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Joint effects of inverse density-dependence and extreme environmental variation on the viability of a social bird species[1]

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Abstract: Environmental stochasticity and density-dependence can have critical synergetic effects on population dynamics, especially when dealing with threatened species. In this study, we examine the effects of these interactions on the dynamics of a vulnerable bird species, the Dalmatian pelican (*Pelicanus crispus*). We conducted demographic analysis and population dynamics modelling of the Amvrakikos pelican population (western Greece) based on a 20-y dataset. Results indicated that annual juvenile survival probability is low (mean = 0.65) and varies according to both negative (regulation) and positive (Allee effect) density-dependent processes. In contrast, adult survival is relatively high (mean = 0.95) and less variable. Deterministic and stochastic population dynamics models based on means, inter-annual variances, and covariances between vital rates revealed that the population is increasing deterministically. Simulations of the extinction risk for the study population and also for various population sizes revealed that short-term extinction risk remains extremely low, even for very small populations of the species. However, when we considered the possibility of rare catastrophic events and their interactions with density-dependence patterns, the projected extinction risk increased dramatically, especially for small populations. Given that many European Dalmatian pelican populations are small, most of them could be at risk for local extinction. Our results illustrate the critical and general importance of considering interactions between all potential factors of extinction in population viability assessments.
Keywords: Allee effect, capture-recapture, carrying capacity, catastrophes, population size, threatened species.

Résumé : La stochasticité environnementale et la densité-dépendance peuvent avoir des effets synergiques critiques sur la dynamique des populations, particulièrement dans le cas d'espèces menacées. Dans cette étude, nous examinons les effets de ces interactions sur la dynamique d'une espèce d'oiseau vulnérable, le pélican frisé (*Pelicanus crispus*). Nous avons effectué une analyse démographique et une modélisation de la dynamique de la population de pélicans d'Amvrakikos (ouest de la Grèce) basées sur un ensemble de données couvrant 20 années. Les résultats ont indiqué que la probabilité de survie annuelle juvénile est faible (moyenne = 0,65) et varie en fonction de processus de densité-dépendance négatifs (régulation) et positifs (effet Allee). À l'opposé, la survie adulte est relativement élevée (moyenne = 0,95) et moins variable. Des modèles déterministes et stochastiques de la dynamique de population basés sur les moyennes des taux vitaux, leurs variances interannuelles et leurs covariances ont révélé que (*i*) la population augmente de façon déterministe; (*ii*) à partir de simulations du risque d'extinction pour la population à l'étude, mais aussi pour différentes autres tailles de population, nous avons montré que le risque d'extinction à court terme demeure extrêmement faible, et ce, même pour de très petites populations de l'espèce. Cependant, lorsque nous avons tenu compte de la possibilité d'événements catastrophiques rares et de leurs interactions avec les patrons de densité-dépendance, le risque d'extinction prédit a augmenté dramatiquement, particulièrement pour les petites populations. Puisque plusieurs des populations européennes du pélican frisé sont petites, la plupart d'entre elles pourraient être à risque d'extinction localement. Nos résultats démontrent l'importance générale et critique de prendre en compte les interactions entre tous les facteurs potentiels d'extinction lors d'évaluations de la viabilité de populations.
Mots-clés : capacité de support, capture-recapture, catastrophes, effet Allee, espèce menacée, taille de la population.

Nomenclature: Mullarney *et al.*, 1999; Dickinson, 2003.

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Introduction

The interaction of density-dependence effects and environmental stochasticity is a key element for population dynamics (Gaillard *et al*., 2000; Gaillard & Yoccoz, 2003; Saccheri & Hanski, 2006). In particular, the interaction between extreme environmental (or catastrophic) events and intrinsic population properties can be critical to population viability assessments. By driving populations to lower densities, catastrophic events may give rise to a number of proximal, deterministic, and stochastic extinction factors. Firstly, demographic stochasticity (arising from random differences among individuals in survival and reproduction) is one of the most important causes of extinction in populations of fewer than several hundred individuals (Shaffer, 1987; Lande *et al*., 2003a). Secondly, it has been widely documented that low population size or density can lead to reduced individual survival rates or breeding outputs in several social species (Green, 1997; Komers & Curman, 2000). An inverse density-dependence (or Allee effect) may be observed in cases where per capita growth rate and population density are positively correlated (Stephens & Sutherland, 1999). The most important corollary of the Allee effect is that social groups that are driven (or maintained) below a critical threshold will have a lower chance of recovery and an elevated risk of extinction (Courchamp *et al*., 1999b; Reed 1999; Berec *et al*., 2001). While demographic stochasticity and Allee effects significantly affect small populations, they may also affect large populations when facing strong environmental temporal variability. Previous work has shown that the risk of extinction can be magnified by the interplay between proximal extinction factors and environmental variation (Liebhold & Bascompte, 2003).

Most population viability assessments examine either the effects of proximal factors on the risk of extinction in small populations or the effect of environmental variation on large population dynamics, but rarely are both types of processes examined at the same time. It is, however, important to integrate these different processes to examine the viability of a species with several populations of various sizes. As extreme environmental variation may induce strong changes in population size, including this factor in population models is also an important issue. While moderate environmental stochasticity (*i.e.*, excluding severe events) and negative density-dependence are commonly treated in population viability analyses (Lande, Engen & Saether, 2003; Saether *et al*., 2005; Benton, Plaistow & Coulson, 2006), severe environmental variation and its interaction with complex density-dependence effects is usually ignored (Coulson *et al*., 2001). The main reason for this is that the frequency, distribution, and possible consequences of such events are rarely known (Ludwig, 1998), principally because the relatively short period of most monitoring programs (generally less than 30 y) is insufficient to provide this kind of information. Thus, the development and use of population models that can deal with such eventualities is becoming a necessity for 3 main reasons: 1) severe environmental perturbations may have high frequencies in natural populations (Reed *et al*., 2003) and are expected to be a major extinction factor, especially in populations larger than a few hundred individuals (Lande, 1993; Lande, Engen & Saether, 2003); 2) under the current global change scenarios, extreme events are expected to become more frequent in the near future (Diffenbaugh *et al*., 2005); and 3) as stated above, the effects of these extreme events are expected to be exacerbated by proximal mechanisms such as demographic stochasticity and Allee effects. Considerable attention should therefore be given to understanding the combined effects of such parameters on extinction probability (Inchausti & Halley, 2003; Pike *et al*., 2004).

In this paper we examine the viability of a vulnerable colonial species, the Dalmatian pelican (*Pelecanus crispus*). Following a radical decrease in its worldwide population over the last century, the species is currently patchily distributed in mostly small, decreasing populations (Crivelli *et al*., 2000). However, no demographic analyses were done for any of the current populations, and there is no viability assessment available for the species. The aim of our study is to use both demographic analysis and population dynamics modelling to provide a first assessment of the viability of the species. At each stage of the analysis, we focused on those ecological and environmental processes that are expected to predominantly affect short- and medium-term risks of extinction, such as demographic stochasticity (Shaffer, 1987), Allee effects (Courchamp, Clutton-Brock & Grenfell, 1999), environmental catastrophes (Coulson *et al*., 2001), and the level of correlation among demographic parameters (Ferson & Burgman, 1995).

Although several populations of the species occur in Europe (for which census data are available), reliable demographic data (involving long-term reproductive monitoring and capture-mark-recapture data) are only available for the Greek populations (Crivelli *et al*., 2000). However, local demographic rates, current population sizes, and carrying capacities may vary among populations of the same species (Dhondt, 2001; Frederiksen, Harris & Wanless, 2005). In addition, the 20-y-period database that we are using in this analysis does not provide enough information about rare catastrophic events. However, environmental catastrophes have already been documented for pelican species, in which increased mortality rates are associated with pathogens (*e.g*., West Nile virus on American white pelicans, Sovada *et al*., 2008), severe climatic events, such as droughts (*e.g*., Australian pelicans, Blakers, Davis & Reilly, 1984), or cold and windy conditions (*e.g*., American white pelicans, Sovada *et al*., 2008). The synergistic effects of environmental stochasticity and disease also should be considered (Rolland, Barbraud & Weimerskirch, 2009), especially in colonial species, where diseases can spread quickly during the breeding period (Sovada *et al*., 2008).

In order to address these limitations, we estimated fecundity and survival rates for the study population (Amvrakikos Gulf, Greece), taking care to discriminate those parameters that are dependent on local conditions (*e.g*., regulation) from those that characterize the species' demography and behaviour (*e.g*., patterns of inverse density dependence). We then used population modelling to assess the sensitivity of population growth to each demographic parameter. Finally, we conducted a population viability analysis in which we incorporated quantitative, generic information on rare catastrophic events. In an attempt to generalize the current analysis for other European populations of the species, we examined different scenarios of interactions between various population sizes, density-dependence, and the presence of severe events. Our results demonstrate the critical importance of considering the interaction between environmental variation and density-dependence patterns in assessing short and medium-term population viability.

Methods

STUDY SPECIES AND DATA COLLECTION

The Dalmatian pelican (*Pelecanus crispus*) is a long-lived colonial bird species that is patchily distributed in the Palearctic, from Montenegro to Mongolia (Crivelli *et al*., 1991). Historically, Dalmatian pelicans were abundant in the Palearctic, but the species declined significantly throughout the 19th and 20th centuries, principally due to disturbances caused by human activities (Crivelli, Hatzilacou & Catsadorakis, 1998). In Europe, it is considered to be a vulnerable species (IUCN, 2001), with most of its populations being small and having stable or decreasing trends, except for the 2 Greek populations, which are increasing (Crivelli *et al*., 2000). In this study, we used data from the population situated in the Amvrakikos Gulf in northwestern Greece (39° 05' N, 20° 50' E), which is the second most important population in Europe (116 breeding pairs in 2005).

We used records of 904 individuals marked at nests between 1985 and 2005. Marking was performed 3-5 weeks after hatching, using plastic rings with a unique code for identification. During the first 5 y of the monitoring period, all birds were marked with 1 ring. However, from 1990 to 2005, individuals were marked with 2 plastic rings (1 on each tarsus) to avoid problems due to ring loss. Resightings occurred through distant observations of marked individuals ($N_{obs} = 3786$) during the breeding period. Breeding data used in this analysis were obtained from monitoring of the entire population (marked and unmarked birds) and consisted of yearly counts of breeding pairs and fledged chicks for the period 1985-2005. Individuals are thought to reach sexual maturity at 2 y of age but actually start breeding after 3 y of age (Crivelli, 1987). Annual productivity is low (1 brood per breeding pair). Fecundity was defined as the average number of fledged young per female in each year.

CAPTURE-MARK-RECAPTURE MODELLING

We used Capture-Mark-Recapture (hereafter CMR) models including information from live resightings only to estimate survival rates (Arnason, 1972; 1973; Hestbeck, Nichols & Malecki, 1991). In typical CMR models, marked individuals that have lost their ring can no longer be identified, which may result in under-estimations of survival and/or resighting rates. We managed to address this problem by using multi-strata models, where the different strata corresponded to the number of rings carried by individuals (Kendall, Conn & Hines, 2006; Le Gouar *et al*., 2008). In a given year, a marked individual could be resighted with 1 (stratum 1) or 2 rings (stratum 2). These CMR models provided survival (*s*), resighting (*p*), and strata transition (ψ) probability parameters. All analyses were performed using MARK (White & Burnham, 1999).

GOODNESS-OF-FIT (*GOF*) *TESTS AND MODEL SELECTION*

As a biological starting point, we tested the multi-state JollyMoVe (JMV) model (s_{t*ring}, p_{t*ring}, ψ_{t*ring}) (Pradel, Gimenez & Lebreton, 2005). Model notation is based on Lebreton *et al*. (1992). The notation "ring" indicates different survival (*s*), resighting (*p*), and/or transition (ψ) probabilities according to ring state (*e.g*., s_{ring} denotes that $s_{2rings} \neq s_{1ring}$). The fit of this model to the data was tested using the U-CARE software (Choquet *et al*., 2004). This analysis showed that the JMV model fitted the data poorly ($\chi^2_{99} = 273.792$, $P < 0.001$), indicating an age-dependent effect (Test 3G.SR: $\chi^2_{18} = 141.772$, $P < 0.001$). The overdispersion factor $\hat{c}$ for the age-dependent model was estimated as 1.630, a relatively safe value for comparing models ($\hat{c} \leq 3$, Lebreton *et al*., 1992). We used the Quasi-likelihood Akaike's Information Criterion ($QAIC_c$) method to compare models (Anderson, Burnham & White, 1994; Burnham & Anderson, 1998).

We performed a stepwise backward elimination of parameters to select our best model, *i.e*., we started from the most parameterized model (s_{a2*t}, $p_{a2*t*ring}$, ψ_{a2*t}) and we subsequently tested several simpler models to obtain the most parsimonious model structure. We first compared different model structures for the nuisance parameters, *i.e*., resighting probability (*p)* and ring loss (ψ*)*, keeping the initial structure for survival probability (s_{a2*t}). The most parsimonious structure for the nuisance parameters was then used to compare survival models. We tested constancy, age, time, and ring effects for resighting and transition probabilities. For survival probability, no ring effect was considered, as we had no evidence that the ring stratum can influence survival. A strong age effect was expected for this species, for both survival and resighting, as we know that juveniles pass their first year away from the main wintering areas. We therefore tested models with 2 age classes (juveniles and older individuals, denoted as a_2). Differences in survival between immature individuals and adults were also tested, through models with 3 age classes (juveniles, 1-y-old, and older individuals, denoted as a_3), or 2 age classes, testing for equal survival among juveniles and 1-y-old individuals (denoted as *a*2(imm,ad)). Given our 20-y data set, we expected a time effect in both survival and resighting, especially for juveniles. The additive effects between components (*i.e*., age and time effects, noted as *a*+*t*) were tested for the best-fitting models.

As we obtained several models with equivalent support from AIC-based selection, the annual survival rates of each age class were estimated through model averaging of all tested models (Wasserman, 2000; Johnson & Omland, 2004). The total temporal variation (σ_{tot}^2) in a series of annual survival rates includes 2 components, process (σ^2) and sampling variation (σ_s^2). While the first represents the true biological variation in a series of parameters, the second depends on the sample size of marked individuals and should thus be removed in order to get a robust, less-biased estimate of the mean survival rate (Gould & Nichols, 1998; Burnham & White, 2002). This is possible through MARK by using a random effect (variance components) approach. Performing a decomposition of the variance assumes that the survival rates are considered to be a random sample from a distribution with mean and variance equal to the process variance (White *et al.*, 1999; Loison *et al.*, 2002). The method used in MARK assumes that survival estimates are obtained from a general model with no constraints on the parameter estimates affecting the process variance estimate (White, Burnham & Anderson, 1999). Mean survival rates were therefore estimated from the best time-dependent model using random effect models.

TESTING DENSITY-DEPENDENCE EFFECTS

The existence of density effects on survival was examined by using the number of breeding pairs per year as a covariate. Two scenarios of density-dependence were tested: a linear and an Allee effect. The Allee effect was tested as a quadratic effect of the number of breeding pairs per year. The amount of inter-annual variation in survival rates explained by density-dependence was estimated using 2 methods: 1) we used the Analysis of Deviance (ANODEV) function implemented in MARK to determine if the covariates tested explained a significant part of the year-to-year variation. We estimated the proportion of the total inter-annual variation in survival probabilities explained by the density covariate as $(DEV_c – DEV_d)/(DEV_c – DEV_t)$, where *c*, *d,* and *t* indicate models with no temporal variation, with the covariate, and with time-dependence respectively (see Frederiksen *et al*., 2008). This approach does not distinguish between process and sampling variance. 2) We estimated the proportional reduction in process variance when the covariate was introduced to the random effect models. We first ran the random effects model, assuming a constant mean to obtain the process variance, and then we ran the same model, assuming that the mean depends on the covariable, which allowed us to obtain the residual variance (σ_{res}^2). The percentage of the variance explained by the covariable was then calculated as $(\sigma^2 - \sigma_{res}^2) / \sigma^2$ (see Loison *et al*., 2002).

POPULATION VIABILITY MODELLING

We assessed the viability of the Amvrakikos pelican population using projection population models. Most analyses were done using a stochastic individual-based model (see below), which provided flexibility in modelling the combined effects of population regulation, demographic and environmental stochasticities, and possible correlations among demographic rates. However, as a first step, a one-sex, age-structured deterministic model was used to infer equilibrium population properties (in the absence of population regulation and demographic and environmental stochasticities). The model was based on a 3 × 3 extended Leslie transition matrix (pre-breeding census and detailed life cycle presented in Appendix I and Results) implemented using the ULM program (Legendre & Clobert, 1995). While the number of breeders per year was a known parameter, no information was available for the total population size that would allow us to estimate the proportion of breeders in the population (γ). Thus, we used the simulated parameter γ that was determined by calibrating population model projections to field data as explained below.

In each time step (year), the reproductive status (*i.e.*, breeder or non-breeder) of each adult (≥ 3-y-old) was stochastically determined according to specific probabilities estimated from our field observations of fledgling and breeder abundances. Male and female breeders were randomly paired according to a monogamous mating system. We simulated the proportion of breeders in the population by testing a number of different values from 0.6 to 0.9, in increments of 0.05. The reproductive success of each pair was determined according to a Poisson distribution (parameter *f*). The sex of each newborn individual was randomly determined according to a 1:1 mean sex ratio. Reproduction was followed by the differential mortality of individuals according to age-specific annual survival rates. Each individual survival event was drawn from a Bernoulli distribution according to the age-specific survival rate (s_0 or s_a). Details of the parameters used are presented in Table I.

MODELLING CATASTROPHIC EVENTS FOR VARIOUS POPULATION SIZES

As we are interested in assessing the viability of both the Amvrakikos population and any other Dalmatian pelican population, we focused on those parameters that (*i*) have a major effect on extinction risk, (*ii*) are the most likely to vary among populations, and (*iii*) have the greatest degree of uncertainty. These parameters are (1) the impact of severe negative environmental events, (2) the initial population size, and (3) the carrying capacity of the population. Carrying capacity is important in assessing how long-term population size and regulation will affect projected viability. While it is not useful to precisely compute the value of *K* from real populations, it may be possible to determine its order of magnitude from field observation (estimation of the quantity of resources locally available, detection of stationary dynamics based on time series of population size, observation of competing behaviour, etc.). One final parameter, the correlation among parameters, was

TABLE I. Annual parameters used for modelling population dynamics. SE and SD refer to the standard error and standard deviation calculated from random effects models. Simul. param. denotes the calibrated simulated parameter γ.

Parameter	mean	SE	SD	Reference
Juvenile survival (s_0)	0.645	0.046	0.206	This study
Immature survival (s_1)	0.952	0.017	0.070	This study
Adult survival (s_a)	0.952	0.017	0.070	This study
Age at maturity	3.000	-	-	(Crivelli, Hatzilacou & Catsadorakis, 1998)
Female breeding success (*f*)	0.865	0.033	0.150	This study
Percentage of ≥ 3-y-old breeders (γ)	0.700	-	-	Simul. param.

also initially considered as an important factor for population dynamics, but no significant impact was revealed in our case. The protocol used and the results obtained are presented in Appendix II.

Environmental stochasticity was modelled by drawing survival rates at age x in each year from a Beta distribution with expectation and variance given by the mean and process variance of the previously estimated demographic rates. For fecundity, we assumed a truncated Normal distribution, and we used the total inter-annual variance in fecundity to model environmental stochasticity (see Table I and Discussion). The Normal distribution was truncated to avoid negative values, but this did not induce any substantial bias in the realized mean or variance with the parameters used (mean = 0.865; SD = 0.15, see Table I) (the probability of drawing a negative value was $< 10^{-8}$).

In addition to moderate temporal environmental variation, the effect of rare and severe negative events on long-term population viability was also considered (Shaffer, 1987; Lande, 1993). This was achieved by assuming that punctual catastrophes occur randomly with a probability p_c at each time step (t) to reduce population size by a proportion C (random truncation). The severity of each catastrophic event (C) was drawn from the empirical severity distribution of Reed *et al.* (2003), who documented punctual population decreases of 50% or greater in 88 species of vertebrates. Population regulation was considered either by using empirical equations linking juvenile survival and population size (see Equation 1 as resulted from model 5 in Table II) or by limiting the overall population size to K (using a simple random truncation in each time step).

In each case, the number and age structure of the initial population was derived from the number of breeding pairs actually observed in the year 1985 and an asymptotic age-class distribution obtained from the deterministic matrix model for the set of parameters investigated. Extinction occurred when population size was equal to zero. Changes in population size and extinction risk were investigated using Monte Carlo simulations in which 2500 population trajectories were drawn over a fixed time horizon (200 y).

Results

DEMOGRAPHIC PARAMETERS

A final set of 20 models were used in the survival analysis (Table II). The most parsimonious model assumed an additive time-dependent effect between juveniles and individuals older than 1-y-old, for both survival and resighting probabilities (model 1). Models with different age structures for survival were also considered, but they fitted the data less well (models 2 to 10). Models with 3 age classes were not supported by the data (models 8 and 10), whereas models with 2 age classes for immature individuals and adults fitted the data better (models 2, 3, and 6). However, when testing for additive effects among components, the model with differential survival between juveniles and older individuals had the best fit (see models 1 and 2). The inter-annual variations in survival rates are presented in Figure 1. In models where both survival and recapture probabilities are time-dependent, terminal estimates cannot be estimated separately (β term; Lebreton *et al.*, 1992), and thus this last estimation is not shown in Figure 1. Juvenile survival varied significantly during the period of this study. We observed

TABLE II. Model selection from tag loss models, based on $\hat{c}$ =1.63.

Model	$\Delta QAIC_c$	Model likelihood	Number of parameters	QDeviance
1. $s_{a2+t}, p_{a2+t}, \Psi_c$	0.00	1.000	45	876.03
2. $s_{a2(\text{imm,ad})+t}, p_{a2+t}, \Psi_c$	2.85	0.241	45	878.88
3. $s_{a2(\text{imm,ad})*t\_c}, p_{a2+t}, \Psi_c$	6.29	0.043	62	845.98
4. $s_{a2*t\_c}, p_{a2*t}, \Psi_c$	6.60	0.037	62	846.29
5. $s_{a2(\text{Quadratic dd-Juv})*t}, p_{a2*t}, \Psi_c$	27.56	0.000	63	865.09
6. $s_{a2(\text{imm,ad})*t}, p_{a2*t}, \Psi_c$	31.71	0.000	79	834.27
7. $s_{a2(\text{Linear dd-Juv})*t}, p_{a2*t}, \Psi_c$	31.93	0.000	62	871.62
8. $s_{a3*t\_c}, p_{a2*t}, \Psi_c$	33.35	0.000	81	831.49
9. $s_{a2*t}, p_{a2*t}, \Psi_c$	36.10	0.000	79	838.66
10. $s_{a3*t}, p_{a2*t}, \Psi_c$	57.83	0.000	97	820.19
11. s_{a2*t}, p_t, Ψ_c	72.33	0.000	61	914.17
12. $s_{a2*t}, p_{t*ring}, \Psi_c$	96.12	0.000	80	896.47
13. s_{a2*t}, p_{a2}, Ψ_c	97.91	0.000	44	976.06
14. $s_{a2*t}, p_{a2*ring}, \Psi_c$	99.01	0.000	46	972.93
15. $s_{a2*t}, p_{a2*t*ring}, \Psi_c$	102.81	0.000	116	821.71
16. $s_{a2*t}, p_{a2*t*ring}, \Psi_{a2}$	105.38	0.000	118	819.64
17. $s_{a2*t}, p_{ring}, \Psi_c$	145.32	0.000	44	1023.46
18. $s_{a2*t}, p_{a2*t*ring}, \Psi_t$	149.02	0.000	152	782.54
19. s_{a2*t}, p_c, Ψ_c	156.68	0.000	43	1036.94
20. $s_{a2*t}, p_{a2*t*ring}, \Psi_{a2*t}$	230.95	0.000	188	774.89

Subscripts indicate whether parameters varied according to time, age, or ring stratum. Age dependence is indicated by "*a*" followed by the number of the age classes considered, *i.e.*, "s_{a2}" for survival models with 2 age classes: juveniles and older individuals. For models with different age structure more information is given in the parenthesis. "*t*" denotes time variation among years, "*c*" denotes constancy, and "*t_c*" denotes a time effect for the first age class and constancy for the following age class(es). Interactions between factors are denoted by an "*", while "+" indicates models where only the main effects are considered (additive models). "Quadratic dd-Juv" denotes an Allee effect, whereas "Linear dd-Juv" denotes a linear density effect on juvenile survival. Example: model 5 denotes a model with 2 age classes, with a quadratic density dependence effect on juvenile survival and time dependence effect on older individuals' survival.

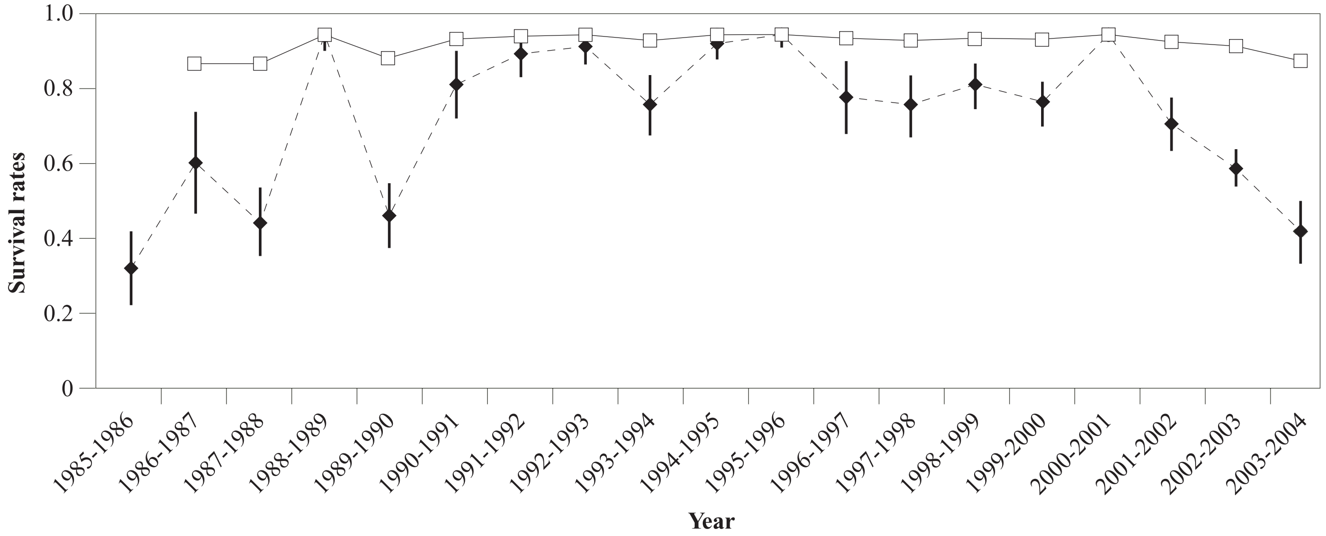

FIGURE 1. Estimated survival rates for the 2 age classes, *i.e.*, juveniles and older individuals derived from the best models selected based on $QAIC_c$ (Table II). Error bars indicate the standard error (SE). Dashed line, filled diamonds: juvenile survival. Solid line, open squares: survival of older individuals.

lower survival probabilities for the first and last years of the study, potentially indicating that density-dependence mechanisms act on this parameter. Survival of immature individuals older than 1 year and adults were equal and relatively stable, with small inter-annual variation. Mean juvenile survival was estimated as 0.645 (SE = 0.046) and survival of older individuals was 0.952 (SE = 0.017).

We also tested several hypotheses for resighting probability (models 9, 11-14, 17, and 19). A strong age and time effect were supported by the data (model 9). No ring effect was revealed (models 9, 11 *versus* 14, 12). Resighting probability was estimated for juveniles as 0.319 (SE = 0.031) and for older individuals as 0.629 (SE = 0.021). Finally, models for the transition parameter (models 15, 16, 18) revealed no age or time effects and ring loss was 0.11 (SE = 0.037).

EFFECT OF DENSITY-DEPENDENCE

The model that assumed a quadratic relationship (model 5 in Table II) between juvenile survival and density (number of breeding pairs) explained 48.4% of the total inter-annual variation ($P = 0.005$). After variation decomposition, 21.7% of the process variance in juvenile survival was explained by the quadratic density effect, according to the equation

$$s_0 = 0.0134 \cdot Npairs - 0.0001 \cdot Npairs^2 + 0.3378 \qquad [1]$$

This indicates that juvenile survival was reduced for both very low and very high densities in the Amvrakikos population. This result is consistent with the presence of both positive (Allee effect) and negative (regulation) density-dependence. The ANODEV showed that the linear density-dependent effect was also significant for juvenile survival but explained a smaller portion of the inter-annual variation (35.7%, $P = 0.007$). No relationship between survival and density was observed for older individuals.

We also tested for density-dependence patterns in annual fecundity estimates (see Figure 2). The number of breeding pairs per year was used as a factor of density. No statistically significant relationship was observed between fecundity rates and population density ($r = 0.27$, $P = 0.23$). Although density-dependence may not yet have been an issue for this particular population, it may become important if the population continues to increase in size.

POPULATION VIABILITY ANALYSIS

DETERMINISTIC GROWTH RATE AND STOCHASTIC EQUILIBRIUM

In the absence of density-dependence and inter-annual variation in demographic parameters, the population increased with a high asymptotic growth rate $\lambda = 1.099$. Although our analysis revealed density dependence in juvenile survival, no such pattern was revealed in adult survival, which was relatively high and stable over time. We expect that in long-lived species, population growth rate depends more on the mean value and temporal variation of adult survival. Given that breeder proportion was calibrated so that model projections would fit observations of the field population, this high growth rate was mainly due to adult survival (elasticity = 0.895) and depended less on juvenile survival (elasticity = 0.105) and fecundity (elasticity = 0.105). Parameter values used for the deterministic matrix model analysis are presented in Table I.

The best agreement between simulated and observed dynamics (assessed by computing the sum of the squared differences between projected and actual numbers of breeding pairs for each scenario) occurred when 70% of adults were considered to be breeders ($\gamma = 0.7$ was assumed in all subsequent analyses). A comparison between actual and projected short-term dynamics is presented in the presence (Equation 1) and absence of density-dependence in Figure 3. Incorporating density-dependence into our model, leads to the prediction that the Amvrakikos population should stabilize to about 150 pairs (which represents less than 500 individuals).

MODELLING CATASTROPHIC EVENTS FOR VARIOUS POPULATION SIZES

Both the frequency of catastrophic events and population carrying capacity have important effects on the extinction rate (Figure 4). While large populations ($K > 500$) have a less than 5% probability of extinction for realistic frequencies of catastrophic events (see below), substantial extinction risks are expected for populations with fewer than several hundred individuals (*i.e.*, most of the European Dalmatian pelican populations; see Crivelli *et al.*, 2000).

The analysis of Reed *et al.* (2003) on the frequencies and severities of population die-offs (decrease of > 50% of population size) in 88 species of vertebrates indicates that the probability of a severe die-off for a particular population is approximately 14% per generation. This estimate corresponds to a rate of 1.5% per year when considering the generation length (T) of the Amvrakikos population obtained from the deterministic matrix model ($T = 9$ y). Integrating this frequency of population die-offs into our model revealed a substantial impact of the Allee effect on the extinction rate (Figure 5). Even for large populations (*e.g.*, $K = 1000$), the extinction rate was substantially higher after accounting for the Allee effect, with extinction probabilities 70% to 120% higher based on the initial population size. For small populations (*e.g.*, $K \leq 200$), the probability of extinction was always significant (> 10%) with or without accounting for the Allee effect.

Discussion

In this study, we performed a demographic analysis for the Dalmatian pelican. Through population dynamics

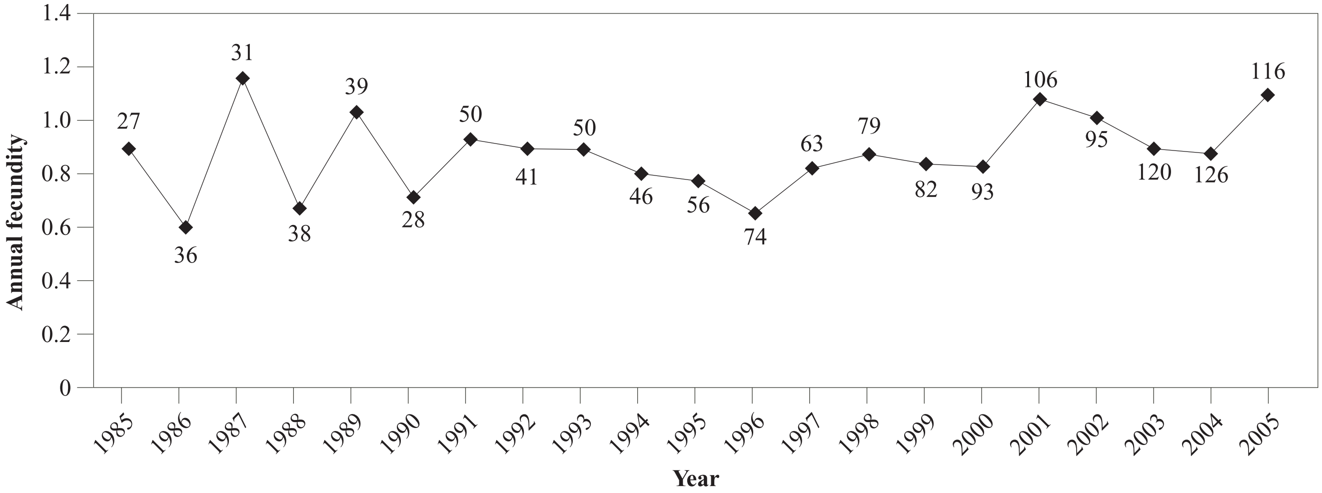

FIGURE 2. Annual estimates of fecundity (number of young fledged per breeding pair). The numbers of breeding pairs per year are given near the point estimates. No standard error is available for this metric, as fecundities were obtained from a global population survey.

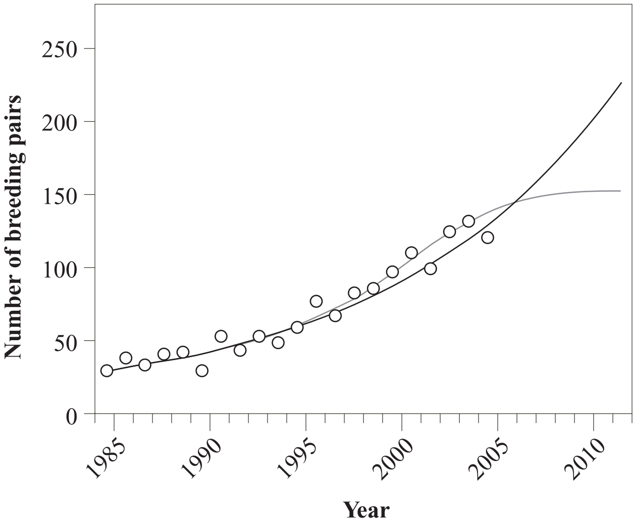

FIGURE 3. Observed and projected population dynamics of the Amvrakikos Dalmatian pelican population (number of breeding pairs) between 1985 and 2010. Modelling results obtained using an individual based model that included both demographic and environmental stochasticity (Table I). Open circles: recorded number of pairs. Black line: density-independent model (juvenile survival independent of population density). Grey line: model including positive and negative relationships between juvenile survival and density (Equation 1).

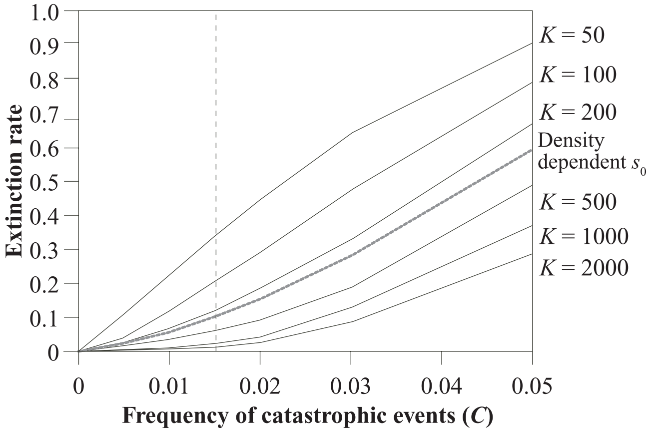

FIGURE 4. Projected 200-y extinction risk of Dalmatian pelican population, according to the annual frequency of catastrophic events (C). Results obtained from an IBM model that included both demographic and environmental stochasticity (Table I) and showed no correlation between demographic rates. The severity distribution of catastrophic events was determined according to Reed *et al.* (2003)'s empirical distribution. The vertical dashed line indicates the mean frequency expected according to Reed *et al.*'s analysis (see text in Results). Black lines: density-independent demographic rates with random truncation to the carrying capacity K. Grey line: positive and negative density-dependent juvenile survival observed for the Amvrakikos population (Equation 1).

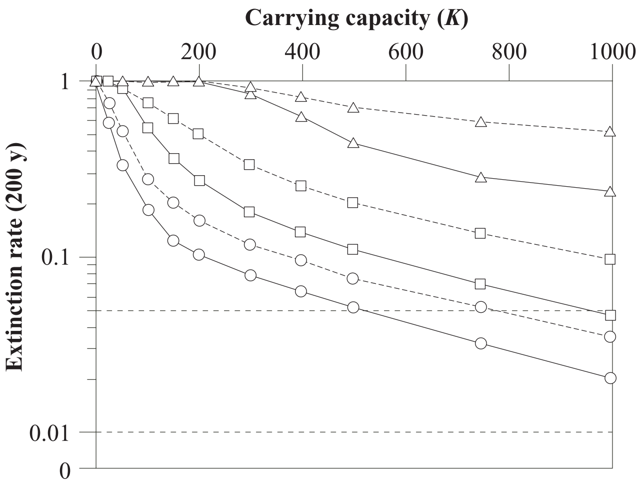

FIGURE 5. Projected 200-y extinction risk for the Dalmatian pelican population (logarithmic scale), according to the population carrying capacity (*K*, truncation model). Results were obtained using an IBM model that included demographic and environmental stochasticity (Table I) and random catastrophic events (C = 0.015). The severity distribution of catastrophic events was determined according to Reed *et al.* (2003)'s empirical distribution. Circles: $N_0 = K$. Squares: N_0 = 5% of K. Triangles: N_0 = 1% of K. Continuous lines: no Allee effect (s_0 independent of density). Dashed lines: Allee effect implemented using an empirical relationship between juvenile survival (s_0) and the number of breeding pairs (N_{pairs}) (see Appendix III for details). Dashed lines indicate extinction probabilities of 1 and 5%

modelling we examined effects of the interaction of density-dependent processes and extreme environmental events on the extinction risk of populations of various sizes.

Our survival analysis revealed both positive (Allee effect) and negative density-dependence on juvenile survival. In social species like the Dalmatian pelican, high population densities can be advantageous for young individuals, providing protection from predation and/or assuring thermoregulation of chicks while adults forage away from the nest (Courchamp, Clutton-Brock & Grenfell, 1999; Courchamp, Grenfell & Clutton-Brock, 1999). In cooperative species, recruitment may be reduced within small groups due to higher juvenile mortality (Clutton-Brock *et al.*, 1998). A positive correlation between fecundity and colony size has been documented for Dalmatian pelicans, indicating that breeding success is also better assured within larger groups (Catsadorakis & Crivelli, 2001). Many studies have demonstrated that early life conditions can often influence the future survival and reproductive success of individuals (see for example Lindstrom, 1999; Cam *et al.*, 2003; Serrano *et al.*, 2005). Favourable early life conditions can permit the development of social feeding abilities of young birds and higher first-year survival. The negative density-dependence suggests, however, that a further increase in density should result in competitive regulation of the population size around the carrying capacity of the site. In both cases, severe environmental stochasticity can have an important effect on the species dynamics by reducing resource availability in terms of food and/or nests or by causing a decrease in population size to densities where the Allee effect has a significant impact.

This study gives evidence of simultaneous variation in survival rates for juveniles and older individuals, supporting the assumption that environmental conditions have similar impacts on both age classes. However, such an effect has little or no impact on the viability of the population in cases where adult survival shows low temporal variation, as in the case of the Amvrakikos population (see Appendix II). Nevertheless, the effect of this correlation may have a far more important impact on the viability of populations in the case of higher temporal variation in adult survival, where we expect higher inter-annual variation in growth rate and thus a lower stochastic growth rate (Doak & Morris, 2002). We therefore suggest that such correlations should be taken into consideration in future analyses (Fieberg & Ellner, 2001).

Sensitivity analysis revealed that population growth depends primarily on adult survival. This is a commonly expected result for a long-lived species like the Dalmatian pelican (Heppell, Caswell & Crowder, 2000). Sensitivity analyses have traditionally been used to help focus management efforts on the vital rate to which λ is most sensitive, in order to increase population growth rates (Marschall & Crowder, 1996; Plissner & Haig, 2000). However, recent studies argue that this approach is insufficient to give effective guidelines for management (Coulson *et al.*, 2001; Katzner, Bragin & Milner-Gulland, 2006). It has been shown that λ is most sensitive to the least variable vital rates (Pfister, 1998; Stearns & Kawecki, 1994). Growth rate is relatively less sensitive to vital rates with greater variability, which can be affected by density-dependence factors or environmental stochasticity (Gaillard, Festa-Bianchet & Yoccoz, 1998; 2000). As natural and anthropogenic processes may cause a shift in the key vital rate from one demographic parameter to another (Eberhardt, 1977; Albon *et al.*, 2000) demographic models should focus not on a single key vital rate, but rather on all vital rates given the population concerned (Caswell, 2000; Norris & McCulloch, 2003). Conservation measures have been applied to the Greek populations over the last 20 y and have focused on eliminating the main causes of mortality (illegal shooting and persecution) and improving breeding success (Crivelli, Jerrentrup & Mitchev, 1988; Crivelli, 1996). These mortality causes persist for many of the declining populations of the species worldwide (Crivelli *et al.*, 2000). Other indirect disturbances may also occur from surrounding human activities, such as agriculture and fish farms, potentially influencing the fish stock of sites where the species forages (Crivelli *et al.,* 1995).

By exploring the synergistic effects of severe environmental variability and density-dependence on population viability, we show that in neglecting such catastrophic events, the risk of extinction is highly underestimated both for large and small populations. Moreover, the Allee effect and initial population size have a greater impact on population viability in the presence of catastrophes (see Figures 4 and 5). More specifically, small populations of fewer than 200 individuals had a considerable extinction risk (> 10%) due to the fact that small and isolated populations are more subject to environmental, anthropogenic, or intrinsic factors over time (Coulson *et al.*, 2001). Given that most Dalmatian pelican populations in Europe are small (fewer than 200 individuals) (Crivelli *et al.*, 2000), a substantial proportion of these populations may have a large risk of local extinction.

The actual extinction risk of other European populations may be significantly higher in some cases since we assumed that all populations have the same demographic rates as the population analyzed in the current study. This is a clearly optimistic assumption as conservation measures over the last 20 y at the Amvrakikos site may have induced substantial improvements in both survival and reproduction rates. Hence, the actual extinction risk may be significantly higher for populations for which no conservation measures have yet been taken. We believe, however, that if conservation measures can ensure demographic rates similar to the ones described in this analysis, the 200-y extinction risk could be maintained between 1 and 5% for relatively large populations (500 individuals).

There have been few empirical studies that have treated extreme environmental stochasticity in populations dynamics (*e.g.*, Frederiksen *et al.*, 2008; Nevoux, Barbraud & Barbraud, 2008). In species related to the one presented here, such as shags (*Phalacrocorax aristotelis*), it has also been documented that heavy rainfall during the breeding season may cause mass mortality among unfledged shag chicks, presumably due to hypothermia (Frederiksen *et al.*, 2008). It has also been suggested that the persistence of vulnerable species like the Mauritius kestrel in the Bambous mountain range may be threatened by a potential increase in the frequency or severity of cyclones (Sutherland & Norris, 2002). Heavy rains associated with cyclones can flood nest sites and result in reproduction failure. Population persistence might therefore be affected by the frequency and severity (in terms of nest mortality) of cyclonic events, especially if population size falls below the minimum needed to recover after a cyclone (Sutherland & Norris, 2002). Populations and individuals at the edge of their species range may also be more significantly affected by an increased frequency of extreme events, such as an increase in the number of days that lie outside the physiological tolerance of a particular species (Hoffmann & Parsons, 1997; Scharr *et al.*, 2004). Further empirical knowledge of the impact of such events on population dynamics will be critical for management efforts in the future. Moreover, as demonstrated by the current study, considerable attention should be given to interactions between rare catastrophic events and density-dependence patterns, as they may significantly change our predictions of viability analyses.

We therefore believe that population modelling should show more flexibility in dealing with severe environmental stochasticity. We suggest that the most adaptive way of doing so may not necessarily be to wait until such events are documented for specific populations, but rather to predict their effect on population dynamics by means of generic data. Several studies have documented relatively high average frequencies of population die-offs in vertebrate species and have provided guidelines to determine biologically reasonable frequencies as a function of the ecology of the target species (Young, 1994; Erb & Boyce, 1999; Reed *et al.*, 2003). Using a plausible probability of occurrence for severe environmental stochasticity in population modelling may help in improving management guidelines by providing optimistic and pessimistic estimates of extinction probabilities (*i.e.*, in the absence and presence of catastrophic events respectively) over a fixed time horizon. Such analyses may also provide important insights into how environmental variation interacts with other factors, such as population growth and density-dependent mechanisms, to reduce population viability. Consequently, the focus of management efforts should be on improving those parameters that interact the most with environmental variation to yield a more flexible and adaptive system of management.

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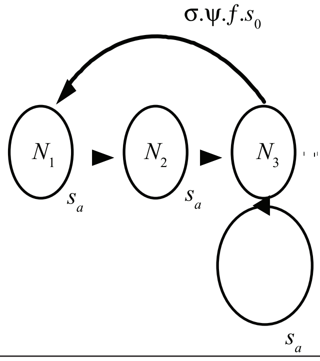
APPENDIX I. Species life cycle and transition matrix used for the Dalmatian pelican population at Amvrakikos.

ϕ: female breeding success.
s_0: juvenile survival.
s_a: immature and adult survival.
γ: % of breeders among 3-y-old females and older.
σ: expected sex ratio at birth.



$$\begin{pmatrix} 0 & 0 & \sigma.\psi.f.s_0 \\ s_a & 0 & 0 \\ 0 & s_a & s_a \end{pmatrix}$$

APPENDIX II.

As the demographic analysis revealed the occurrence of correlations among different survival rates, we considered these relationships using correlated variables to model annual variation in these rates. The effect of correlations among parameters on the risk of extinction was examined by comparing different levels of correlation between s_0 and s_{ad} (*i.e.*, survival of immature and adult individuals [older than 1-y-old]) in conjunction with other demographic variables. Correlation values varied from 0 to 1, with an interval of 0.25. Results indicated that correlations had very minor effects on extinction in comparison to other parameters such as the frequency of catastrophes (*C*), the carrying capacity (*K*), and the initial population size (N_0). Results are presented in Figure II-1.

The following protocol was used to draw juvenile ($s_{0(t)}$) and adult ($s_{a(t)}$) survival rates for the year *t*, assuming that (*i*) these rates were distributed according to β distributions (with means and variances [μ_0,σ_0^2] and [μ_a,σ_a^2] for juvenile and adult survival, respectively); (*ii*) the coefficient of correlation among these rates was *r*.

(1) first, $s_{0(t)}$ was drawn from $\beta\ (\mu_0,\sigma_0^2)$.

(2) a random variable $s'_{0(t)}$, correlated with $s_{0(t)}$ was computed as

$$s'_{0(t)} = r\ (s_{0(t)} - \mu_0) + (\mu_0,\sigma_0^2\ (1 - r\ \surd 816)) \qquad \text{[II-1]}$$

(3) $s'_{0(t)}$ was transformed to obtain $s_{a(t)}$ with the required mean and variance, according to

$$s_{a(t)} = \frac{\sigma_a(s'_{0(t)} - \mu_0)\ 824}{\sigma_0} + \mu_a \qquad \text{[II-2]}$$

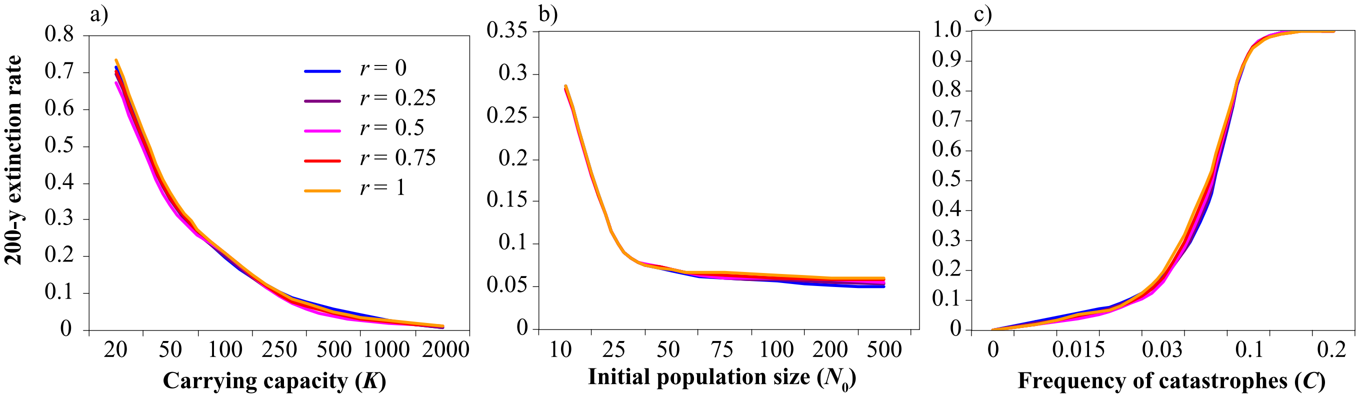


FIGURE II-1. Variation in projected extinction risk according to various demographic and environmental characteristics, for different coefficients of correlation (*r*) between juvenile (s_0) and adult (s_a) survival rates. Results were obtained using an IBM model and included both demographic and environmental stochasticity (Table I). The severity distribution of catastrophic events was determined according to Reed *et al.* (2003)'s empirical distribution (density-independent models with random truncation to the carrying capacity *K*). a) Variation in the carrying capacity *K*, with $N_0 = K$ and $C = 0.015$ in all cases. b) Variation in the initial population size N_0, with $K = 500$ and $C = 0.015$ in all cases. c) Variation in the annual frequency of catastrophic events *C*, with $N_0 = K = 500$ in all cases.

APPENDIX III.

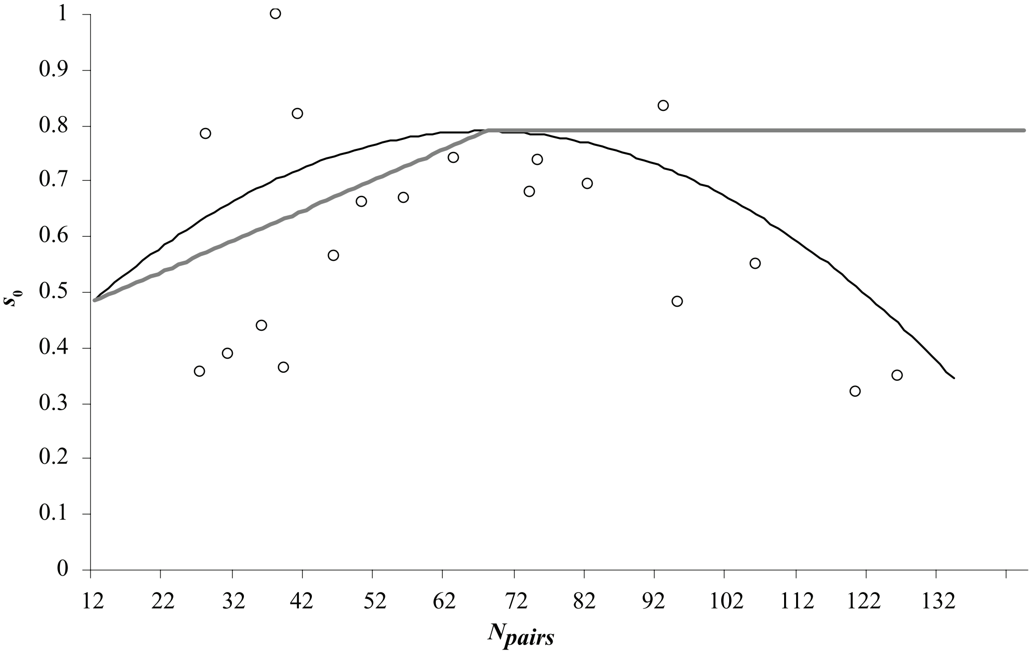


FIGURE III-1. Observed and modelled relationship between density (N_{pairs}) and juvenile survival. Circles: Survival rates resulting from the most parsimonious time-dependent model. Thin black line: model including positive and negative relationships between juvenile survival and density (model 5). Thick grey line: model including only positive density-dependence. The equation for positive and negative density-dependence was obtained from the Mark program (see model 5, Table II): $s_0 = 0.0134 * N_{pairs} - 0.0001 \cdot N_{pairs}^2 + 0.3378$. The equation for positive density-dependence was obtained by fitting a linear regression model to the increasing portion of the relationship between N_{pairs} and s_0 (*i.e.*, for values of N_{pairs} lower than the value associated with the mode of the distribution) and assuming a fixed maximal value of s_0 for all other values. The resulting equation was $s_0 = \mathrm{Min}(0.79; 0.0055 \cdot N_{pairs} + 0.4182)$.