

An investigation of matrix population model
assumptions: wrens (*Troglodytes troglodytes*) as a case
study

Mark Nicholas Trinder

Thesis submitted for the degree of Doctor of Philosophy
in the School of Biological and Environmental Sciences,
The University of Stirling.

August 2003

Abstract

A simulation matrix population model of a small population of wrens (*Troglodytes troglodytes*) is presented. The field work methods used to obtain and analyse the demographic rates are provided. This includes a description of the use of miniature radio tags to track juvenile (post-fledging) survival and dispersal, and capture mark recapture analysis of an eight year dataset to estimate adult survival rates, taking into account environmental variation and density dependence. Age related reproductive rates were obtained from detailed nest surveys. Using these demographic rates (means and variances), and information on density dependence in survival and breeding, a simulation matrix model was developed using Matlab (The MathWorks, Inc.). The operation of this model and its outputs are explained in detail, with particular reference to the methods employed to incorporate both density dependent survival and reproduction and environmental and demographic stochasticity. This model is then used to illustrate how, under plausible conditions of density dependence and stochasticity, large discrepancies are obtained between the deterministic, density independent elasticities of the population growth rate (λ) and the stochastic, density dependent elasticities of the equilibrium population size, extinction probability and invasion exponent. Since the elasticities of λ are often used to guide the management of endangered species, these results are particularly relevant to workers in the field of rare species conservation. While the importance of including environmental variation in the form of stochastic population simulations seems to now be generally accepted, the role of density dependent population regulation is still infrequently considered. Since one of the most common causes of population decline is habitat destruction,

leading to an increase in population density within the remaining areas of habitat, this omission may rarely be justified. It is recommended that when elasticity analysis is conducted as part of species conservation efforts, both density dependence and stochasticity are included. Failure to do so may result in the misguided management of endangered species.

Statement of originality

The work described in this thesis is original research carried out by myself and has not been submitted for consideration previously for a higher degree at this or any other university. Any references henceforth used have been appropriately acknowledged.

Mark Trinder

August 2003

Acknowledgements

Many people in the biology department have made useful suggestions (not always work related...) at some stage or another during my time in Stirling and I would like to thank all of them for their help - you know who you are. Obviously my main sources of guidance have been my supervisors, Matthew and Tim, who have always made the time to see me and have even on occasion provided good advice! I have certainly learned a lot from them, and if nothing else I'm sure my initial shortcomings in the areas of birding and modelling (not unimportant for this project) provided them with some amusement over the years. Amongst the other people who have been willing and able to help me along the way, Andy Beckerman's name inevitably stands out - he's been a good friend and his enthusiasm and support has been ever present (if sometimes slightly alarming!). Others who have helped out with my fieldwork over the years have included Rachel Atkinson, Kate Buchanan, Andy Dowse, Jonathan Fairbairn and Kirsty Park - thank you all for your time and friendship. Finally I'd like to thank all my friends and family who have supported me over the last (nearly) four years, and of course not forgetting Fi who has become my best friend (and latterly my financial backer!). Its been a long final year, but you have always been there - thank you.

Contents

	Page no.	
Abstract	II	
Statement of originality	IV	
Acknowledgements	V	
Chapters		
1	Introduction	1
2	Estimation of adult wren demographic rates	12
3	Estimation of juvenile wren demographic rates	50
4	Description of density dependent, stochastic simulation matrix population model	85
5	Elasticity analysis of density dependent, stochastic model	142
6	Discussion	183
	References	191
	Appendix 1: Simulation model code	213

Chapter 1

Introduction

The rapid expansion of the human population during the last few hundred years from an estimated world-wide total of 600 million in 1700AD to over 6 billion in the year 2000 (source: US Census Bureau) has brought large scale change to almost all natural habitats on the planet. In addition to the modification, pollution and destruction of ecosystems brought about through the increasing requirements of the human population for food, energy and other natural resources, there is growing evidence that our actions are influencing the climate on a global scale (source: IPCC). There is little doubt that the conditions thus created have led to a rate of species extinction between 100 and 1000 times greater than the estimated background rate (source: IUCN). It appears that the scale of these man-induced changes is such that we are now in the midst of the 6th mass extinction of species (Akcaakaya et al, 1999; Chapin et al, 2000). Current estimates suggest that 24% of all mammal species and 12% of all bird species are threatened with extinction (IUCN red list, 2002). While birds and mammals are the best documented groups, the threats are not confined to them. All the major vertebrate taxonomic groups have been at least partially assessed, and show similar, or worse, trends: 30% of fish species; 25% of reptile species and 21% of amphibians are threatened with extinction, and similar proportions are reported for invertebrate groups and plants. For the level and range of threats to be reduced, major alterations to the way we utilise natural resources and manage the natural environment are required. For example recent research suggests that many fisheries currently have a biomass of only about 10% of their pre-industrial fishing levels (Myers and Worm, 2003), and recovery will only come about through considerable reductions in fishery effort (Pauly et al, 2002). With approximately 40-50% of the ice-free land surface transformed by humans (Chapin, et al, 2000), loss and

fragmentation of natural terrestrial habitats is perhaps the greatest contributor to species declines (Opdam and Wiens, 2002). Presently there appears to be insufficient political will to take the large steps needed to slow and reverse the current trends in resource use, and even if such changes are made there will inevitably be delays before their effects are felt. The status of many species is such that they will almost certainly be extinct (at least in the wild) long before such changes can take effect, and there is thus a need for immediate intervention, often on a case by case basis. The necessity for urgent action to monitor, and if necessary attempt to reverse, population declines has seen an increase in the application of ecological theory, and in particular population modelling, to conservation problems. Through analysis of population models developed using a species' demographic rates, the outcomes of alternative management strategies can be considered. Often these theoretical experiments would be impossible, impractical or simply take too long, to perform on field populations. Thus the growth in population modelling theory and application has provided an extremely valuable additional tool for conservation managers, who previously may have had to base important decisions on little more than their own intuition. Population projections can also play a part in guiding policy makers, who might otherwise only have information on past declines on which to base decisions.

Matrix population models have become established in the last 20 years as the most common form of population model for studying endangered species (Beissinger and Westphal, 1998). A typical matrix model consists of a series of difference equations presented in matrix form for convenience (fig. 1). Population studies are often conducted

by regular censusing of a population with the data categorised by age or stage. Data collected in this way usually requires little additional analysis for the calculation of mean demographic rates (e.g. fecundity, survival and growth rates), which are then entered into a population matrix. If this matrix of mean vital rates is multiplied by a vector containing the number of individuals in each age (or stage) class then the result is a second vector of the numbers present in each class after the time period (typically one year) over which the rates operate (fig. 1b). Repetition of this process will yield a sequence of such vectors and thus a projection for the population into the future (hence population matrices are sometimes referred to as ‘projection’ matrices). After an initial period of fluctuation, a constant (λ) defining the rate of population growth (whether positive or negative) can be calculated from such a projection. λ may also be derived analytically through eigenanalysis of the population matrix (performed using a software package such as MATLAB); λ is the dominant eigenvalue of the matrix. Two additional characteristic values for the matrix can also be found in this way: the right and left eigenvectors represent the stable age distribution and the reproductive values for each age class respectively (Caswell, 2001). The value of λ provides valuable information about the status of the population. A decreasing population has a λ value less than one, while an increasing population has a λ value greater than one. This is not the limit of such a model’s usefulness however. The contribution (either absolute or proportional) which each of the mean demographic rates within the matrix makes to the overall rate of population growth can also be calculated. Such proportional contributions are known as elasticities (de Kroon et al. 1986), and these can be used to rank a species demographic rates according to their relative contributions to population growth. The theory of

a

$$n_1(t+1) = F_1n_1(t) + F_2n_2(t) + F_3n_3(t)$$

$$n_2(t+1) = P_1n_1(t)$$

$$n_3(t+1) = P_2n_2(t) + P_3n_3(t)$$

b

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix} (t+1) = \begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix} * \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix} (t)$$

c

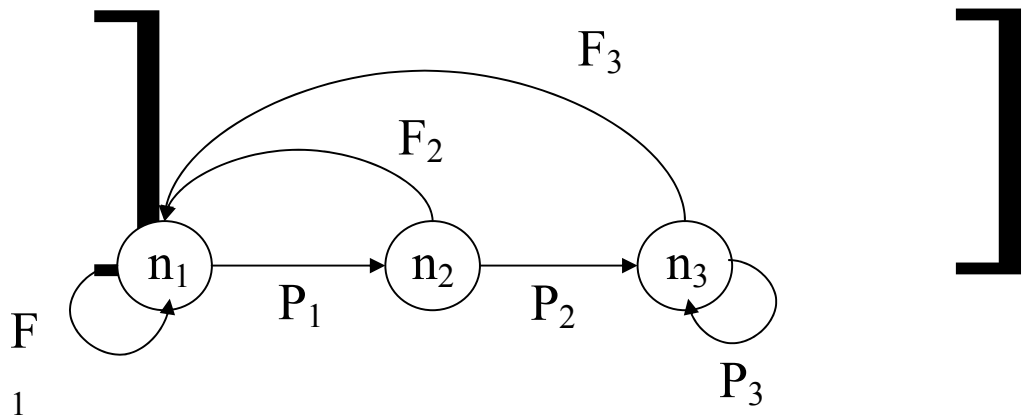


Figure 1. Post-breeding matrix model presented in 3 different formats. a) difference equations for the age structured population; b) matrix model formulation of (a) with population vectors and transition matrix; c) life cycle graph of (a). In each diagram ‘t’ represents the time step interval (e.g. annual) and there are 3 age classes: n_1 (0 year olds, representing e.g. fledglings); n_2 (1 year olds); n_3 (2 year olds and older). In each case P_X are survival transitions and F_X are fecundity rates (fecundity rates are composites of the age class survival and fertility rates (m_x), e.g. $F_1 = P_1m_1$; $F_2 = P_2m_2$, etc.).

elasticity analysis states that a proportional increase in the vital rate with the highest corresponding elasticity value will produce the greatest subsequent increase in λ (Caswell, 2001). Clearly this type of information is of great appeal to conservation managers, and elasticity analysis has played a significant role in promoting the use of matrix models in conservation.

However, all models make assumptions about the form of data used and how it is analysed, and these assumptions must be borne in mind during interpretation of their results. A deterministic, density independent calculation of λ and its associated elasticity values, as described above, makes two important assumptions: that the environment is unchanging and that the rate of population growth is unaffected by population density. Neither of these assumptions can be justified from the point of view of real population processes, only from that of model simplification. While models should be kept as simple as possible (Starfield, 1997), it is also important that, where data permit, assumptions made during an analysis are investigated. Techniques for calculating elasticities for density dependent, stochastic matrix models have recently been developed (Grant, 1997; Grant and Benton, 2000; Grant and Benton, 2003), and thus it is now possible to test the assumptions of traditional elasticity analysis.

Grant and Benton, using both theoretical models (Grant and Benton, 2000) and one previously developed by Dennis et al. (1995) for experimental populations of the flour beetle (*Tribolium castaneum*; Grant and Benton, 2003) have shown that under certain conditions, density dependent, stochastic elasticities can be significantly different from

the deterministic, density independent elasticities of λ , even to the extent of having the opposite sign. There are, however, no published accounts of the application of these techniques to models developed using data from field populations. This study was undertaken in order to address this issue.

An ideal candidate species from a modelling point of view would be one for with a long time series of data, comprising of good quality information for all demographic rates across all age classes, and showing wide variations in population density. We would also have detailed information on exchange rates between different populations and the relationship between demographic parameters and habitat quality indices. This would enable us to have a high degree of confidence in model structure and performance. Unfortunately the wren dataset used in this study does not fall into this description. However, since data of such a high quality is rarely available, particularly in the case of rare and endangered species, the use of a more limited dataset for the purposes of illustrating what can still be achieved in such circumstances is still extremely useful.

The data for this study was derived from a population of wrens (*Troglodytes troglodytes*). Wrens lend themselves to this task because, despite being one of the commonest bird species in Britain, their populations show large fluctuations in size between years and thus data for modelling stochasticity in vital rates is readily obtained. In addition, studies of wren populations have found evidence that both winter weather and population density influence survival rates (Greenwood and Baillie, 1991; Newton et al, 1998; Peach et al, 1995) and population density also limits reproduction (Wesolowski, 1983). Thus wrens

appear to be an ideal candidate species for investigating the roles of density dependence and stochasticity in elasticity analysis. The study population chosen peaked at around 120 in mid summer and was modelled as an isolated population, despite the fact that it was not actually an island population. In effect the model started from the premise that this was the last population of wrens, and the modelling was undertaken to identify the most appropriate management for this situation. This approach was chosen in order to make the results as applicable as possible to a hypothetical rare bird scenario.

Since wren populations experience both density dependent regulation and fluctuations between years due to environmental variation, a wren population model without these features would omit vital components of wren population dynamics. The fact that in addition these two features may combine in their population dynamic effects, as described for an increasing range of other systems (Higgins et al, 1997; Leirs et al, 1997; Grenfell et al, 1998; Coulson et al, 2001), provides a further incentive for performing this research.

Thesis overview

The main aim of this study was to compare the results of elasticity analysis for a wild population performed with and without density dependence and stochasticity, in order to assess the importance of their inclusion in demographic studies, with particular reference to rare and endangered species conservation. The data collection and the model development and analysis are described in the remaining chapters of this thesis, as briefly described in the following section.

Chapter 2

To develop and parameterise a simulation model, demographic rates from a suitable population were required. A population of wrens in a wood near to the Stirling university campus were selected for this purpose (fig. 2). Adult survival rates were estimated using leg rings (BTO and colour), capture – mark – recapture techniques, and analysis using program MARK. Reproductive rates were obtained by mapping individual territories, carrying out intensive nest searches within each territory and subsequently monitoring active nests through to completion.

Chapter 3

Juvenile survival rates were investigated using a combination of observation, capture – mark – recapture methods and radio tracking using miniature tags with a maximum life span of 8 weeks. A sample of nestlings were selected for radio-tracking, and were fitted with tags at or around the date of fledging. In addition to investigating the post-fledging survival period the tags were also used to study juvenile survival rates during their first winter. All fledglings were leg ringed, and return rates as adults were used in conjunction with the radio tracking data.

Chapter 4

A simulation matrix population model was written in Matlab (The Mathworks, Inc), using the demographic rates and variances collected from the study population, along with additional parameters derived from the field study (e.g. the number of territories and the breeding bird sex-ratio). The model explicitly incorporates environmental and

demographic stochasticity, vital rate covariance and density dependent survival and reproduction. Model outputs are presented for a range of density dependent and stochastic settings, and these are discussed with relevance to their roles in real populations.

Chapter 5

Density dependent, stochastic elasticity analysis using the model described above was carried out using three alternative methods. Each method uses a different population metric to calculate the elasticity values (invasion rate of a mutant type, mean equilibrium population size, extinction probability). The results from each of these techniques, and those derived by the traditional analytical approaches, are compared and contrasted across a range of density dependent and stochastic model scenarios. The causes of both agreements and disagreements between the methods are discussed in relation to their suitability to different applications and requirements.

Chapter 6

The conclusions of the work carried out are summarised, the implications of the main results discussed and possible directions for future work building on this study will be suggested.

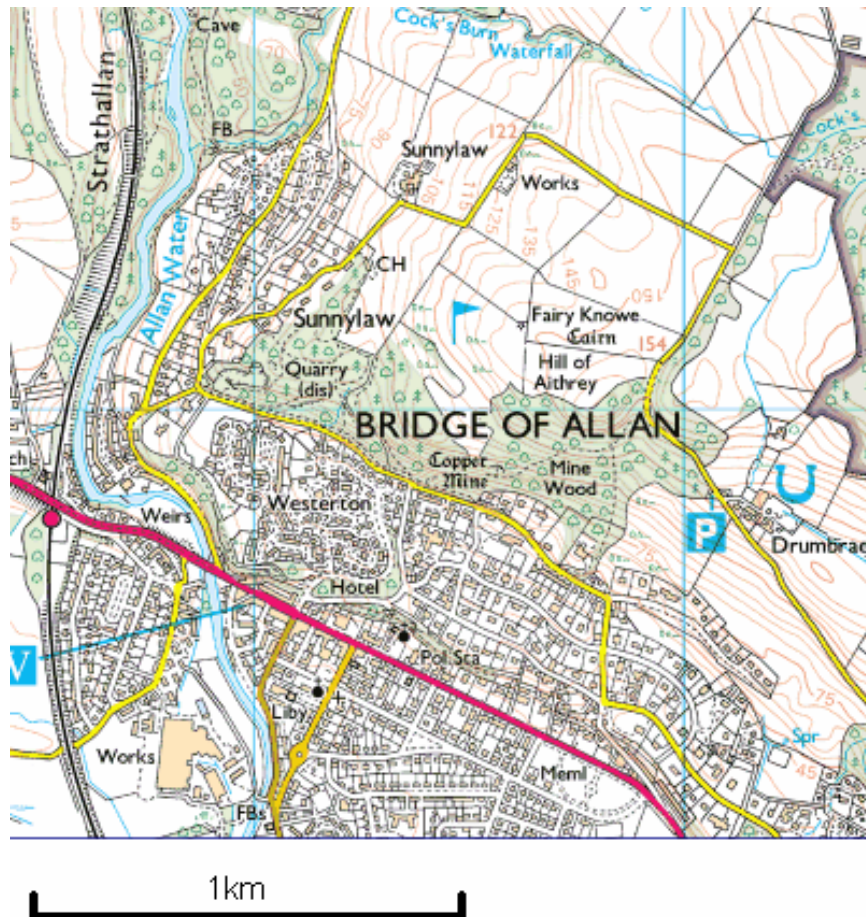


Fig. 2. Ordnance survey map of Bridge of Allan, Stirlingshire, showing the Mine wood study site (centre). The wood lies on a south facing slope and is bordered to the south and west by roads, houses and gardens, to the north by a golf course and to the east by rough pasture.

Chapter 2

Estimation of adult wren demographic rates

2.1 Introduction

The European wren (*Troglodytes troglodytes*) is the only representative of the wren family outside of the Americas and is widely distributed through middle latitudes in the western Palearctic. In the UK wrens are one of the most numerous bird species and are most commonly found in woodland and hedgerows, although they have also been recorded in many other habitats (Armstrong, 1955). The aim of this study was to collect demographic data from a small population of wrens, occupying an area of woodland near to the Stirling University campus, Bridge of Allan, Scotland, with which to parameterise population models. After a brief description of the wren breeding season (March – September covering the main period during which data was collected), the methods used to analyse the data will be described. This chapter deals with the survival and reproduction data collected for adult wrens, defined here as birds aged one year and older. The next chapter considers data for juveniles, comprising the period from leaving the nest to the commencement of breeding at one year old.

Wren life cycle

During spring, males surviving their first winter establish themselves on suitable, available territories. Previous observations have found that, with rare exceptions, males in possession of a territory in one season will remain there until they die (Armstrong, 1955). Spring is thus also the time when older males, surviving into their second or later years, re-establish the boundaries of their territories. Singing and territory defence increase during the spring reaching a peak in May and June. No formal measurements of territory size were made in this study, but territories

were typically in the region of 1-2 ha in size. The main determinant of territory size in woodland appears to be the density of understorey vegetation (Evans, 1997a). Territory sizes in the more open, primary forests of Bialowieza National Park in Poland are reported to be up to 5 times as large as those in the secondary woodland of the UK (Wesolowski, 1981). The total area of the study site was approximately 25 hectares, and the average adult numbers for the whole study site in the spring was 32 (s.d 3.7, n=4). This gives an approximate adult pre-breeding population density of 1.28/ha. During April and May males begin to build nests on their territories, only a small proportion of which will be selected for nesting by females (Armstrong, 1955). The males' 'cock' nests are an important component of the display for females (Evans and Burn, 1996), and the number built by any particular male is determined through a combination of the availability of suitable nest sites and the individual's nest-building ability (Evans, 1997b). Once a female has selected a male and a nest, she lines it with feathers prior to egg-laying. The first clutches are laid around the beginning of May, incubation of the eggs lasts for 16 days and the nestlings fledge after a further 14 days. The female incubates the eggs and feeds the young on her own, while the male continues to build nests until June or July and attempts to recruit more females to use these nests for breeding. Most females which have successfully raised an early first brood to independence or lost their first clutch through predation or poor weather, undertake a second breeding attempt. The last nests are initiated in early July with the latest broods fledging in early August. Brood size is highly variable, with anywhere between 2 and 7 young fledging successfully. The female, often with the male in attendance continues to feed the young for up to two weeks post-fledging, after which the family groups break up and the juveniles begin to disperse. While most of the features of the wren life cycle

remain the same throughout their range, the extent to which males successfully recruit more than one female with which to breed appears to depend on the productivity of the habitat (Wesolowski, 1983). Latitude plays a part both in the timing of events, and also in determining the extent to which wrens are year round residents or undergo seasonal migration. In the UK wrens are near to the northern limit of their permanent resident range. At higher latitudes within continental Europe they show an increasing degree of southerly winter migration as the minimum temperature declines, with the cut-off point for residency found around the -7°C January isotherm (Armstrong, 1955).

2.2 Methods

Data collection – population census and breeding

Male wrens have a loud and distinctive song, making mapping of territories in the spring a relatively straightforward operation. The wren population used in this study had been studied since 1995, and thus most individuals present in previous seasons had already been fitted with leg rings - both a unique metal BTO ring and also individual colour ring combinations to permit identification with binoculars. After the commencement of territorial behaviour in the spring the study area was surveyed to identify which of the territory holding males possessed colour rings (survivors from previous years with a known history) and which did not. The latter, un-ringed individuals were caught in mist nets using a recording of male song as a lure to assist in their capture, since territory holders respond vigorously to the apparent presence of another male. Once a bird was caught it had leg rings fitted and was aged as either being in its first year or older (this is the only age distinction which is

possible, based on plumage characteristics; birds in their first year can be identified as such until the end of summer moult in the year after they hatched, when they are approximately 14 months old, see Svensson, 1992 for details). In addition the following morphological measurements were taken (tarsus (to the nearest 0.1 mm), tail length (0.1 mm), wing length (1 mm), weight (0.1 gm)). Males and females have identical plumage and, since birds other than the specifically targeted territory owner were also caught, a means to distinguish the sexes was required. Sweeney and Tatner (1996) developed a discriminant analysis for sexing wrens based on morphological measurements which they report had a 96% success rate. Using their methods, morphological measurements were used to assign sex. Once all the territory holding males were colour ringed, observations enabled territory maps to be drawn up. These were used and updated for the remainder of the season as guides for nest searching. Each male territory was visited every 5 to 7 days between April and July and a thorough search for nests was carried out. Male wrens build small dome nests (c. 15 cm diameter) in a wide range of possible locations. Typically nests are built within dense vegetation, beneath root-plates, under loose tree bark and below logs. Nests were also located through observation of males actively engaged in building. Each nest was plotted on a map and visited every few days for the remainder of the breeding season to check for signs of breeding activity. Once a breeding attempt was identified, efforts were made to catch the female in mist nets placed near the nest. Once caught, measurements were taken and, if necessary, leg rings (BTO and colour rings) were fitted. Chicks in the nest were weighed and ringed at around 11 days after hatching. One day before the expected fledging date all the chicks from each brood were removed from the nest and placed in a catching bag. One (in 2000) or two (in 2001) individuals from each brood were then removed

randomly from the bag and had a radio tag attached. After tag attachment all the nestlings were placed back in the nest or released to fledge together depending on the stage of development of the birds and their willingness to be returned to the nest (the details of radio tagging and juvenile data collection are discussed in chapter 3).

M Evans, as part of on-going research into mate choice decisions, recorded demographic data for the wrens in the study population from 1995 until 1999. The area covered varied slightly between years, as did the level of detail:

Conducted by M Evans:

- 1995 - all males, all females, all breeding attempts
- 1996 - all males, all females, all breeding attempts
- 1997 - all males, some females, some breeding
- 1998 - males in half the wood only
- 1999 - males in half the wood only;

Conducted by M Trinder:

- 2000 - all males, all females, all breeding attempts (as 1995/96)
- 2001 - all males, all females, all breeding attempts (as 1995/96)
- 2002 - all males only

Survival analysis

Ideally demographic rate estimates for the study population would be calculated for both sexes independently, using the data collected over the full span of years. However males were recorded to a much greater extent than females, due in large part to difficulties in surveying for females. With the exception of 2 years (1998 and 1999, when a reduced area was surveyed), the same area of the wood was surveyed

for territorial males in each year of the study, providing a good time series for survival analysis. Females were only recorded in detail for 4 of the 8 years, in 2 separate blocks of 2 years (1995-96 and 2000-01). Thus analysis of female survival is severely compromised, due to difficulties in separating emigration from death. A survival analysis for both sexes combined, using all of the available data could be carried out, but in order for this approach to be valid it is necessary to be confident that both sexes experience the same survival and re-capture probabilities. If the sexes differ then estimates will be affected and we should therefore treat each sex separately in our analysis. Although bird ringers throughout the UK commonly catch and ring wrens, very few workers sex them, so we cannot use national data to look for sex related differences in survival or movement. For many bird species females show lower site fidelity between years (and therefore lower re-trap rates) than males (Greenwood, 1980). There is some evidence of this in wrens from a Dutch study which found that males were more faithful to breeding territories both within and between years than females (Kluijver et al., 1940). If this is the case for the population studied here, then an analysis combining males and females could lead to an underestimation of survival rates, due to the inclusion of female emigration. For this reason survival was estimated for males only.

Survival rate estimation

Program MARK (White and Burnham, 1999) incorporates a range of survival rate estimation methods, allowing different formats of data to be analysed. The standard Cormack-Jolly-Seber (CJS) capture, mark, recapture model which calculates apparent survival (ϕ) and recapture probability (p) from live recaptures or re-sightings was selected from the range of survival models available, and an arbitrary

annual census date set as a point at the beginning of the breeding season. Survival in the CJS model is estimated as apparent survival (ϕ), which is a combination of permanent movement out of the study area along with true mortality, and so has a tendency to underestimate the true survival probability (White and Burnham, 1999). If emigration rates are high this can significantly influence survival estimation, however male wrens exhibit a high degree of site fidelity and movements between territories between years are uncommon (Armstrong, 1953; Kluijver, 1940; Peach et al, 1995). In this study 74 territory holding males (counting each male only once) were monitored over 8 years and only 2 were recorded moving to different territories within the wood between breeding seasons. In addition, all new territory holders were birds in their first year, thus we have no reason to reject the hypothesis that recording of presence or absence of territorial males is a good proxy for survival. A table representing the territories and their owners over the course of the study is provided in fig 1.

Territory	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Year																							
1995	R	OPI	Y	P	G	B	B	W	BL	RY	RR	?	?	OO	OY	RB	RW	RBk	?	?	OR		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
1996		BLY	?	BLB	BLB	BW	GG	W/BR	GO	GW	RR	GPI		GBL	(BR)	RB	?				GP		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
1997	WW	BkO	BkY	BLB	BLB	WPI	WBL	BR	PB	GW	RR	PW		GBk	PPI	RB	WR	WO	WY	WG	WP		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
1998	*	*	*	*	*	*	*	?	PB	GW	RW	PW		OB	PPI	OO	OW	OP	OB	OG	BR		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
1999	*	*	*	*	*	*	*	RR	PB	RB	RW	OY		OB	OR	OO	OW	OP	OB	OG	BR	BO	
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2000	YY	YR	BkY	BkBk	BkPi	PiY	YO	BkP	RB	RB		OY	?	PR		PIW	?	OP		BR	BO		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2001	YY			PiBk	BkBk	YR	?	RG	RR	RR		OY	RY		PR	RBk	BkP	RO		BR	RP		
	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2002	YY	?		?	WP	OBk	WO	BPI	RG	PP		RPI	RY		PiO		BkP	PG		BR	RP		

Figure 1. Graphical representation of male wren territories within the Mine wood study site between 1995 and 2002. Each column represents a territory (1-22), and each block of two rows comprises one year. In each year the cross ('+') signifies a change of ownership has occurred, and the first and second lines indicate whether the territory owner is a first year (line 1) or older (line 2) male. The identification letters represent the coloured leg rings worn by each male (key to colours below).

Notes: 1 - Male 'W' disappeared during the breeding season and was replaced by male 'BR'; 2 - In 1998/99 part of the wood was not surveyed due to time constraints; 3 - Male 'YR' moved from his 2000 territory to a different, non-adjacent territory in 2001.

Key to symbols: '?' - unringed male; '+' - previous year's territory holder absent (presumed dead); empty cell - unoccupied territory.

Colour codes: R - red; O - orange; Y - yellow; G - green; B - blue; P - purple; Pi - pink; W - white; Bk - Black; LB - light blue

Data entry into MARK is in the form of individual encounter histories. For the CJS model an individual has just one character for each year, either a '1' – alive and caught/seen, or a '0' – not seen. Thus a male wren first caught on a territory as a 1yr old at the start of the study (1995) and remaining on that territory for the next 2 seasons (1996/7) before disappearing over the following winter would have the following capture history:

1 1 1 0 0 0 0 0

(for further details see Program MARK: A gentle introduction, Cooch and White, 1998).

Each line of an encounter history file contains the capture history for one individual. Adult wrens were aged as either one year olds or older on the basis of plumage characteristics (Svensson, 1984). In the standard data entry formulation as described, individuals can only enter the dataset as 1 year olds. This would lead to the exclusion of all birds older than 1 in the first year of the study (approximately half the territory holders in 1995 were older than one), and similarly exclude those males occupying the area of the wood which was re-surveyed in 2000 after two years of omission. In order to incorporate these older birds it was necessary to divide the input data into two groups. One group consists of birds caught for the first time at 1 year old, the other of birds first caught when older than 1. Through a combination of this grouping and manipulation of the parameter estimation matrices all individuals could be incorporated into the analysis and could contribute to the survival rate estimates. In this study we make the assumption that all adult mortality occurs over the winter, however it is extremely unlikely that this is the case. While more regular censusing of the population would provide further details of the variation in seasonal survival, the most reliable period for the male census is in the spring when they are

exhibiting their peak territorial behaviour, and censuses at other times of year would suffer from a significantly reduced detection rate. Since the majority of population models are based on an annual time step, this simplification in survival analysis does not present subsequent problems in terms of model parameterisation.

Goodness of fit testing

When the CJS model is used for analysing capture-mark-recapture data it is essential to be aware of the four underlying assumptions which the technique makes about the data:

1. all marked animals have the same recapture probability (for the period: $t - t+1$);
2. all marked animals have the same survival probability (for the period: $t - t+1$);
3. marks are not lost;
4. sampling is instantaneous relative to the intervals between samples.

Loss of leg rings in small passerines occurs at a very low rate, and for the purposes of this study we consider assumption 3 is met. Although trapping and monitoring of territory holding males was conducted over a course of 2-3 weeks, this is short compared to the year time step over which rates were estimated, thus assumption 4 is also of little concern. However few wild populations are likely to satisfy the conditions of equal recapture (assumption 1) and/or survival rates (assumption 2) due to trap avoidance or age structure (Cooch and White, 1998). MARK can identify violations of these assumptions by performing tests for the goodness of fit of a model to the data. Goodness of fit is performed on the fully parameterised, time dependent (saturated) model. If an acceptable fit to the data is established then models with improved precision are sought by simplifying the parameter structure

and thus increasing model parsimony. The first step is to compare the deviance for the observed, saturated model with that obtained by parametric bootstrap simulation. The next stage depends on the outcome of this procedure. If the observed data satisfy the CJS assumptions (i.e. the observed model deviance does not lie within the significant 'tail' of deviances from the simulated models), then it is simply a matter of running biologically plausible models of survival and recapture, and comparing their fit to the data with that for the saturated model. However, if the observed model's deviance is sufficiently large that it falls within the statistically significant region of the bootstrap results, this suggests over-dispersed data, and an important lack of fit requiring further investigation. Clearly if age does influence survival and/or recapture rates in the study population then a model structure which does not take this into account has a high probability of failure. MARK incorporates another test program, RELEASE (Burnham et al, 1987), to use when this is suspected. RELEASE also performs goodness of fit tests on the time-dependent CJS model. However rather than simply providing a measure of fit to the data, RELEASE breaks down the fitting process, providing greater insight into the causes of poor model fit to the data, and identification of the CJS assumptions which are being violated. The tests use chi-squared contingency tables to compare expected and observed numbers of survivors. Small sample sizes can present complications, since if the expected value in a contingency table is very low (e.g. < 0.1) then a single observation (i.e. one bird) can produce a large discrepancy in the observed and expected values, and a highly significant chi-squared value. There does not appear to be a solution to this problem (White, 2000) and thus a pragmatic approach towards interpretation of model outputs is necessary.

Mark-recapture data are commonly over-dispersed and it is therefore important to check for its presence prior to model fitting so that any necessary adjustments can be made. The bootstrap simulation results, as well as measuring goodness of fit, also provide a method to correct for over dispersion in the observed data. If the time dependent model fits the data perfectly then the over-dispersion quasi-likelihood parameter \hat{c} (c-hat), has a value of 1.0 (the default value). If the data are over dispersed then a value of $\hat{c} > 1.0$ can be expected. The size of the corrected \hat{c} value can have important implications both for assessing relative model fit and in extreme cases, the applicability of the CJS technique. There are two methods to calculate the adjusted \hat{c} value, the first is based on model deviance:

$$\text{adjusted } \hat{c} = \frac{\text{observed deviance}}{\text{expected deviance}}$$

Where the observed deviance is that from the model $\{\phi(t) p(t)\}$ and the expected is the mean deviance value from the bootstrapped simulations. The alternative method is based on \hat{c} itself and is derived thus:

$$\text{adjusted } \hat{c} = \frac{\text{observed } \hat{c}}{\text{expected } \hat{c}}$$

Where the observed \hat{c} is found by dividing the model deviance by the deviance degrees of freedom ($df=1$) and the simulated \hat{c} again comes from the averaged bootstrap value. There has been no formal work to establish which technique is more valid and in most cases the current recommendation is to accept the larger of the two values (Cooch and White, 1998). However the calculated values of \hat{c} can differ quite markedly when small sample sizes are analysed, caused by high variability in the deviance degrees of freedom across the bootstrap simulations (White, 2000). If this

is encountered it is preferable to use the \hat{c} calculated from model deviance. Values of \hat{c} much greater than one (e.g. $\hat{c} > 3$) indicate substantial lack of model fit to the data, and even at intermediate levels ($\hat{c} > 2$) model fit must be considered carefully (Lebreton et al 1992).

Model fitting

The model building process in MARK is extremely flexible and models can be constructed with the parameters (ϕ and p) varying with age or time, or remaining constant, or combinations of all three. Each model is assessed for its fit to the data using Akaike's information criterion (AIC), balancing model deviance against the number of fitted parameters. The difference in AIC value between each candidate model and the current best-fit model (ΔAIC), is used to rank model fit. To calculate the AIC weights, first the ΔAIC for each model is divided by the ΔAIC summed for all the candidate models (specifically: for model i , $= \exp(-1/2 * \Delta AIC \text{ for model } i) / [\sum \text{ for all models of } \exp(-1/2 * \Delta AIC)]$). This gives a proportional measure of the fit of each model given the data, and the AIC weights are simply these values normalised (to sum to 1), thus providing a straightforward means of comparing fit across all considered models. Likelihood ratio testing can also be performed to look for the presence of significant differences in model fit. Tests are carried out between pairs of nested models with a significant result indicating poorer fit for the reduced model than the more parameterised one, due to a significant increase in model deviance with a decrease in the number of parameters (Cooch and White, 1998).

It is sensible when fitting models to be guided by the biology of the study species and the conditions under which the data has been collected. As previously mentioned, wrens can be aged as either 1-year-olds or older using characteristics of the plumage retained until the end of summer moult at age one. A few known age individuals older than 2 are present in these data with which age specific survival beyond the age of 2 could be estimated (i.e. 2-3, 3-4 years etc.). However these estimates would be of little practical value outside of similarly intensive studies. In addition the actual number of known age wrens older than 2 is very small (four survived from 2 years to 3, one from 3 to 4) and thus confidence in the precision of survival estimates would not be high. For this reason age related survival was considered for only two age groups: one year olds surviving to two years old and individuals aged two or older surviving to the following year.

Male census data runs from 1995 to 2002, giving 7 transition periods for survival estimation. Analysis began with the time dependent (t), single age class model $\{\phi(t) p(t)\}$, with both survival (ϕ) and recapture (p) probabilities calculated independently for each estimation period. This (saturated) model is the basis for comparisons with less parameterised versions: constant (c) survival and recapture for all ages in all years $\{\phi(c) p(c)\}$; two age classes (as described above) each with either constant or time dependent survival and recapture across all years $\{\phi(1c, 2c) p(1c 2c)$, to $\phi(1t 2t) p(1t 2t)\}$; and various combinations of the above.

Winter survival

There is much anecdotal, and some more rigorous, evidence suggesting that passerines, and wrens in particular, experience elevated mortality rates during severe

winter weather (Cawthorne & Marchant, 1980; Marchant et. al 1990; Armstrong, 1955; Greenwood and Baillie, 1991). Peach et. al (1995) used weather variables covering the whole year in their analysis of wren survival. They concluded that the number of winter snow days was the best predictor of wren survival rates. For this study, winter weather data recorded at a permanent station on the University of Stirling's campus (56⁰⁹'N, 3⁰⁵⁵' W) which is approximately 2 km SE of the Mine wood study site was used. Since Peach et al (1995) only found evidence for an effect on survival of winter weather, and the population was only censused in the spring, it was decided that only winter variables would be used in this analysis. The variables and their values are listed in table 1. Monthly means for each variable in each winter (1995-2002) were calculated and summed into a 6 month (October-March) total. Figures for the 3 month period December-February were also calculated, but during subsequent analysis it was found that this failed to provide any additional explanation of survival beyond that from the 6 month totals and thus these have been omitted. Principle component analysis (PCA) of the weather variables identified those factors contributing most to the between year variation and also produced an overall weather score for each winter, derived from the data and the principal component coefficient values. By entering either the weather data or the PCA scores into the design matrix in MARK, survival (and/or recapture) rates are constrained to be linear functions of the variable entered. To investigate combined effects multiple co-variates can be added to the design matrix. It is important to scale the variables entered to lie between 0 and 1 prior to testing to ensure the numerical optimisation algorithm finds the correct parameter estimates.

Table 1. Winter weather data from meteorological station, University of Stirling, Stirlingshire. The six month mean values are shown (October - March), all readings were taken at 9am each morning. A rainday was defined as one in which 1mm or more rain fell, a snow day as one with at least 50% of the ground covered with snow and a frost day as one with the ground predominantly covered in ice. The principle component score was calculated using all of the weather data in Minitab.

Winter	Temperature		Precipitation			Frost		Principal component score			
	Mean minimum temp ($^{\circ}\text{C}$)	Mean maximum temp ($^{\circ}\text{C}$)	No. days max $<10^{\circ}\text{C}$	No. days max $<5^{\circ}\text{C}$	Total rainfall (mm)	Rain days	Snow days		Consecutive snowdays >4	Frost days	Consecutive frost days >4
1995-96	2.22	8.55	116	39	468	62	25	3	5	0	0.601
1996-97	2.87	9.39	103	22	648.9	86	3	0	0	0	0.117
1997-98	4.07	10.31	100	17	498.9	77	1	0	0	0	0.088
1998-99	1.95	9.47	94	13	595.9	93	6	0	0	0	0.085
1999-2000	2.69	9.94	91	12	649.3	93	2	0	15	2	0
2000-01	1.80	8.55	124	29	495.7	80	22	3	19	1	0.54
2001-02	2.32	10.10	94	17	555.6	93	6	0	4	1	0.072

Reproduction

The number of young fledged per nest in each year of nest monitoring (1995,1996, 2000, 2001) was considered in various ways. Number of offspring was considered separately for each sex, with either two age classes (1 year olds and 2 years or older, as used for survival estimation) or all ages combined. Using the same age and sex divisions, investigations of the rate either per individual or per breeding attempt were also conducted. The data was analysed for trends within and between the groupings using Residual maximum likelihood testing (REML) in the statistical package Genstat. The mean and standard deviation across all years for each group was then calculated to provide fecundity parameters for population modelling.

2.3 Results

Goodness of fit testing

The observed deviance for the starting model $\{\phi(t) p(t)\}$ was 42.74. This corresponds to the 753rd model of 1000 bootstrapped simulations. Thus there was no reason to reject the time dependent, non-age structured model ($P = 0.247$), as there is a reasonable likelihood of observing a deviance this large. However with the aim of obtaining age class survival rates (violating CJS assumption 2) for parameterisation of age-structured population models in mind, further tests of the CJS assumptions using RELEASE was carried out. A small number of the individual tests gave significant results for lack of fit, however these were all attributable to occasions where single observations for small expected values result in large chi-square values and the overall test statistic failed to reject the saturated model. Thus while there is no statistical support to justify adopting age structure in the survival rate analysis, the small sample size limits the power of the tests to detect structure in the data.

Over-dispersion

The deviance based adjustment calculation yields a \hat{c} value of:

$$\frac{42.74}{36.71} = 1.164$$

Where the observed deviance (42.74) is that from the model $\{\phi(t) p(t)\}$ and the expected (36.71) is the mean deviance value from the bootstrapped simulations. The deviance calculated using \hat{c} itself was found thus:

$$\frac{42.74}{13.01} = 3.283$$

Where the observed \hat{c} (42.74) is found by dividing the model deviance by the deviance degrees of freedom ($df=1$) and the simulated \hat{c} (13.01) comes from the averaged bootstrap value.

Because of the small sample size in this study, rather than use the larger of the two \hat{c} values, the deviance based method is preferred, therefore the adjusted value of \hat{c} used for the remainder of the model fitting was 1.164. This is substantially lower than the critical values of \hat{c} indicating substantial lack of fit ($\hat{c} > 3$), and also lower than the intermediate level ($\hat{c} > 2$) when model fit must be considered carefully (Lebreton et al 1992). Thus in this study it appears that model fit is not an area of concern.

Model fitting

Single age class models

Table 2a presents the results of the initial adult survival analysis. Models 1 to 4 consider survival and recapture rates for all individuals together, with all possible combinations of time dependent and constant rates. The best fitting model (no. 4: $\phi(t) p(c)$) has time-dependent survival, and constant recapture probabilities and receives almost twice the support of the next best, constant rates model $\{\phi(c) p(c)\}$. The degree of relative support inferred from the AICc weight is reduced slightly due to a \hat{c} value slightly greater than 1.

Two age class models

The next step in the analysis was to investigate age related survival. As previously stated, known age wrens older than two are not well represented in the data. Therefore a two age class structure was adopted, with the first class containing one year old males (estimating survival from one to two) and the second all males aged two or older (estimating survival from two to three, and all subsequent survival). The results of this analysis can be seen in table 2b. The starting point is the previous best-fit model ($\{\phi(t) p(c)\}$, model 4, table 2a) against which models with a range of age specific parameter structures (nos. 5-12) were compared. Three age-specific models (5,6,7) have higher AICc weightings than the single age starting model. Model 5 $\{\phi(1t 2c) p(1c 2c)\}$ has the highest AIC weight, with over 4 times the support of the next best model, $\{\phi(1c 2c) p(1c 2c)\}$.

Table 2. Models of adult survival rates of male wrens in Mine wood 1995-2002. The best fitting (minimum) models are highlighted in bold.

Notes: phi=apparent survival probability; p=recapture probability; t=time dependent; c=constant; 1=first age class; 2=second age class; QAICc=Quasi Akaike's information criterion; Delta QAICc=QAICc difference to minimum model; QAICc weight=proportional model likelihood; LRT=Likelihood ratio test. In all cases the over dispersal parameter (\hat{c}) has an adjusted value of 1.164. Covariates: maledensity = measure of population size at beginning of winter; min temp = mean minimum daily temp; max temp = mean maximum daily temp; days<5C = no. days temperature fell below 50C; days<10C = no. days temperature fell below 10C; raindays = no. days rain>1.0mm recorded; snowdays = no. days snow lying at 9am; snowdays>4 = occasions snow lay for 4 or more days consecutively; rain = total winter rainfall.

Model no.	Model structure	QAICc	Delta QAICc	QAICc Weight	No. Par.	QDeviance	LRT	Result
(a) Single age class								
1	phi(t) p(t)	157.0	11.1	0.00	14	36.7	-	Starting model
2	phi(c) p(t)	154.6	8.6	0.01	8	49.3	2 vs.1: $\chi^2 = 12.6$	p = 0.04
3	phi(c) p(c)	146.9	1.0	0.38	2	55.0	3 vs.1: $\chi^2 = 18.3$	p = 0.1
4	phi(t) p(c)	146.0	-	0.61	8	40.7	2 vs.1: $\chi^2 = 4.0$	p = 0.67
(b) 2 Age classes								
5	phi(1t 2c) p(1c 2c)	141.4	-	0.64	10	31.4	5 vs.6: $\chi^2 = 16.9$	p = 0.009
6	phi(1c2c) p(1c2c)	144.5	3.1	0.14	4	48.4	6 vs.8: $\chi^2 = 4.3$	p = 0.03
7	phi(1t 2c) p(c)	145.0	3.6	0.11	9	37.4	7 vs.5: $\chi^2 = 5.9$	p = 0.01
4	phi(t) p(c)	146.0	4.6	0.07	8	40.7	-	starting model
8	phi(1c 2c) p(c)	146.7	5.2	0.05	3	52.7	8 vs.4: $\chi^2 = 11.9$	p = 0.04
9	phi(1t 2t) p(1c 2c)	155.2	13.8	0.00	16	29.4	9 vs.6: $\chi^2 = 14.6$	p = 0.26
10	phi(1t 2c) p(1t 2c)	157.2	15.8	0.00	16	31.4	10 vs.4: $\chi^2 = 16.9$	p = 0.15
11	phi(1t 2t) p(c)	158.2	16.8	0.00	15	35.2	11 vs.4: $\chi^2 = 5.5$	p = 0.59
12	phi(1t 2t) p(1t 2t)	186.3	44.9	0	28	21.7	12 vs.4: $\chi^2 = 19.0$	p = 0.52
(c) Winter weather and population density covariates								
5	phi(1t 2c) p(1c 2c)	141.4	-	0.79	10	31.4	-	starting model
13	+ raindays	148.9	7.4	0.02	10	38.8	-	n.s.
14	+ rain	150.9	9.4	0.01	10	40.8	-	n.s.
15	+ days<5	152.1	10.7	0.00	10	42.0	-	n.s.
16	+ days<10	154.4	13.0	0.00	10	44.4	-	n.s.
17	+ pca	154.7	13.3	0.00	10	44.6	-	n.s.
18	+ snowdays>4	155.2	13.8	0.00	10	45.1	-	n.s.
19	+ min temp	155.9	14.5	0.00	10	45.9	-	n.s.
20	+ snowdays	156.3	14.9	0.00	10	46.3	-	n.s.
21	+ mdensity	157.5	16.1	0.00	10	47.4	-	n.s.
22	+ max temp	158.2	16.8	0.00	10	48.2	-	n.s.

Winter weather and population density

Table 2c lists the results of adding weather and population density co-variables to the design matrix prior to model fitting. The starting model was the best-fitting 2 age class time dependent model ($\{\phi(1t\ 2c)\ p(1c\ 2c)\}$, model 5, table 2b). The explanatory variable is treated as a linear constraint on survival. None of the variables investigated improved model fit above the starting model, indeed all the co-variate models receive limited AIC support. The highest ranking weather co-variate model (total winter raindays) is over 40 times less supported than the starting model based on AIC weight. Combinations of weather co-variables and weather and density co-variables were also tested, but model fit was not improved. Likelihood ratio testing of nested models provides further support for age structure in the study population. These tests were not performed on the weather analysis as the lack of fit based on AIC values was such that Likelihood ratio tests for significance of fit were unnecessary.

Survival rate estimation

The rates generated by the survival analysis were needed for development of structured population models and this first required selection of the most representative age structure. Both AIC and LRT support the 2 age class structure adopted in this analysis above that of a single age class. Model 10 $\{\phi(1t\ 2c)\ p(1c\ 2c)\}$ receives a substantially higher AIC weight ($0.64/0.07 = 9.1$ times the support) and fits significantly better ($\chi^2=9.3$, d.f.=2, $p=0.009$) than the best fitting single age class model $\{\phi(t)\ p(c)\}$.

Before adopting mean rates from any particular model it is important to consider uncertainty in model selection (Buckland et al, 1997). In MARK this is achieved through model averaging of common parameters using AIC weights taken from the candidate models. Weighted parameter estimates are calculated which are not conditional on any particular model. Lebreton et al (1992) suggest that candidate models should lie within one AIC unit of the optimal model. However the best-fit model has an AIC value considerably larger (3.08 AIC units) than the next best model indicating that model averaging is both unsupported by AIC values and also unlikely to substantially alter parameter estimates because of the strong weighting in favour of the optimal model. Thus vital rates were taken just from the optimal model.

The high degree of support for the optimal model suggests its parameter structure is very important. The contrast of time dependent survival from ages 1 to 2 with a constant rate for the older age class is an indication of greater variability in survival of the younger class than the older and leads to careful consideration of how to best derive mean age class rates and variances. The overall mean rate for the first age class was calculated from the 7 estimates in the model $\{\phi(1t\ 2c)\ p(1c\ 2c)\}$, each one representing a single survival period. The second age class rate was taken straight from the model output as this is already a mean value across the years. The standard deviation of the two mean values thus derived can be calculated from the standard errors provided by the survival analysis. However these standard error values over-estimate the true temporal variation as they include both sampling error and process error (Gould and Nichols, 1998). The contribution to the overall error value from each source is calculated using variance component analysis of the rates

from time dependent models (note: this procedure requires multiple estimates and is therefore not possible with constant rate models). Due to problems related to the small number of older (>2 years) birds in this study this could only be carried out on the combined age model $\{\phi(t) p(c)\}$ and for the first age transition (from age 1 to 2) in the 2 age class model $\{\phi(1t\ 2c) p(1c\ 2c)\}$. The proportion of total error attributable to sampling error for the combined age model is 17.6% and in the 2-age class model for the first age class is 14.8%. The close agreement of these two estimates suggested that the adoption of an error reduction of 15% in the subsequent calculations would be appropriate. Table 3 lists the analysis output and calculated mean rates. Survival is slightly higher for the first transition (mean: 0.52; s.d. 0.25) than the second (mean: 0.46; s.d. 0.21), although not significantly so. As would be expected for a detailed study of a territorial species, the recapture (re-sighting) probabilities are high (estimated by MARK to be 1.0 for age 1; 0.62 for age 2+). The lower value for re-sighting older birds is a consequence of the reduced surveying carried out in 1998 and 1999, and is unlikely to represent a real difference in detection rate between the age classes.

Reproduction

Tests for significant differences in reproductive output between age groups were conducted using REML testing in the statistics package Genstat, which permits multiple random terms to be entered into the analysis. Thus year and individual can be entered as random terms in the model and the non-independence introduced through the repeated measurements of a few individuals in more than one year can be accounted for. Age and number of breeding attempts were entered as fixed factors with offspring number the response variable.

Table 3. Male survival (a,b) and recapture (c) rates from model $\{\phi(1t\ 2c)\ p(1c\ 2c)\}$. Corrected standard deviation found by reducing the standard error estimate by 15% to account for process error. See text for details.

a) time dependent annual survival probabilities (ϕ) from 1 to 2 years

	Estimate	SE	Lower CI	Upper CI
1995 - 1996	0.13	0.13	0.015	0.578
1996 - 1997	0.56	0.18	0.232	0.838
1997 - 1998	0.27	0.14	0.082	0.611
1998 - 1999	1.00	0.00	1.000	1.000
1999 - 2000	0.75	0.23	0.207	0.972
2000 - 2001	0.50	0.27	0.108	0.892
2001 - 2002	0.44	0.18	0.162	0.768
mean	0.52			
std	0.29			
se	0.11			
process se	0.09			
corrected std	0.25			

b) constant annual survival (ϕ) from 2+ years

all years	0.46	0.09	0.286	0.636
mean	0.46			
se	0.09			
process se	0.08			
corrected std	0.21			

c) recapture probabilities (p)

from 1-2	1.00	0.00	1.000	1.000
for 2+	0.62	0.17	0.291	0.871

Each sex was analysed separately as the range in the number of breeding attempts was not evenly partitioned between the sexes (male range: 0-5; female range: 1-2). The random terms (individual and year) were found to be non-significant and thus removed from the analysis, leaving only age and breeding attempt. Dropping individual from the analysis could have introduced pseudo-replication into the calculations, but the actual number of individuals for which fecundity data was recorded in successive years was sufficiently low (<10%) that this was considered to be of little concern. Because the term for individuals has been removed, there is no longer any need to perform a mixed-effects model and we can carry out a standard GLM, testing for an influence of age and number of breeding attempts on the number of offspring per individual. Of these only number of breeding attempts has a detectable significant effect (males: $F = 9.22$, $P < 0.001$; females: $F = 8.79$, $P = 0.004$). An analysis with the number of breeding attempts set as the response variable was also conducted. Year and individual were again found to be non-significant and removed from the model. Male age is found to be significant, with older (2+ years) males having a higher number of breeding attempts than one year old males ($F = 5.93$; $P = 0.018$), but this is not found for females ($F = 1.07$, $P = 0.306$). Table 4 lists the summary statistics for wren fecundity. The values are averaged across all years and are divided into age and sex groups and presented per individual or per breeding attempt. The number of fledged young is given as both the total number fledged and also half the total, as a measurement of same sex reproductive rates (i.e. female production of females). These sex specific values were calculated for use in two-sex population models, with an assumed fledging sex ratio of 0.5. The number of breeding attempts is averaged across years for each age class.

Table 4. Average reproductive output for wrens in Mine wood (1995,1996,2000,2001). The per breeding attempt, per individual and total and half divisions were made to parameterise different formulations of simulation model. The 'half' offspring values are for use in models where each sex is considered to produce same sex offspring only (i.e. females produce daughters, males sons).

Sex	Age class	No. offspring per breeding attempt		No. offspring per individual		No. breeding attempts					
		total	half	total	half	total	half				
		mean	s.d.	mean	s.d.	mean	s.d.				
Male	1st year	3.25	0.55	1.61	0.27	4.07	0.59	2.04	0.30	1.19	0.14
	2nd year & older	2.50	0.96	1.25	0.48	4.32	1.76	2.16	0.88	1.70	0.11
Female	1st year	3.57	0.69	1.78	0.34	4.76	1.07	2.38	0.54	1.32	0.05
	2nd year & older	2.81	1.58	1.40	0.79	3.38	1.69	1.69	0.91	1.21	0.21

2.4 Discussion

Census techniques - reliability

Performing a census of male wrens is relatively straightforward. This is in large part due to their loud and frequent singing during the spring and summer as part of their territorial behaviour. Catching singing males is assisted through the use of tapes of male song played next to mist nets, taking advantage of their willingness to confront potential rivals. Subsequent identification by observation of coloured leg rings is similarly assisted because males tend to sing from obvious perches. As a result confidence in the completeness of each years' survey is high, despite the change in observer between the first five years and the last three. Female wrens on the other hand present much greater difficulties. Apart from the occasional capture of females in mist nets set for males, the presence and capture of females tended only to be possible once active nests were found. Females have no need to spend time advertising their presence from obvious locations but instead spend much time in dense vegetation, thus even when colour-ringed, females are difficult to locate and identify. Allied with a tendency to range over larger areas than males (Kluyver et al, 1940) this makes studying female wren population dynamics very difficult. In one of the few other published studies where wrens were sexed, Peach and co-workers (1995) were similarly unable to analyse female survival due to low numbers of female re-traps. They suggest the reason for this is the greater distances reported for female movement, which accounts for the observed disparity in re-capture rates between the sexes. The 'active' approach adopted here of catching females engaged in breeding, through intensive nest monitoring, addresses some of the problems of their inconspicuous nature, however the time and effort required meant that this was

impractical to carry out in all years. Additionally only breeding females are found and it is very likely that some nests will be missed.

CJS survival Modelling

Despite the limitations imposed by its assumptions, live re-sighting data as presented here is still most appropriately analysed using the standard CJS model approach. Indeed violation of the assumptions can sometimes lead to interesting observations about the study in question (Cooch and White, 1998). However small sample sizes present difficulties in analysis. This is evident in the results of the RELEASE goodness of fit tests, which do not provide reliable guidance due to the presence of single observations in several of the chi-squared tests (White and Burnham, 1999). Importantly, however, there is no consistent pattern of significant results, which might otherwise indicate lack of model fit. The advantage of testing goodness of fit using the bootstrap procedure is that sample size problems are of less concern, and in addition we are provided with a means to correct for over-dispersed data through the provision of an adjusted value of the quasi-likelihood parameter \hat{c} . The bootstrap results provide a high degree of confidence in the data because the observed deviance does not lie within the significant tail of the simulated model deviances and after adjusting for over dispersion we can have further confidence in the model fitting procedure.

Although the larger of the two estimated \hat{c} values of 3.283 is high enough to suggest that we might be concerned about a substantial lack of model fit (Lebreton et al 1992, recommend reconsidering model suitability with $\hat{c} \gg 3$), the lower estimate of

1.164 does not appear to indicate a severe lack of fit. One consequence of a $\hat{c} > 1.0$ is that MARK becomes more 'conservative' in its model support, based on AIC weights. Less parameterised models receive proportionately greater support, and the interpretation of AIC weights is affected: for any given magnitude of relative difference between models the support inferred by the difference decreases with increasing values of \hat{c} (Cooch and White, 1998). For example, if we consider a hypothetical situation, with a $\hat{c} = 1.0$ and an AIC weight value of 0.8 for our best model and 0.1 for the next best we can state that the best model receives 8 times the support of the next model. However, when \hat{c} is greater than 1.0 the relative degree of model support decreases with increasing \hat{c} , and we could no longer make the same assertion. The exact reduction is not a straightforward one, but the result is grounds for careful consideration of the results from model fitting. In this case changing \hat{c} from 1.0 to 1.164 makes only a slight change to the rank order of models (with $\hat{c} = 1.164$, models 6 and 7 swap places) and the AIC weight for the best fit models is reduced by approximately 25%. Thus overall the goodness of fit testing lends acceptable support to the starting (saturated $\{\phi(t) p(t)\}$) model and subsequent adjustment of \hat{c} corrects for the small degree of over-dispersion in the observed data, but does not alter the final outcome.

Winter weather and survival

No aspect of winter weather was found to explain the observed inter annual variation in survival rates. This is an unexpected result, considering the strong relationship between harsh conditions and wren survival previously reported (Cawthorne and Marchant, 1980; Peach et al 1995; Newton et al, 1998). One explanation for the current failure to identify any significant factors is the short time series for analysis (8 years). Both Peach et al (1995) and Newton et al, (1998) used datasets comprising over 20 years for their survival analyses, and thus will have been able to include a wider range of both survival rates and weather conditions. Extended periods of cold temperatures over winter are commonly cited as causing low passerine survival (Marchant et al, 1990), with a particular emphasis for wrens on occasions of snow lying for several days. The variable in this study which comes closest to predicting survival is the number of rain days between October and March, with survival apparently increasing as the number of days with greater than 0.1 mm of rain recorded increased. It seems unlikely that this is a reflection of a real relationship between wren survival and the frequency of rain in winter. What seems more plausible is that the same sensitivity to harsh weather exists in the study population, but that the best ‘indicator’ of a mild winter (and therefore one promoting improved wren survival) is one during which precipitation falls more often as rain than as snow. Another possibility is that longer term studies, covering a greater number of severe winters than this study, are better able to detect trends relating to weather. Thus with a series of mostly mild winters promoting intermediate levels of survival as experienced in this case, other, less obvious variables become more important for determining observed survival rates.

Sex differences in survival

One of the consequences of being unable to calculate female survival directly from the data is that in order to develop population models which include both sexes, it is necessary to derive female rates from those estimated for males. Thus we must decide what, if any, is the relationship between male and female survival. Dobson (1987) reported that there was no detectable difference in survival between males and females for 13 species of passerine, while seasonal analysis of ring recoveries indicated the presence of two annual peaks of passerine mortality; during the breeding season and over the winter. During breeding male and female wrens perform quite distinct roles, which could lead to differential predation risk. The male contribution to reproduction is through territory defence and nest building, both of which may lead to an increase in their conspicuousness to predators. The female is less conspicuous during early stages of the breeding cycle than the male, but may come to the attention of predators over the course of the more than 30 days spent visiting a nest site (covering the period for nest-lining, egg laying, incubation and provisioning of the young). Quantifying and comparing the predation risks associated with these different activities was beyond the scope of this study and indeed, as Peach et al (1995) state “there is little evidence to suggest that small passerines experience significant mortality during the breeding season”. Analysis of carcasses from Sparrowhawk nests found that wren remains were greatly under-represented in relation to their abundance in the habitat (Tinbergen, 1946). Mustelid predation of passerines is well documented (Akande, 1972; McDonald et al, 2000; King, 1980), although identification of avian bones to species level has not proved practical, and thus the extent to which wrens suffer from this form of predation is unknown. It seems plausible that the wren’s terrestrial foraging habits would bring it

into contact with stoats and weasels, but at the same time adult wrens are presumably well adapted to avoid capture whilst foraging in dense undergrowth. There are also suggestions that during the summer wrens tend to feed higher off the ground in the available foliage than during the winter (Armstrong 1955), and thus perhaps distance themselves from immediate contact with mammalian predators. In Hawthorn and Mead's (1975) report of monthly recoveries of dead wrens the lowest values are found over the summer months (May – September), and their highest during mid to late winter (January – April), although this information may reflect variation in the probability of detection between seasons. Thus we are left without consistent agreement between the various sources of information. Until better understanding of wren survival during breeding can be gained, and in the absence of evidence to the contrary, the most parsimonious course is to assume that survival rates at this time of year are low (relative to over winter rates) and the same for both sexes.

However, the different roles of males and females with regards to nest building (males) and provisioning young (females) may be of more importance in determining the condition in which adult wrens enter the winter. Most studies which have looked for differential mortality rates brought on as a consequence of biased parental investment have considered monogamous species (Owens and Bennett, 1994) in which parental investment is, superficially at least, shared equally. The division of labour between male and female wrens makes the assessment of each sex's breeding effort very difficult, and consequently the extent to which each sex suffers from breeding induced reductions of body condition remains unknown. Against this we should note that the last traces of behaviour associated with breeding

have been observed by the middle of September, leaving three or more months recovery period before the onset of the winter weather (snow) most closely associated in other studies with wren mortality (Greenwood and Baillie, 1991; Newton et al 1998; Peach et al, 1995). Taking all of these pieces of information together, and until evidence can be collected to the contrary, the most parsimonious course of action is to assume that male and female survival rates are comparable.

Age structure, reproduction and life history effects

Support for age structure is strong with the three best fitting models all incorporating age structure. A larger study might detect a more defined adult age structure than the two age classes described here, although in this population at least, very few male wrens survive beyond the two years of age. Although the time averaged first rate is slightly higher than the second (0.52 c.f. 0.46), it is the variability between years which is more striking. The fully time dependent survival model $\{\phi(1t\ 2t)\ p(1c\ 2c)\}$ receives almost 1000 times less support (from AIC weights) than the optimum model. Thus we have overwhelming support for a model of constant survival rate for older birds, and time dependent survival for younger ones, with a degree of support large enough to suggest this is not just a product of the smaller sample of older birds. One mechanism which might lead to this pattern would be that in most years survival is low for all ages giving rise to an underlying survival curve based on the survival of only the fittest individuals, leading to low numbers of birds aged two and older. In years with milder winter conditions survival rates are elevated across all ages, but a greater increase is seen for younger birds simply because there are more one year old birds present, and thus the scope for increase is greater, with the extra survivors being those individuals unlikely to survive in an average or below average winter.

One possible explanation for the lower survival of birds older than two is that this indicates the onset of senescence. Further support for this comes from the observation that of 49 males first caught as one year olds between 1995-2001, 22 survived to their second year, but only 4 to their third and just one (known age) bird was recorded alive at four and then five years old. Thus we can see a marked age

related decline in survival rate appears to set in before birds reach their 3rd year. This pattern of age related survival has previously been recorded for many bird groups (Martin, 1995), although the early onset seen for this study population is an extreme example, perhaps reflecting the marginal status of wrens as year round residents in northern Britain. However the likelihood of recording birds older than two is partly compromised by the fact that censuses of the whole wood were only conducted for maximum consecutive periods of three years. We can at least be relatively confident that this pattern is not caused by older wrens becoming more adept at avoiding capture, since 're-captures' are actually re-sightings of individual colour ring combinations.

If we consider together the results of the survival and reproduction analyses presented here, along with the conclusions of previous studies of wren ecology it becomes possible to suggest some interesting theories regarding wren life histories. There are three significant trends in the reproduction analysis. For both males and females the only predictor of the number of offspring per individual is the number of breeding attempts in a season and for males this increases significantly with age. While this study failed to detect an increase in the number of young fledged (by males) with age (probably due to the small sample size), other studies have provided evidence that male reproductive success increases with age. Evans (1997b) found that individual males tended to build more nests as they got older and individuals with more nests attracted more females (Evans and Burn, 1996). Thus we have evidence that older males build more nests, attract more females and have greater numbers of breeding attempts than males in their first year, and it seems reasonable to suppose that this additional effort results in higher numbers of fledged young. If

this is the case it does not appear to come without a cost however, as evidenced by the lower survival of older males.

Why don't we see similar age related breeding effects in females? The most likely answer is that females are much more constrained by time within a season than males, with respect to the numbers of breeding attempts per year. The polygynous breeding system commonly seen in wren populations allows males to make multiple breeding attempts with different females overlapping in time, whereas a female can only raise one brood at a time and has to leave a period of 1-3 weeks between attempts. Therefore it is not surprising that detecting an increase in the number of female breeding attempts with age has proved difficult, although it is possible that females do increase their reproductive effort with age, by other means (e.g. raise larger broods, increase food provisioning). This hypothesis does cast some doubt on the proposed use of the male derived survival rates for females in population models. However this remains the most reasonable course of action until female survival rates can be estimated directly.

Chapter 3

Estimation of juvenile wren

demographic rates

3.1 Introduction

The first few weeks post-fledging are an extremely important period for avian survival and it is generally believed that mortality rates at this time are very high (Korschgen et al, 1996; Naef-Daenzer et al, 2001; Perrins, 1965). Because of the difficulty in measuring juvenile survival directly during this period most data on the subject has come from analysing return rates of birds (usually to their natal areas) at some point in the future, often as breeding adults, or in a few cases from observing colour marked individuals for a short period post-fledging (Krementz et al, 1989; Magrath, 1991). The use of such approaches has in the main been prompted by the difficulty of making repeated observations of highly mobile, newly fledged birds, along with the problem of distinguishing death from permanent emigration. In the case of passerines, while much of their ecology and behaviour is well documented, it is only comparatively recently that studies of early survival have become possible. Radiotags provide a means to closely monitor juvenile birds during this critical period, but until recently have been too large to use on birds weighing less than 20-30g. Thus data are available on the patterns of juvenile movement and survival for large birds such as buzzard (*Buteo buteo*; Walls et al, 1998), imperial eagle (*Aquila adalberti*; Ferrer et al 1997) and burrowing owl (*Athene cunicularia hypugaea*; King and Belthoff, 2001), but only a handful of passerines have been studied this way, and amongst bird species weighing less than 20 gm the only published studies are for great and coal tits (*Parus major*, *Parus ater*; Naef-Daenzer et al, 2001) and lark buntings (*Calamospiza melanocorys*; Adams et al, 2001). Because the aim of this study was to use demographic parameters derived from the study population to develop simulation models, it was important to obtain high quality estimates of juvenile survival rates. This objective was greatly assisted by recent advances in

radio tag and battery technology which permits the use of radio-tags with small (c. 10g) passerines. When deciding the appropriate size of radio tag for a study, an often quoted guide is that tags should weigh no more than 5% of the animals' body mass (Cochran, 1980). However, an investigation of the energetic costs of carrying radio transmitters has found that use of this weight guideline will tend to lead to an overestimation of the cost of carrying tags for small birds and an underestimation for large birds (Caccamise and Hedin, 1985). They provide a means to select transmitter load using estimates of the flight costs involved for any given species, using the 5% rule as a starting point. Using this method we can have reasonable confidence that tagging 10g wrens with the minimum weight 0.5g tags available at the time of this study was an acceptable practice. It is also important to consider the behaviour and ecology of the study species when selecting radio tags (Naef-Daenzer et al, 2001), since the energetic cost of carrying a tag is likely to be greater for bird species which hunt on the wing than for those which feed on the ground. In this respect the wren's terrestrial habits are not a cause of serious concern with regard to the impact of carrying radiotags.

3.2 Methods

Study site

The study was carried out in an area of woodland near the Stirling University campus, Bridge of Allan. The wood lies on a south facing slope, and contains mostly mature broad-leaved trees: beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus*), with a few smaller continuous blocks of mature pine. The understorey is dominated by large areas of fern, with patches of

regenerating ash trees. To the south and west the wood is bordered by gardens and large houses and to the north and east by a golf course and farmland. Of these the golf course and farmland probably represent the most significant barriers to wren movements, although several hedgerows do provide potential corridors to other areas of nearby woodland.

Radio tags

Radio telemetry of juvenile wrens was carried out in 2000 and 2001. Nests were located as part of an on-going demographic study of adult survival and reproduction (see chapter 2). The progress of active nests was monitored closely in order that an accurate assessment of fledging date could be made. At around 10 days nestlings were weighed and had a BTO (British Trust for Ornithology) leg ring fitted. Juvenile wrens fledge at around 16 days, although they will leave earlier if disturbed by a predator. Catching newly fledged birds is obviously much more difficult and time consuming than taking birds out of a nest, therefore it was decided that nests would be visited the day before the expected fledging date (day 15) so that radio-tags could be fitted. In some cases the nestlings were successfully placed back in the nest after tagging, but on most occasions the disturbance was sufficient to trigger the impulse to leave the nest and all nestlings fledged. This early fledging may have put the birds at a slightly elevated risk of predation for a short period. However, this was considered to be an acceptable trade-off since mist netting newly fledged wrens is difficult and could lead to the fledglings becoming split up, which was also likely to increase the risk of predation. In 2000 one bird per brood and in 2001 two birds per brood were chosen at random for tagging. The tags were supplied by Biotrack UK

Ltd., and had maximum dimensions of 13 * 7 * 3 mm, with a total weight in the range 0.51-0.53g (including the transmitter, cell and 10 cm wire aerial). In order to maximise battery life the tags had a slow pulse rate (approximately 20 per minute) and a short pulse duration (12 ms.). With these settings the tag battery life was extended to up to eight weeks, at the expense of lowered detectability in the field. This set-up was chosen to permit tracking of individuals for a longer post-fledging period, and the ability to rapidly pinpoint individuals was not important in this respect. Tag reception range was highly variable, being strongly influenced by an individual's location and behaviour. Maximum detection distances were around 3-400m.

Tag attachment

A range of tag attachment methods have been used with birds (e.g. Sykes et al, 1990). In many studies there has been the time and resources available to conduct detailed investigations into the relative merits of different techniques, however for this study only a very limited test was possible and a review of tag attachment techniques was conducted to assist in the selection process. Harnesses have often been used on large birds (Walls et al, 1998) and sometimes on smaller birds (Hill et al, 1999), particularly in studies when tag retention periods of longer than 1-2 months are sought. After a period of fine-tuning to perfect the fitting process they rarely fall off (Naef-Daenzer et al, 2001) which maximises data collection, but they can also present a high risk to the long-term health of tagged individuals, particularly if recapture is uncertain. In this respect the wren's terrestrial habits raise the possibility of harnesses becoming snagged on vegetation. For these reasons

harness attachment was rejected. Tags can also be mounted to either the legs or tail feathers, but neither of these is appropriate for a bird as small as a wren. The remaining possibility is to fix the tag directly to the bird's back with glue (a range of adhesives have been tried in other studies e.g. surgical cement, eyelash adhesive, cyanoacrylate – 'superglue'), and of these cyanoacrylate provides the strongest attachment. Johnson et al (1991) in an investigation of the efficacy of glue techniques for radiotags reported no ill effects from the use of superglue. Tags can be glued either onto, or for improved retention, beneath the outer feathers, which can then lie over the tag, reducing its profile and associated drag effects. Sykes et al (1990) compared harness and gluing methods for common yellowthroats (*Geothlypis trichas*) and found that gluing was preferred for both the birds' welfare and for maximising tag retention times. Glued tags were naturally shed after around 30 days, pulling out the attached feathers and stimulating visible feather growth within 2 to 4 days. They also found that using a fabric layer between the tag and the bird improved the retention times.

A test tag was fitted to an adult territorial male in the spring of 2000, using the following method. First the outer feathers on the spinal tract in the intrascapular region of the bird's back were lifted and pushed forward. These were held out of the way while a patch of feathers the same size as the tag was trimmed down to leave a 'stubble' about 1 mm long. Using cyanoacrylate a piece of velcro (the 'soft' half) the same size as the tag was glued 'furry' side up to the trimmed feathers and then the tag was glued to the fabric. The outer feathers were then allowed to lie back over the tag. This bird was monitored closely over the next few hours for indications of ill-effects, but none were observed and it appeared to adapt rapidly to the tag. After 3

weeks the bird was recaptured to check its condition and to remove the tag. No adverse skin reaction was visible at this or subsequent recapture occasions and full feather re-growth was seen within a few weeks. This procedure was therefore used for fitting tags to juveniles, although it was decided that the tag would be glued directly to the bird, omitting the velcro layer. As well as reducing the total weight, this allowed the tag to fit underneath the outer feathers much more neatly, and there is no apparent reduction in tag retention times (plate 1).

If a tag came off after only a few days post fledging and observations of the brood suggested that the tagged individual was still alive, efforts were made to re-catch either the originally tagged bird or one of its siblings in order to extend data collection. Once the brood had begun to split up (around 10-14 days post fledging), locating and catching brood members was rarely possible and further attempts to recapture and re-attach prematurely shed tags were made only occasionally. In the first year of the study the aim was to tag one bird per brood and in the second year two birds per brood (although this was not always possible). Thus in 2000, 19 juveniles (from 16 broods) were tagged and tracked for 1 to 63 days and in 2001, 18 juveniles (from 11 broods) were followed from 1 to 54 days. Radio-tagged individuals were also fitted with a unique colour ring combination on one leg to enable positive identification in the absence of a radio signal should the tag fail or be shed.

a



b

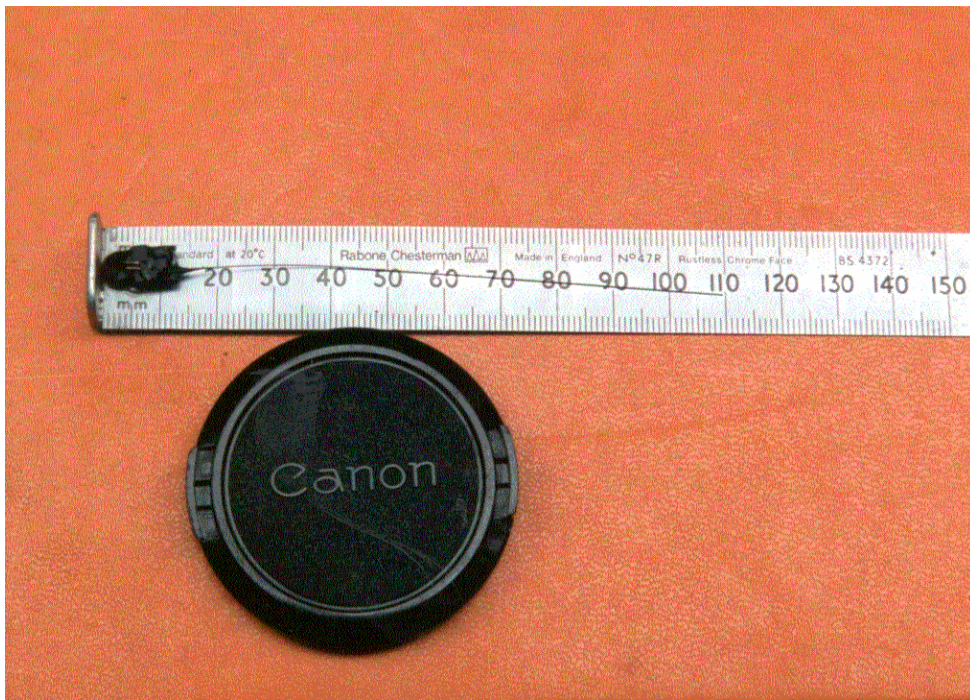


Plate 1. (a) Juvenile wren with radiotag glued to back, the tag lies close to the body underneath the outer contour feathers, and the aerial is visible extending backwards from the rear of the tag. (b) Type of radiotag used for the wren radiotracking study. Each tag weighed approx. 0.5g, with dimensions 12*7*2mm, and an aerial of 100mm.

Radio tracking

Because of the tags' short transmission range and the expectation that the juvenile birds would leave the natal area at some point during the life of the tags regular checks were made in order to minimise the risk of losing individuals due to extensive movements. In 2000 each bird was located 3 times per day (morning, afternoon and evening), the last occasion being at or just after roosting. Based on the data collected in the first year of the study, in the second year only two daily locations (morning and afternoon) were collected, as the additional roosting information collected in 2000 did not significantly enhance bird re-location the following morning. During the day detected birds were approached until visible contact was made to confirm the bird's status and the location was recorded using a GPS receiver. Birds suspected to be roosting were not closely approached in order to minimise disturbance, but instead had their location estimated (through a combination of rough triangulation and listening to the signal characteristics) and noted down for position recording at a later date.

Juvenile wrens continue to be fed by the female (and occasionally the male) for several days after leaving the nest and may remain in their parent's territories for up to 3 weeks, often in close association with brood mates (Armstrong, 1955). This made locating tagged birds relatively simple for the first few days as movements tended to be quite limited. When a tag was not detected in the expected area (based on previous fixes) an extensive search was conducted, first throughout the remainder of the woodland study site and then in the surrounding areas. This was conducted as soon as possible after a tag had failed to be detected in its previous location to minimise the time for possible further movement out of the study area. Once a

missing bird had been re-located it was monitored closely over the next few days for indications of continuing dispersal and if the signal was lost again immediate efforts were made to relocate it.

Home range and dispersal monitoring

In this study natal home range is defined as the area used by a juvenile until the initiation of dispersal (Anders et al, 1998). To identify the time at which dispersal occurred, the distance between each positional fix and that individual's 'focal' point (usually its nest site, or regularly used roosting location) was calculated. Dispersal was judged to have taken place when there a marked increase, relative to the previously recorded distances, in the distance between the bird and its focal point (i.e. a movement away from the focal point which was >3 times the previous average distances), followed by a return to shorter movements in the new area. Fixes collected before dispersal were used to plot natal home range size using a minimum convex polygon method (outer points were connected unless the distance between two consecutive edge points was greater than $\frac{1}{4}$ of the maximum range width, in which case the next inner point was taken as the next point). Where possible, points collected after dispersal were similarly analysed to measure the post-fledging dispersal range. As a measure of the distance travelled during dispersal, the shortest distance between the centres of the natal range and the post-dispersal range was calculated. The arithmetic mean position of each range was used as the central location, calculated as the average of all the 'x' co-ordinates and the average of all the 'y' co-ordinates.

Post-fledging survival

During the study period tagged birds became classified as either dead (body or remains recovered) or censored (fate unknown). Birds were recorded as censored for one of several possible reasons as follows: the tag was found undamaged with no indication of injury to the bird (probably due to tag removal by the bird); the bird disappeared with no trace of its radio-signal (potentially due to: tag destruction by a predator; failure of the tag; a fully discharged battery; or undetected dispersal). The expected life of the tag batteries based on the pulse strength and frequency was around 56 days, which closely matched the maximum duration recorded in the field (57 days). Survival was estimated from day 0 (fledging) to day 44 (earliest apparent battery expiration) for all tagged wrens. Analysis was conducted using the non-parametric Kaplan-Meier failure time estimator which avoids the need to choose a specific probability distribution and is also reasonably robust to the high levels of censoring encountered in this study.

Independence of observations

In the first year only three out of sixteen broods had more than one juvenile tagged, as a result of the first tag being shed. The original tags were shed in these cases at 2, 5 and 13 days. In each case the brood was observed within the natal area, the previously tagged individual was identified and a second brood member was successfully caught. The three extra birds were included as extra individuals in the survival analysis, since it was not felt that their inclusion would have a major impact

on the estimated survival rate. In the second year the tagging of multiple brood members could have given rise to higher levels of dependence. However, there was no detectable relationship between the death (or suspected death related censoring) of one brood member and that of its sibling (indeed only 3 birds were recorded as dead in 2001, all from different broods). Thus all tagged birds were entered into the analysis and treated as independent data points.

Survival covariates

In other species a combination of fledging body mass and date have been found to predict individual survival (Naef-Daenzer et al, 2001; Krementz et al, 1989). The existence of variables explaining the variance in juvenile wren survival was investigated here using regression with life data (Minitab). This technique fits one of a range of common distributions to the data and looks for predictors of ‘failure time’, in this case death. The exponential distribution was found to be a reasonable fit to the survival data, and the predictive variables tested were: fledging body mass (on day of tagging), early or late fledging date. In addition the body mass of parents was tested to see if body condition or size might also predict fledgling survival. It was not possible to fit tags at exactly the same time of day nor the same stage of development, and this must be borne in mind when considering this aspect of the study.

Annual survival

One of the main aims of the field data collection was to derive annual survival rate estimates to be used in the parameterisation of population models. Thus, while the post-fledging period is generally accepted as being the most critical time for juvenile survival, in order to calculate wren survival for the whole of the first year (from fledging to one year of age) a means to extrapolate from the end of the radio-tag period until the following breeding season was required. Several long-term studies have obtained this parameter for other species using the return rate of one year old birds previously ringed on the study site as juveniles (e.g. Perrins, 1965). Preliminary analysis of the Mine Wood data suggested that this approach was likely to underestimate the true survival rate by a considerable margin, due to apparently high levels of emigration. Two alternative means to calculate survival from fledging to one year old were used instead. By 6 to 8 weeks post-fledging juveniles are fully independent and known age birds observed at this time were indistinguishable in general behaviour from older wrens, thus the first approach calculates an annual rate as the product of 12 monthly survival rates, the first two months of which were derived from the radio tracking analysis reported here, and the remaining 10 come from the mean monthly estimates of survival of birds in their second year of life (see chapter 2 for adult survival estimates). Variance around this mean value was estimated by calculating the annual rate using the survival values at the upper and lower 95% confidence intervals for both the post-fledging period and the adult rate. The second method makes the assumption that the study site lies within a larger area of similarly suitable (and therefore equally productive) wren habitat. This leads to an assumption of balanced immigration and emigration of first year birds across the boundaries of the study area. Survival was thus estimated as the

total number of first year birds present within the wood in year $t+1$ divided by the total number fledged in the wood in year t . It was expected that the first method would be a more robust estimate of survival, but that the second would provide a general indicator of the range of values within which the actual survival rate would lie. As an additional attempt to gain information on survival from fledging to one year of age, a further period of fieldwork was undertaken during the autumn and winter of 2001-2. This work aimed to extend the radio tracking of juveniles through their first winter, so that weekly or monthly survival rates could be obtained for comparison with those derived from method one above. Thus, beginning in October attempts were made to catch juveniles using mist nets and to then fit them with radio tags. Little is known about the movements and ranging behaviour of wrens (particularly juveniles) during autumn and winter. They are at their least conspicuous at this time of year, as they exhibit minimal territorial behaviour and their plumage makes them ideally camouflaged for foraging amongst fallen leaves. Consequently the capture rates of juveniles was extremely low, with only 5 juveniles tagged between October 2001 and February 2002, and this was not assisted by poor weather restricting opportunities for mist-netting. Daily tracking followed the same protocol as that described above.

3.3 Results

Tag retention

Table 1 summarises the post-fledging tag data. In both years there was a high rate of tag loss (50% and 58% respectively) due to premature shedding, which in most cases appeared to be caused by removal of the tag by the bird itself (in such cases there was no evidence of tag damage and only feather shafts were attached to the tag). Although this is obviously a disappointing result, there is currently no alternative attachment method which offers a combination of improved retention times with an acceptable level of animal welfare. It was thus decided to be preferable to err on the side of the birds welfare rather than ensuring that data was collected for the complete length of the tag battery life. Since censored observations can be incorporated into the survival analysis this need not detract from the information gained.

Home range size and dispersal

Measurements of dispersal were only possible for those individuals which retained their tags for three or more weeks and which also moved into readily accessible locations, thus only five birds in 2000 and one in 2001 could be analysed (table 2). Dispersal occurred on average after 23.8 days (s.d. 5.4), often took less than half a day (n=3), with a mean distance travelled of 431m (s.d. 178m). Two of the individuals in 2000 moved a second time, one further away (further distance of 1823m from initial post-dispersal range, 11 days after first dispersal) and the other returned to an area close to its natal

Table 1. Tag attachment and retention times for juvenile wrens in Mine wood, summers 2000 and 2001.

* observations of remainder of brood strongly suggest predation resulting in tag destruction

	Tag/individual fate	No.	Number of days since fledging of last contact
2000	Battery expired (presumed)	3	44,53,57
	Found dead	3	3,9,16
	Disappeared, presumed dead *	3	1,7,8
	Disappeared	1	27
	Tag shed	10	1,2,3,4,11,12,13,13,15,31
	Total	20	
2001	Battery expired (presumed)	1	47
	Found dead	2	1,3
	Disappeared, presumed dead *	1	3
	Disappeared	4	8,8,17,27
	Broken	2	18,18
	Tag shed	14	4,6,6,7,10,10,12,12,12,12,12,14,16,33
	Total	24	

Table 2. Dispersal measurements for juvenile wrens in Mine wood.
 The distance is calculated as the minimum between the arithmetic mean
 locations of the pre- and post- dispersal ranges.

* - initial dispersal distance. Bird moved a second time after 1-2 weeks.
 See text for details

	Dispersal distance (m)	No. days post-fledging	Duration of dispersal (days)
2000	593	19	<1
	256*	21	<0.5
	572*	29	<0.5
	375	31	<0.5
	204	18	<1
2001	552	25	<1
average	431.0	23.8	
sd	178.47	5.4	

range (return distance of 619m after 16 days). The distances reported are possibly biased on the low side since an individual travelling further than a few hundred metres within the space of a few hours would be unlikely to be located before it had time to move outside of the searchable area, due to the short detection range of the tags. The only way to minimise this problem was to carry out extensive searches of the surrounding area. There was no consistent direction in dispersal movement (Rayleigh's z test: $P > 0.5$, $n = 7$) across individuals. Two individuals were observed making 'exploratory forays' one day prior to their dispersal, each moving a little less than half their subsequent dispersal distance. These movements were in the same direction as their subsequent dispersal, but the birds returned to roost in their natal areas before leaving permanently on the following day. Figure 1 plots typical representations of the daily movements of two individual birds for 35 (fig 1a) and 56 (fig 1b) days. An exploratory movement can be seen in fig. 1b, occurring the day before the individual dispersed. For birds which retained their tags long enough to cover the dispersal period, it was possible to compare the home range size before (natal home range) and after dispersal (post-dispersal home range). When considering these ranges however, it is important to note that in no cases did the home range size reach an asymptote before either dispersal or censoring occurred. Table 3 gives the sizes for all measured ranges, calculated using the maximum convex polygon method. If a bird became censored prior to dispersal, but had a similar number of natal position fixes as others which retained their tags for longer, then a natal home range estimate is included. The average natal range area was 1.38 ha (s.d. 1.0). There is considerable variation in the natal range areas between birds (from 0.38 to 3.57 ha), which is possibly a reflection of variation in habitat suitability. Previous studies of

Figure 1a

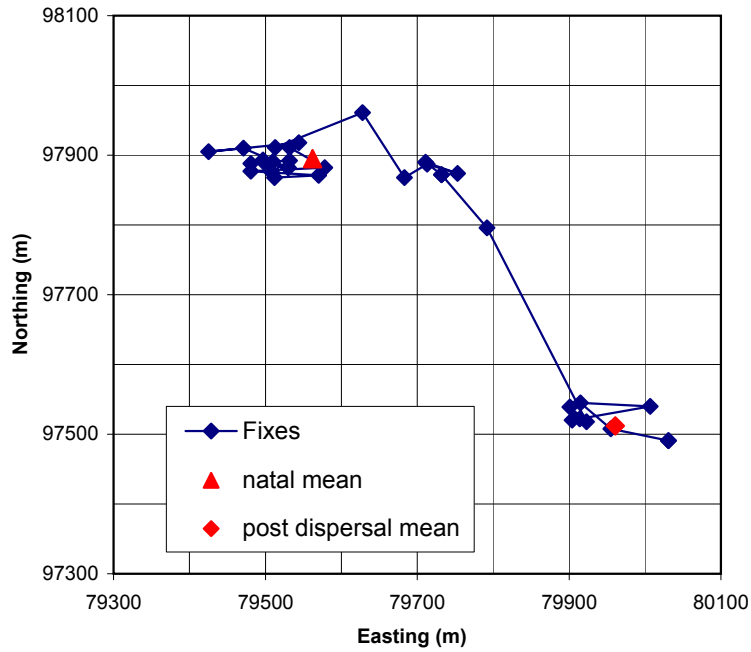


Figure 1b

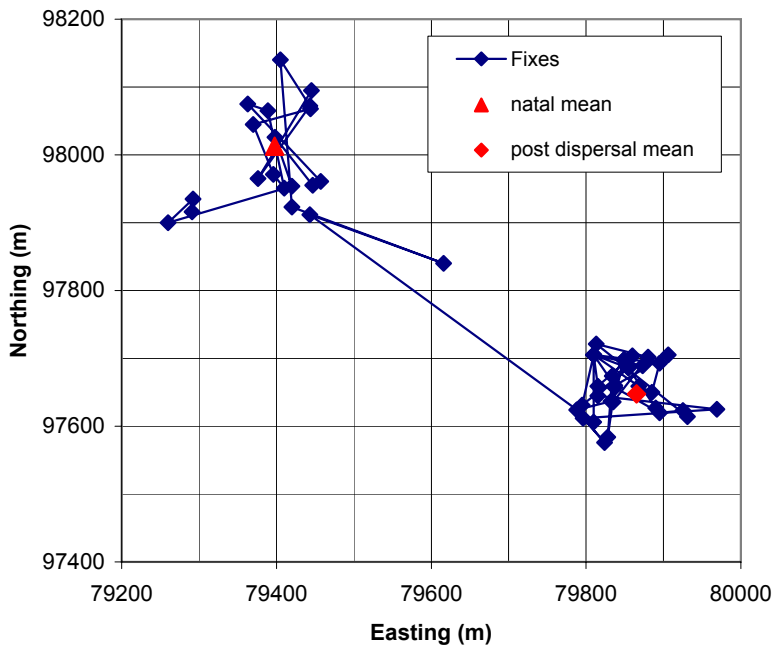


Figure 1. Plots representing the movements of two juvenile wrens in Mine wood. The axes use Ordnance Survey grid references. Dots provide daily position estimates and the lines indicate the order in which they were recorded. The arithmetic mean positions for the pre- and post-range are also marked.

Table 3. Areas for natal and post-dispersal home ranges, calculated using the minimum convex polygon method. Individuals 2 and 4 moved twice, and an area estimate is given for each post-dispersal range.

Individual	Natal home range			Post-dispersal home range		
	Area	Number of:		Area	Number of:	
		Days	Fixes		Days	Fixes
1	1.07	16	35	2.19	35	74
2	0.38	20	45	1.61	13	27
				3.13	9	19
3	0.71	17	30	-		
4	2.55	28	63	1.26	15	33
				1.37	20	47
5	3.57	30	62	3.26	12	26
6	0.53	15	32	-		
7	0.57	16	37	-		
8	0.57	13	34	4.94	18	39
9	1.55	25	40	-		
10	1.43	30	44	1.71	24	33
11	2.49	24	30	0.41	8	11
12	1.12	17	21	-		
mean	1.38	20.92	39.42	2.21	17.11	34.33
s.d.	1.00	6.17	12.59	1.36	8.46	18.24

wrens have found that adult male territory size is related to the vegetation structure (Wesolowski, 1981), and the natal area used by juvenile birds is likely to be strongly influenced by the parents' territory size. The average post-dispersal area was 2.21 ha (s.d. 1.36), which is larger than for the natal areas, although not significantly so (two-sample t-test, $P = 0.16$), probably due to the small sample size.

Survival analysis

Post-fledging survival

Nineteen juveniles were tagged in 2000, and eighteen in 2001. Comparison of the Kaplan-Meier survival curves by year showed no detectable difference in survival between the two years (log rank test, $P = 0.34$), so the years were combined for rate estimation. The Kaplan-Meier combined survival curve is presented in fig. 2. There were no recorded deaths after 16 days in either year, which may partly be a reflection on the high level of censoring encountered. The overall survival probability for the 2 month post fledging period is taken as the final rate from the graph (0.704, s.e. 0.087). Of the nine deaths across both years, only three could be assigned to known causes, two to predation by birds and one by a mammal. The other six were due to unknown losses, but for which there was a sufficiently high probability of predation that they were treated as deaths rather than censored observations. In these cases the individuals disappeared within a few days of fledging, while their brood mates were still present in the natal area. At this age they were judged to have been too immature to have successfully

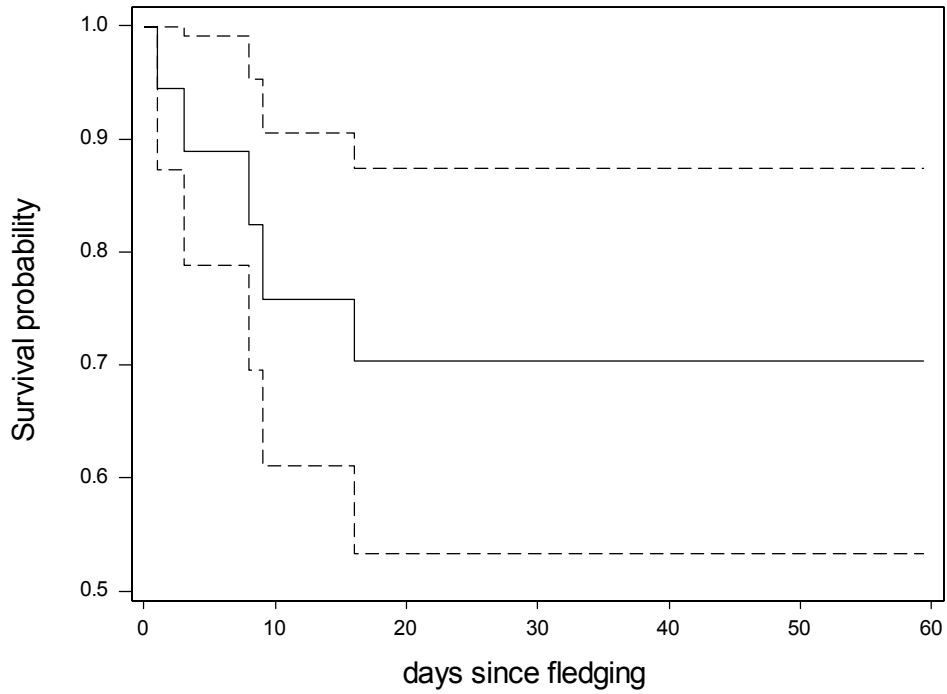


Fig 2. Kaplan-Meier post-fledging survival curve for juvenile wrens from 0-60 days, data combined for 2000 and 2001. Mean survival (solid line), and upper and lower 95% confidence intervals (dotted lines) shown.

dispersed and the failure to either detect the tag's radio frequency or observe the tagged individual directly led to the conclusion that tag had been destroyed by a predator.

Regression with life data was used to investigate the influence of a range of possible co-variables in juvenile survival. None of the variables tested (fledging body mass, father's body mass, mother's body mass, early or late fledging date) were found to explain the observed variation in survival. This is probably due to the small sample sizes in this study as previous passerine studies of survival rates have found strong relationships, particularly with body mass at fledging and date of fledging (Naef-Daenzer et al, 2001). It did not prove possible to fit tags at the same time of day or on the same day of development, and this may also account for the lack of relationship.

Annual survival rate estimation

Method 1

Observation of the behaviour of radio-tagged juveniles towards the end of the radio tracking period (5-8 weeks post-fledging) led to the decision that application of the next older age class survival rate (1-2 years) would be appropriate from the age of 2 months. Table 4 gives the starting parameter values and the calculations performed to derive an average juvenile annual survival rate of 0.43 (s.d. = 0.11). Although this is quite a high estimate for a small passerine, note that it is bound by wide confidence intervals due to the limited sample size.

Table 4a. Survival rates estimated from radio tracking data and capture-mark-recapture data (see chapter 2)

Survival period	Survival rate			
	Mean	s.e.	lwr 95% c.i.	uppr 95% c.i.
Juvenile 0-2 months	0.704	0.087	0.533	0.874
Adult 1-2 years	0.521	0.0934	0.338	0.704

Table 4b. Annual juvenile survival estimated using the rates in (a) above. The monthly adult survival rates (upper and lower) are calculated by raising the annual rate to the power 1/12. The monthly rates are raised to the power 10 and multiplied by the juvenile rates for 2 months, to give upper and lower estimates of the juvenile annual survival rate.

Survival period	Calculation	Rate
Estimates of adult monthly survival:		
lower	$(0.338^{1/12})$	0.913
upper	$(0.704^{1/12})$	0.971
$(\text{annual rate})^{1/12}$		
Estimates of adult survival for 10 months:		
lower	(0.338^{10})	0.404
upper	(0.704^{10})	0.746
$(\text{monthly rate})^{10}$		
Estimates of juvenile annual survival:		
lower	$(0.533 \cdot 0.404)$	0.215
upper	$(0.874 \cdot 0.746)$	0.652
$(\text{adult 10 month rate} \cdot \text{juvenile 2 month rate})$		
mid	$0.215 + (0.652 - 0.215) / 2$	0.434
s.e.	$(0.434 - 0.215) / 1.96$	0.111
$(\text{mid-point between upper and lower annual rate estimates})$		

Method 2

For the years 1996 and 2001 the total number of first year breeders present in the wood could be compared to the total number of birds fledged in the previous year, and for 1997 and 2002 the number of first year male breeders in the wood could be compared to half the total number fledged in the previous year. Tables 5a and b lists the data and the estimated survival rates, 5a for all first years (assuming emigration and immigration are balanced) and 5b for recruits only (birds ringed the year before in the wood as fledglings). The mean annual survival rate for all birds is 0.3 (s.d. 0.06). This is lower than the mean rate calculated using method 1 above, but lies within the estimated range of values. We might expect this value to be lower than the empirically derived one if our assumption of balanced immigration and emigration is not in fact the case, particularly if the more likely scenario of the wood being a 'source' relative to the surrounding area's 'sink'. If only first year recruits within the population are considered then much lower values are obtained, with a mean survival of 0.07 (s.d. 0.04). This is a reflection of the low number of recruits recorded during the study, with a maximum number in any one year of 3.

Over winter radio tracking

Five juveniles were caught between 11th October 2001 and 14th February 2002. The tagging was staggered through the period to maximise the duration of observations. Two of the birds had been radio-tagged during the preceding summer in their natal areas. Both birds had moved from those areas, distances of 680m and 303m, calculated from

Table 5. Juvenile survival rates estimated from the return rates of first year birds. Table (a) calculates the survival rate based on the total number of first year birds recorded in the wood, and makes the assumption that immigration and emigration are equal. Table (b) makes the same calculations but only returning recruits (i.e. birds born in the wood) are counted.

a) All first years

Year	Fledged young	First years in following spring		Survival rate
		Male	Female	
1995	93	11	10	0.23
1996	68	11		0.32
2000	73	9	11	0.27
2001	56	10		0.36
mean	72.50	10.25	10.50	0.30
s.d.	15.42	0.96	0.71	0.06

b) Recruits only

Year	Fledged young	First years in following spring		Survival rate
		Male	Female	
1995	93	1	2	0.03
1996	68	3		0.09
2000	73	1	2	0.04
2001	56	3		0.11
mean	72.50	2.00	2.00	0.07
s.d.	15.42	1.15	0.00	0.04

their arithmetic mean positions in the summer and winter as described for dispersal measurements. No mortality was recorded during the tracking period and analysis of the birds locations gave no indication of any continuing dispersal movements. No tags were found shed by the birds, with all tags simply failing to be located after tracking periods for the five birds of: 18,22,29,37 and 43 and 9 days. The last two were for the same bird, covering a total period of 77 days with a gap of 25 days between initial tag failure and subsequent re-capture and re-tagging. On re-capture the bird was found to have shed the first tag and was growing new feathers. This bird and one of the other tagged birds (both males) held territories in the spring following the tracking period in the same respective areas of the wood as they were tracked during the winter. The tags used during this work probably had reduced battery life compared to those used for the summer tracking, since they were up to 6 months old and some had been partly used and recovered. Thus all of these censored results could have resulted from expired batteries. Since no mortality was recorded survival analysis was not possible, however the adult monthly survival rate estimates (lower = 0.913, upper = 0.971, table 4) are sufficiently close to the effective survival rate of 1 recorded here for this to be a valid result.

Winter home range size

Two of the birds did not have their range sizes estimated, one because it had an almost entirely linear home range (most of the fixes came from along two perpendicular hedgerows) the other because very few precise locations were obtained. The three home range areas calculated were 0.41 ha, 0.53 ha and 2.95 ha. The variation in home range size for these birds does not appear to be related to the

number of fixes as each one covers a period of at least 30 days. However, the time of year is not consistent for each of these estimates, although it is of interest that the range areas decrease with progress towards mid-winter. As mentioned previously habitat factors play an important role in determining foraging areas, and the range contraction may be a reflection of the vegetation in the wood dying back.

3.4 Discussion

Radio-tag attachment methods and influence on survival

A serious concern with any radio tracking study is that the tags themselves may influence the results, and this could be expected to be particularly true of small, newly fledged passerines. Previous research comparing the survival of tagged fledglings (great and coal tits) with their un-tagged siblings (Naef-Daenzer et al 2001) found there were no differences in survival attributable to the presence of the radiotags. They also report no detectable reduction in the flight performance of the tagged individuals. It was not possible to conduct a similar test for tag effects in this study and this must be kept in mind when considering the results obtained. However, observation of tagged birds (both the adult male used to test the attachment method and the tagged juveniles) revealed no apparent differences in behaviour from untagged individuals and thus provides a reasonable level of confidence in the study's results. Birds that had been radio-tagged were among the one year old recruits in both years which followed summer tracking periods, and two birds which were tagged both in the summer and the winter of their first year went on to hold territories in the following spring. Thus there is no evidence to suggest that wrens

which carried a radio tag (for periods of up to several weeks) experienced reduced survival.

Tag retention times in this study were probably shorter than those which might have been possible using a harness. However the potential for adverse effects of harnesses (e.g. possibility of snagging, increased weight, difficulty of bird re-capture for tag removal) compared to those from gluing tags (temporary feather loss and possible skin irritation), suggests that, in the absence of field tests of alternative methods, the gluing method (erring on the side of animal welfare) is preferable. While tag losses after 10-12 days were higher in the second year of the study than the first, this is of less concern than it might have been since the results from the first year of study indicate that most of the post-fledging mortality occurs within two weeks of leaving the nest, and thus this critical period is covered by the data. Naef-Daenzer et al (2001) report a similarly concentrated period of high mortality in great tits and coal tits, with a third of all post-fledging mortality occurring in the first 4 days. Thus despite the high level of censoring we have a good degree of confidence in our estimate of post-fledging survival.

Post-fledging survival

The survival of juvenile wrens until eight weeks post-fledging found in this study (0.704) is higher than that reported for many other passerines (table 6). Only two of these studies made use of radio tags, for the wood thrush (Anders et al, 1997) and Naef-Danzer et al's (2001) study of great and coal tits. It is interesting to note that both these studies report rates higher than the rest, and importantly the rate for great

tits derived from the radio tracking study (0.47; Naef-Daenzer et al, 2001) is almost twice that from the passive observation and mark-recapture study (0.252; Dhondt, 1979). Thus we could reconsider the statement that the results from this study are high, with the contrary suggestion that those from some of the other studies are low, possibly underestimating survival due to unaccounted losses through emigration. Another explanation could be that wrens generally suffer lower levels of predation than the other species considered, particularly from avian predators (because of their small size and terrestrial habits). We would expect newly fledged wrens to be more vulnerable than adults, but this distinction may only last for a relatively short time after which low juvenile mortality is seen. Although the low number of birds tagged beyond 4 weeks could lead to a situation where any mortality occurring during the second half of the tagging period (i.e. weeks 5-8) is missed purely by chance. However, Tinbergen (1946) reported that wren remains were greatly under represented in the remains associated with sparrowhawk nests, whereas larger and more conspicuous species such as great tits were over represented. A possible explanation for why these apparently higher post-fledging survival rates do not result in considerably larger wren populations than those of other species of woodland passerine, is that their small size causes them to experience much lower over-winter survival. Obviously caution should be exercised when comparing results from different studies and different species, but as more radio-tracking studies are undertaken it is possible that a reappraisal of post-fledging survival rates may be necessary.

Table 6. Examples of passerine post-fledgling survival.

Species	Survival estimate	Duration	Authors
Wood thrush	0.423	8 weeks	Anders et al (1997)
Yellow eyed junco	0.321	10 weeks	Sullivan (1989)
Zebra finch	0.33	5 weeks	Zann and Runciman (1994)
Starling	0.429	7 weeks	Krementz et al (1989)
Great tit	0.252	10 weeks	Dhondt (1979)
Great tit/Coal tit	0.47	3 weeks	Naef-Daenzer et al (2001)

Annual survival rate

Estimating survival for the period of life from independence to the first breeding attempt is extremely difficult for most animals. This is often the time during which dispersal occurs, with permanent emigration compounding estimates of survival based on mark recapture techniques. Until such time that the individual fates of an entire population can be monitored it will remain necessary to derive estimates of vital rates from a combination of available data and reasonable extrapolation. In this case we took the approach that the period of elevated mortality risk experienced by juvenile wrens is relatively short-lived, after which they achieve a level of competence equivalent to that of birds one year older, and survive accordingly. Additionally the post-fledging survival curve has a reasonable fit to an exponential decline, and therefore we can feel justified in the use of the adult monthly survival rate (0.947) as an extension of this curve. Dividing up a population into distinct age classes can in some ways be regarded as an artificial structure, and thus our approach could be re-interpreted more in terms of a period of high mortality immediately post-fledging, followed by an improved survival probability (the period from juveniles through to young adult) before a final decline in the survival rate with the possible onset of senescence. Obviously this too is a simplification, since most mortality will occur seasonally (over winter) rather than as a gradual reduction. However, qualitative observations of juvenile wrens from 4 weeks after fledging, through their first winter, suggest this is a reasonable pattern to adopt.

The difference between our 12 month estimate of survival calculated by method 1 (mean 0.43, s.d. 0.11) and that from method 2 (mean 0.3, s.d. 0.06) is probably a reflection of several factors. Firstly method 2 assumes that immigration and

emigration balance each other out across the borders of the wood, however we have no evidence for this. If it was the case that the study site is in fact better quality wren habitat than the surrounding areas then a ‘source-sink’ situation might be seen, with the wood producing a surplus of wrens which disperse from the wood, but the less productive surrounding areas cannot produce sufficient numbers to match it. In order to address this question more information on the range of wren dispersal distances and the relative productivity of different habitat types would be needed. Another explanation for the lower estimate is that surviving males are only recorded if they become territory holders. Juvenile males only become territory holders if vacant territories become available through the death of the previous occupier. Thus survival measured this way is in fact a combination of juvenile survival and adult (territory holder) survival. The result of this is that the estimates are biased on the low side, since in years of high survival for all age classes, fewer territories will become available, less first year birds will be present and thus survival will be underestimated. The failure to identify any explanatory covariates for juvenile survival is again probably due to the small sample size. Studies of post-fledging survival which have found relationships between nestling body mass and survival have typically had sample sizes 5-10 times that for this study (Naef-Daenzer, 2001, Kremenetz et al, 1989).

Home range size and dispersal

During the period in which natal home range areas were defined (up to an average of 20 days from leaving the nest), observations indicated that the juveniles were becoming less dependent on their parents and were also seen less often in

association with their siblings. There was no detectable consistency of direction between dispersing individuals, although the distance travelled initially was broadly similar (204-593m). Although two of the birds settled within the boundaries of the study wood, most of the known locations where dispersing birds settled tended to be of a less high quality than the natal woodland. This included gardens, woodland edges, hedgerows and an area of gorse scrub within a field. This variation in post-dispersal habitat is reflected in the range of different sizes for the post-dispersal home range areas. Adult male territorial behaviour is maintained throughout the breeding season, and this may be directed at their own offspring once they are no longer recognised as such and have become independent. Most territories in the study site shared boundaries with others, thus a dispersing juvenile in most cases has to pass through areas defended by other males. The observation that most birds settled in apparently marginal areas perhaps indicates that these were the first places the juveniles encountered in which they were not subjected to antagonistic behaviour from a resident bird.

It is possible that the dispersal distances recorded are biased on the low side due to the difficulty of re-locating birds which moved rapidly out of the study area. Efforts were made to control for this through extensive searching of the area around the wood to a distance of up to 3 km, but the limited tag detection range imposed by the small tag size meant that birds moving over 1 km from the study site would have a high probability of avoiding detection. Of 8 birds which were suspected of moving away from their natal areas and were initially lost, 5 were re-located outside the wood within 1-2 days. Of the 3 which were not re-located, 2 had tags which could have run out of battery life (40 and 54 days), leaving one bird with an unknown fate.

Thus we can feel confident that in most cases dispersing birds which remained alive were detected during the initial stages of dispersal. The locations of the 2 birds re-tagged during the winter lend further support to the idea that wrens from the study area were not travelling distances over which re-location was compromised by the short tag range. The distances travelled from their natal areas (303m and 680m) are similar to those recorded for initial dispersal movements during the summer tracking period, although it is possible that these birds had travelled more widely during the intervening period (2-3 months).

Chapter 4

Description of density dependent, stochastic

simulation matrix

population model

4.1 Introduction

Population modelling

Demographic models have become a common component of wildlife management techniques over the last twenty years (Beissinger and Westphal, 1998). Population models are employed in a variety of situations where the goals of management may be: in the case of rare and endangered species, to minimise extinction risk (e.g. Inchausti and Weimerskirch, 2001) or increase the population's size or growth rate (λ ; e.g. Wisdom and Mills, 1997); for exploited species, to maximise the potential harvest (e.g. Hamilton and Moller, 1995) or in the case of pest species, to reduce the size of a population in order to minimise detrimental effects (e.g. Brooks and Lebreton, 2001). Population models provide a means to investigate questions which might otherwise be impossible or impractical to address. No model is ever 'right' or 'wrong' in terms of the outputs provided (McCarthy et al, 2001), and indeed an approach to model development based on these assessments is misplaced. Instead models should be chosen for their ability to act as problem solving tools (Starfield, 1997) and as a means for comparing alternative management options.

The aim of a simple form of population model is to provide an estimate of the population size or growth to be expected at some point in the future based on the current population size and estimates of the rates of survival and reproduction (e.g. Jones, 2002; Velando and Freire, 2002; Inchausti and Weimerskirch, 2001). These demographic rates are usually obtained from census data (typically annual), with the rates often categorised by sex and age (or size). Matrix models are ideally suited to make use of this age or (stage) based, discrete time data, and in their simplest form require little additional data manipulation. Consequently they have become a common tool in population management. The application of matrix algebra methods for

modelling populations was first proposed by Leslie (1945) and their popularity increased following the publication of 'Matrix Population Models' (Caswell, 1989). This coincided with a general increase in the application of modelling in the management of threatened and endangered species. A central feature in the popularity of matrix models is the simplicity with which it is possible to derive analytical results. For example a common form of analysis is to calculate the sensitivity of the population growth rate to change in a species' demographic rates (e.g. Martien, et al 1999; Wisdom and Mills, 1997; Crowder et al, 1994). Sensitivities, and their proportional equivalents, elasticities, are a measure of each demographic rate's contribution to λ , the population growth rate: the larger the elasticity value, the greater the contribution of that vital rate to population growth (Caswell, 2001). Thus management for a rare species can be directed at the demographic rates which will yield the greatest return in terms of population growth. Clearly this makes matrix modelling and elasticity analysis in particular, extremely attractive to conservation managers.

Matrix model assumptions

Analysis of a matrix model at its simplest assumes each parameter has a constant value, population growth is density independent and deterministic, and elasticity analysis is conducted with reference to a single value of λ . The insights thus provided into population processes are extremely valuable. However, the omission of density dependence and environmental variation has prompted concerns about the technique's validity for populations where these factors play an important part in the population dynamics (Benton and Grant, 1996; Mills et al, 1999; De Kroon et al, 2000; Grant and Benton, 2000). For example a management assessment based only on λ and the factors which affect it, calculated using a

matrix of constant mean rates, will be of limited value if density dependence acts to constrain the population's actual long-term growth rate to lie around 0. It is sometimes argued that species of conservation concern are experiencing either population declines or have sufficiently small population sizes that density dependence is unimportant and therefore an analysis based on λ is justified (e.g. Weilgus et al, 2001) . However, simply because a population is declining or small does not mean that density dependent processes are absent or can be ignored. Indeed, once the causes of a population's decline are understood it may be found that density dependent processes are operating at elevated levels, and their inclusion in the modelling process may become even more important. For example reduction in a species' available habitat will lead to greater competition for resources and thus a period of increased density dependence, until such time as the population re-establishes itself at a new, lower level. Similarly, environmental variability plays an important role in determining optimum life history strategies, and the relationship between environmental variation and the optimum reproductive effort has been found to be highly dependent on a host of population dynamic factors (Benton and Grant, 1999). A consideration of life history strategies may not be of immediate concern when management is concerned with maximising total population size, but in other situations (e.g. commercial harvesting, or maximising output of individuals to 'seed' new populations), such factors are of considerable relevance. Thus the implementation of management prescriptions with the intention of reducing the risk of population extinction, but derived from a density independent, deterministic sensitivity or elasticity analysis, conducted with reference to λ , may not produce the desired results.

If elasticity analysis is used to guide management, it is critically important to assess the techniques' performance under a range of conditions. Various tests of the robustness of linear

elasticity predictions to realistic natural variations have been conducted (e.g. Mills et al 1999; van Tienderen, 2000; Silvertown et al, 1996), and there have been reviews of the outputs and predictions of alternative commercial Population Viability Analysis packages (PVA - e.g. RAMAS, GAPPS, Vortex), which can incorporate stochasticity and density dependence (Mills et al, 1996; Brook et al, 2000). Some studies have used the observed variation in vital rates to perform stochastic simulations (e.g. Doak, et al, 1994; Wisdom and Mills, 1997; Cuthbert et al, 2001), and a few have included density dependence in survival or fecundity (Jensen, 1995; Escos et. al, 1994), but applied studies combining both stochasticity and density dependence in vital rates (excepting the use of ‘black-box’ PVA tools where the methods employed are not generally clear to the end-user) are notable by their absence. This, in spite of the fact that to produce accurate projections of fluctuating populations both density dependent and stochastic effects should be included (Saether et al, 2002).

Methods for calculating density dependent, stochastic elasticity values using data derived from population simulations have recently been developed (Grant, 1997; Grant and Benton, 2000) and applied to a population model of *Tribolium* (Grant and Benton 2003). This work has demonstrated that under certain density dependent and stochastic conditions, the density dependent elasticities of population size can be quite different from the elasticities of λ , even to the extent of having the opposite sign. This work suggests that under some conditions manipulation of a species vital rates might be undertaken with the expectation of a positive response (in terms of population growth or size), but the actual result could be a decline in the size or growth rate of the population. The work presented in this thesis is the first to use data collected from a wild population to parameterise a simulation model suitable for comparing elasticity analyses with and without density dependence and stochasticity. The results of the

elasticity analyses will be presented in the next chapter, but here the model will be introduced in detail. The methods section will describe the model structure and approach taken to incorporate density dependence and stochasticity, while the results section will discuss the outputs obtained for a range of density dependent and stochastic scenarios. The discussion will highlight those aspects of the model which are of particular importance for the system studied here, and the implications for population modelling in conservation. The models are based on data collected during a study of a small population of wrens (*Troglodytes troglodytes*), conducted over a period of eight years in an area of woodland near the Stirling University campus, Bridge of Allan, Scotland. They are short lived, small passerines found throughout the northern temperate regions and are common in woodland and hedgerow habitats. Wrens, particularly males during the breeding season, are highly territorial and their small size (approx. 10g.) causes their survival rates to be highly sensitive to the severity of over-winter weather. Further details of the wren life cycle, data collection and analysis are presented in chapters two and three.

4.2 Methods

Basic matrix model construction

To construct a typical matrix model a species' average survival and reproductive rates, subdivided by age or stage, are entered into a square projection matrix, **A**, with fecundity rates in the top row and survival rates in the sub-diagonal. For this study a simplified form of the age-based 3*3 matrix is as shown:

$$A = \begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix}$$

[1]

Where the F_i terms are measures of the mean fecundity for age class i at time t and the P_i terms are measures of the mean survival probability for age class i , for the transition period $t-1$ to t . In this model, the final age class (P_3) contains all individuals aged 3 years and older. Multiplying the matrix \mathbf{A} of mean rates by a vector \mathbf{n}_t of the numbers in each age class at initial time t , produces a second vector \mathbf{n}_{t+1} of the numbers in each class after the transition period defined by t :

$$\begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix} \times \begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix}_t = \begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix}_{t+1}$$

[2]

or alternatively:

$$\mathbf{A}\mathbf{n}_t = \mathbf{n}_{t+1}$$

[3]

A population projection is obtained by repeating this procedure. The timing of the annual census (either pre- or post- breeding) determines the method used to calculate the fecundity rates. If, as in this study, an annual census is performed post-breeding, the first entry in the population vector (N_1) is the number of newly fledged individuals, and the transition period t comprises the survival period (P), followed by breeding (F) and then the census. Thus only surviving birds breed, and consequently the F_i terms in the population matrix are the product of the P_i survival rates and the i class reproductive rates (m_i fertility rates in life table notation). It should be noted that the matrix used in the simulation model corresponds to a 6*6 matrix, which includes both sexes, subdivided into the 3 age classes. The age specific demographic rates are provided in table 1.

Table 1. Summary vital rate data for wrens of Mine Wood, 1995-2002. All data comes from a small population of wrens, Mine Wood, Bridge of Allan, Stirlingshire.

a) 0-1 survival estimated from radio-tracking data, (see chapter 3 for details); 1-2/2+ survival estimated from colour ring data using capture-mark-recapture methods (CJS) in program MARK (chapter 2).

b) Fecundity estimates and breeding attempt data calculated from 4 years of detailed nest surveys and monitoring (chapter 2).

c) Breeding territory data calculated from six years of complete census data (chapter 2).

a) Survival probabilities

	Age transition (years)			
	0-1	1-2	2+	
Male	mean	0.43	0.52	0.46
(and female)	s.d.	0.11	0.25	0.21

b) Fecundity rates

		Age	
		1	2 / 2+
Per individual			
Male	mean	2.04	2.16
	s.d.	0.3	0.88
Female	mean	2.38	1.69
	s.d.	0.54	0.91
Per breeding attempt			
Male	mean	1.61	1.25
	s.d.	0.27	0.48
Female	mean	1.78	1.4
	s.d.	0.34	0.79
Number of breeding attempts			
Male	mean	1.19	1.7
	s.d.	0.14	0.11
Female	mean	1.32	1.21
	s.d.	0.05	0.21

c) Number of breeding territories

mean	17.67
s.d.	1.97

The long run population growth rate can be calculated both numerically from a population projection and also by eigenanalysis of the projection matrix itself. The dominant eigenvalue of the matrix is λ , and the vectors of the stable age distribution and reproductive value are the right and left eigenvectors respectively. The sensitivity and elasticity of λ to change (respectively absolute or proportional) in each of the matrix elements can be calculated either numerically (see next chapter) or analytically using the eigenvectors (see Caswell, 2001).

Density dependent survival and reproduction in the study population

Previous workers have reported that wren survival is particularly sensitive to winter weather (Armstrong, 1955; Cawthorne and Marchant, 1980), causing wide variations in survival (and subsequently population size) between years. A similar result was also found in this study, for example the estimate of over-winter survival for one-year-old males varied between 0.13 (1995-96) and 1.0 (1998-99). During survival analysis (using Program MARK) covariates coding for weather variables and population density were investigated, but no factors improved model fit. However, further attempts to detect the presence of density dependence in survival rates were performed during the model development and parameterisation described here. These tests were complicated because in two of the study years only a partial census was conducted. While the survival rate estimation procedure in MARK can take account of this, it meant it was not possible to use population counts to test for the presence of density dependence. Male wren territories within the study site maintained approximately the same size and boundaries between years, despite both changes of ownership and seasons of non-occupation. It was also apparent that certain 'core' territories were occupied in all years, while other, 'peripheral', ones were only filled in years of higher population size. Thus it was possible to estimate the number of territories that the wood could support (under the conditions

encountered during the study period) and the number of these that were occupied in any one year. Using these estimates an index of population density was derived, defined in any particular year as the number of occupied territories divided by the number of available territories, within the area of wood surveyed. The presence of density dependence was investigated by testing this index (of the proportion occupied) against the subsequent change in proportion (i.e. prop. occupied in year A vs. prop. occupied in year B/prop. occupied in year A). The potential drawback of this approach is that it relies on consistency in the observer's ability to identify a wren's territorial requirements and the censuses were conducted by two different individuals. However, this risk is minimised by the presence of territory maps for each year. Further discussion on the mechanisms employed in the model for the action density dependent survival are included below.

The territorial behaviour of wrens during the breeding season limits the number of birds which are able to obtain viable breeding territories (for a discussion of wren territoriality see chapter 2), and this regulates the population's overall reproductive output. It is possible that there is a decline in the suitability of territories for reproduction, which will lead to a form of 'buffer effect' (Brown, 1969) as the population increases and all the best territories become full. However, there was insufficient data on reproduction in relation to territory quality for this hypothesis to be tested in this case, and it was decided that for the purposes of modelling, the whole study site would be treated as being of comparable quality. It was also decided to omit any functional decline in reproductive output with increasing population density. Therefore density dependence operated on breeding by the imposition of a limit to the number of territories available in any one year. Although woods are obviously not static in terms of their

structure and how this is translated into the number of territories available for wrens, it was assumed that the average number would remain the same for the duration of each simulation.

Model structure

The model incorporates both sexes, divided into 3 age classes; age class one (zero to one year old), age class two (one to two year olds) and age class three (all individuals older than two years), totalling twelve demographic rates. This division was based on the ability to age wrens in the field and the nature of the data thus collected. The 6*6 matrix, incorporating both sexes is therefore:

$$\mathbf{B} = \begin{bmatrix} fF_1 & fF_2 & fF_3 & 0 & 0 & 0 \\ fP_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & fP_2 & fP_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & mF_1 & mF_2 & mF_3 \\ 0 & 0 & 0 & mP_1 & 0 & 0 \\ 0 & 0 & 0 & 0 & mP_2 & mP_3 \end{bmatrix}$$

[4]

where the coding is as for equation [1], with the addition of the lower case ‘f’ and ‘m’ signifying female or male. The population vector has 6 entries, for the 2 sexes and 3 age classes. The model code was written in Matlab (The MathWorks Inc.) using the built-in functions (see appendix 1). A global flow chart of the model structure is provided in fig. 1. The annual cycle begins at the point immediately after the population census. The first age group is made up of newly fledged individuals, the second and third, birds which have just bred and had a birthday: either their first (age class two) or their second or later (age class three). There follows a period of survival encompassing all of the non-breeding portion of the year (survival subroutine, fig. 2). Surviving individuals in each age group then progress through three stages of breeding: territory allocation (fig. 3), pairing (fig. 4) and reproduction (fig. 5). The end of

the year occurs with a population census and then each breeding age class moves into the next age category and the fledglings enter the first age group. The model can be run with or without stochasticity (environmental and demographic), covariance between vital rates and density dependent survival and breeding. The points at which vital rates are perturbed during elasticity analysis are marked on the diagrams and this aspect of the model performance will be discussed in the next chapter.

Model subroutines: survival

A flow chart of the survival subroutine is provided in fig. 2. Input variables are the vectors of males, females and that year's vital rates (calculated in accordance with settings governing stochasticity, rate covariance and density dependence). If demographic stochasticity is selected the number of surviving birds is sampled from a binomial distribution. If not then the number surviving in each age class is simply the product of the population size and survival rate, rounded to the nearest integer.

Model subroutines: territory allocation

Only territory holders breed, with the number of territories either a constant value at each time step of a simulation, or varying randomly between years (using a function described below). Male territories are allocated in reverse age order, since it was observed that the majority of males in the study wood remained on the territory they obtained as 1 year olds until their apparent death (<3% of males in the study moved to a different territory between years). Thus surviving males in age classes two and three automatically obtain territories and first years fill

any remaining spaces. The survival rates estimated from the field data take all apparent mortality into account, whether it occurred over-winter or during the breeding season. While most mortality does take place over-winter, with a breeding season which lasts for six to seven months there clearly may be mortality and replacement of territory holders during this time too. However, for convenience the model treats survival and breeding separately, with breeding effectively an instantaneous event. Thus no distinction is made in the model between a first year male who obtains a territory in November and another who obtains one in May: both contribute to the overall reproductive output. However, no males were recorded becoming territory holders within the wood for the first time aged two years or older. Thus first years who fail to obtain a territory in their first breeding season are considered to have emigrated and are removed from the population. The situation for females is less well understood, although females appear to be less fiercely territorial (female ranges tend to show a greater degree of overlap, M. Evans, pers. comm.). However, it is likely that the mechanisms determining territory numbers and acquisition will be similar to those for males (Wesolowski, 1983), thus female territory allocation follows the same format.

Model subroutines: pairing

Wrens do not form pairs in the traditional passerine sense (at least not in heavily modified western European habitats, see Wesolowski, 1983). Instead each male builds several nests and encourages as many females as possible to mate with him, and use one of his nests (Evans and Burn, 1996). Similarly females normally have more than one breeding attempt, often with different males. This is not a simple system to model, however, records from the study site suggest that the number of breeding males and females was very similar in most years. Without

better data on the adult sex ratio therefore, the numbers of each sex are constrained to be the same, and breeding only occurs from 'pairs' of birds. Whichever sex is in greater number has its first year breeder numbers reduced to match the minority sex, and the excess are considered as emigrants.

Model subroutines: reproduction

The number of offspring is calculated as the product of the number of breeding birds, the number of breeding attempts per individual and the number of offspring produced per breeding attempt (fig. 5). The sex and age specific number of breeding attempts is either constant in all years (observed mean values) or randomly generated at each time step (using the observed means and variances and distributions matching the field data). The total number of female breeding attempts for the population is calculated as the number of breeding females multiplied by the per individual number of breeding attempts. Since the total number of male breeding attempts must match this figure the following adjustment routine is employed. First, an 'unadjusted' total number of male breeding attempts is calculated in the same way as for females, and then divided into the total female number to produce a correction factor. The original age specific male breeding attempt rates are then multiplied by the correction factor to produce a set of adjusted breeding attempt rates. These adjusted rates are used to calculate the total male reproductive output. The young produced by both sexes are combined and the offspring sex ratio is found either by sampling from a binomial distribution with a probability of 0.5 (demographic stochasticity) or the sexes are assigned equally.

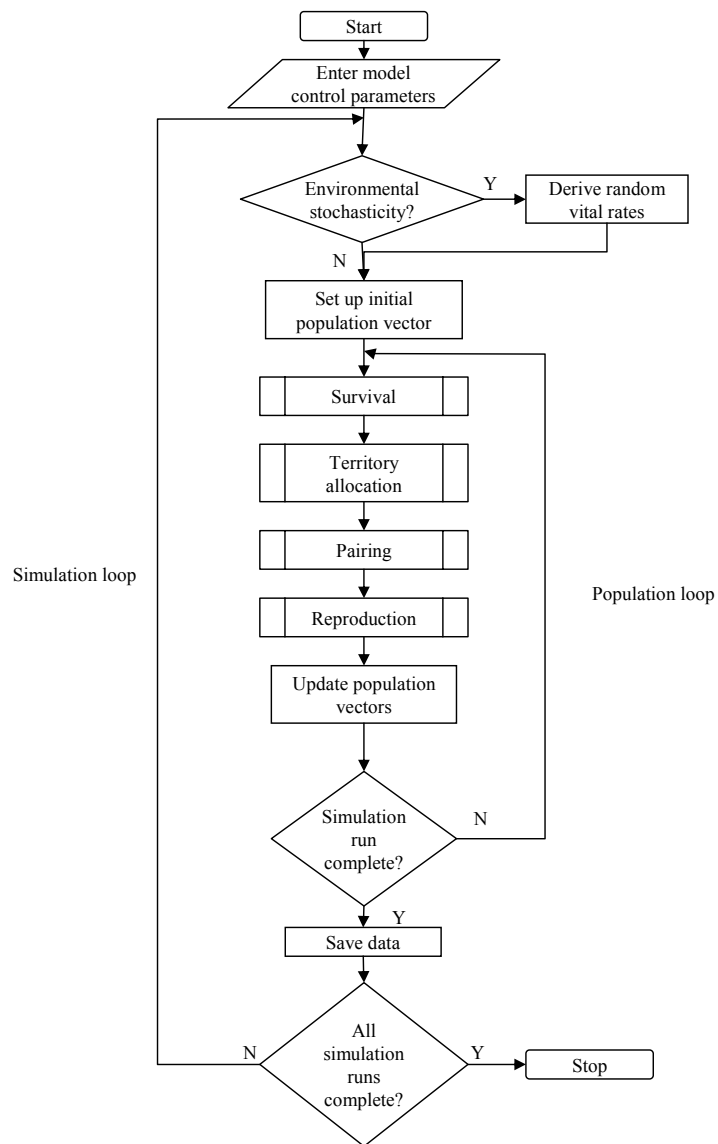


Figure 1. Global flow chart for Wren simulation model. The population loop contains subroutines for survival, territory allocation, pairing and reproduction (detailed in figs. 2-5) which make up the annual time step.

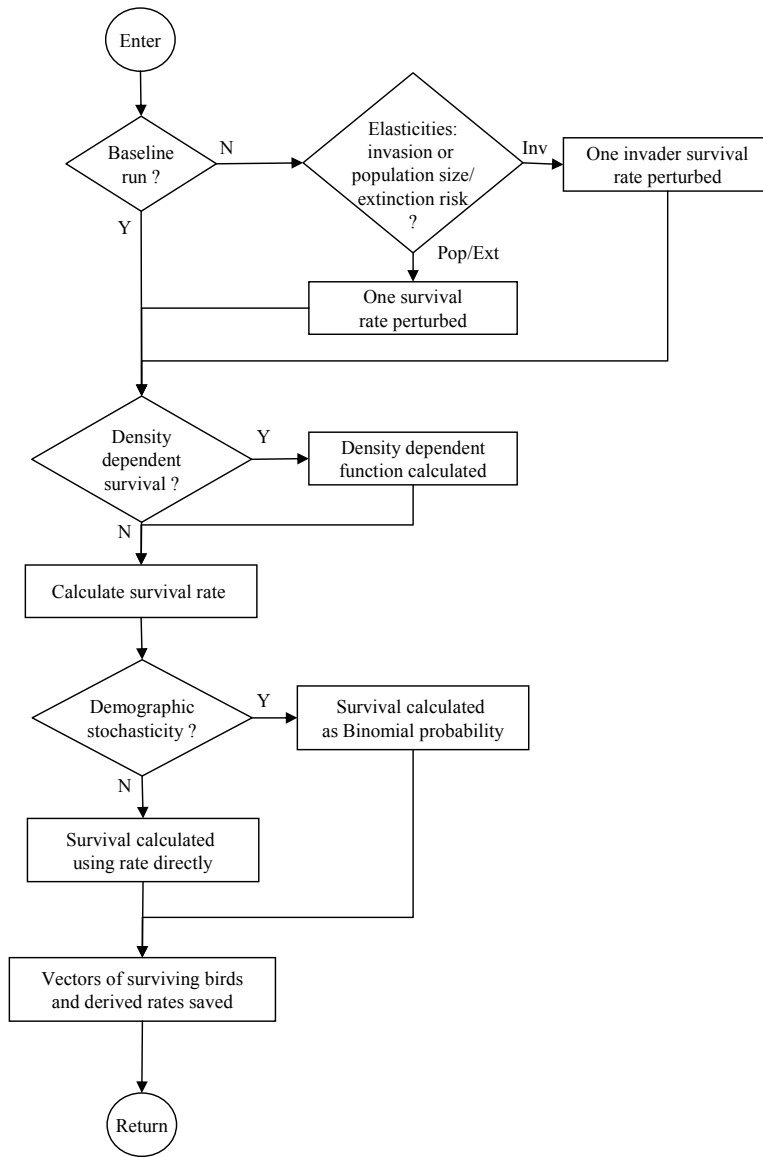


Figure 2. Survival subroutine. In baseline run conditions no vital rates are perturbed. Perturbation runs can be to find either elasticities of invasion, population size or extinction probability.

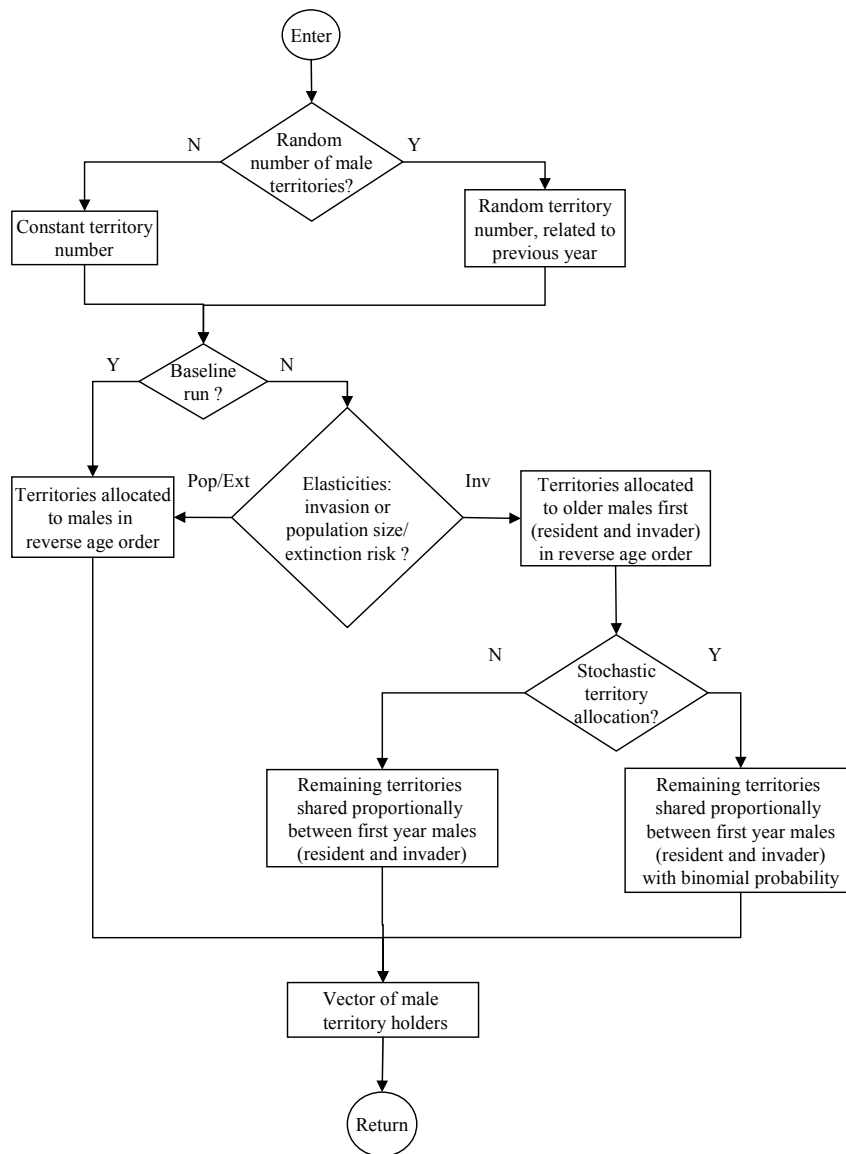


Figure 3. Territory allocation subroutine. Only males are shown but the female routine is identical. The allocation of territories changes depending on whether or not elasticities are being calculated, and if so which kind (invasion, population size, extinction risk). Excess individuals are removed from the population. In a baseline run no vital rates are perturbed, these runs are used for comparison with elasticity runs (when individual vital rates are perturbed).

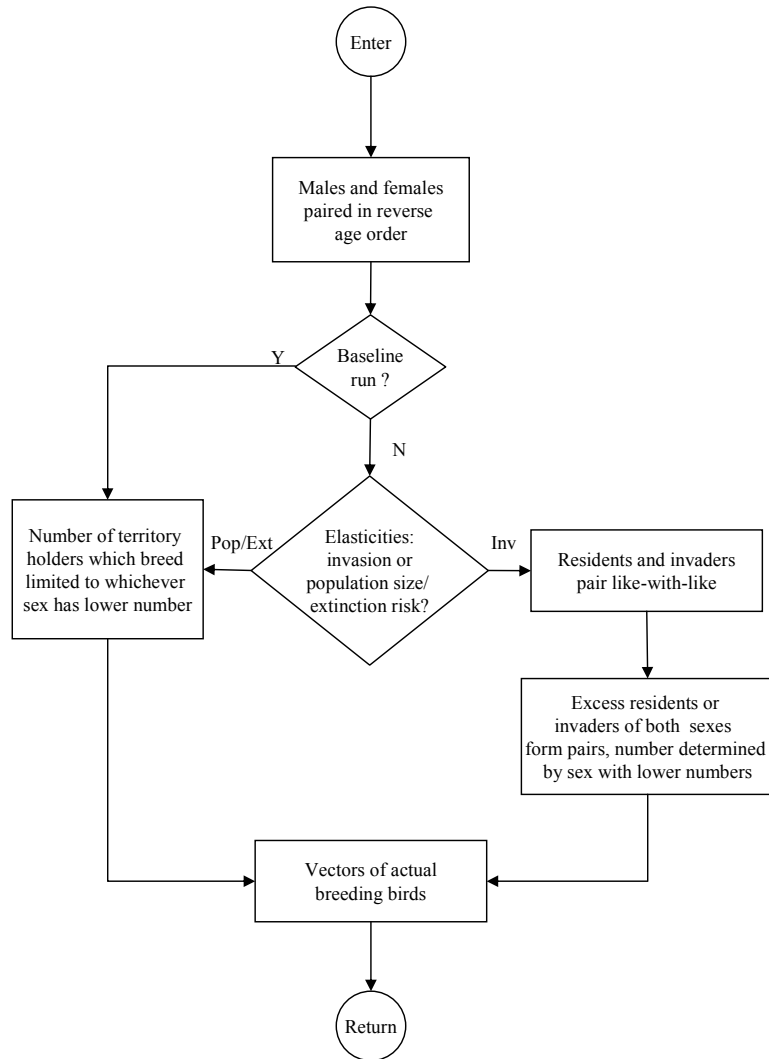


Figure 4. Pairing subroutine. Only an equal number of males and females can breed, excess individuals of either sex which fail to obtain a partner are removed from the population. If elasticities of invasion are being calculated pairing occurs first between same types (i.e. resident with resident, invader with invader), before any excess of either sex of each type pairs with excess of the opposite sex of the other type. Offspring from 'mixed' pairs are assigned equally to resident and invader types.

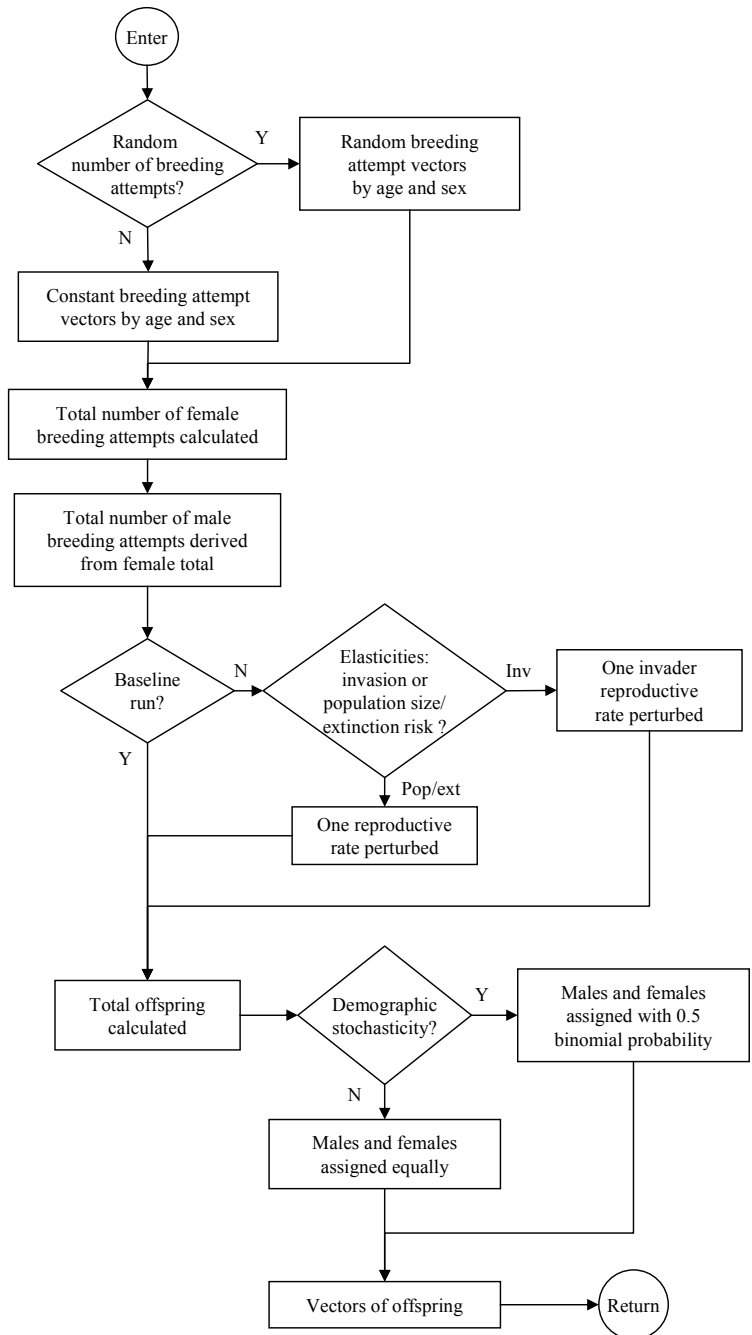


Figure 5. Reproduction subroutine. The number of offspring produced by each sex is calculated separately, with the proviso that only territory holding pairs can breed (see previous sub-routines).

Modelling environmental stochasticity

Simulating environmental stochasticity requires that vital rates are picked from probability distributions, ideally defined by field data. Identification of the study population's vital rate distributions was not possible, making it necessary to select the most appropriate distributions. Fieberg and Ellner (2001) state that in many cases there is no significant difference in the probability densities produced by commonly used alternative distributions for vital rates (e.g. for survival: beta, uniform; for fecundity: lognormal, gamma), and conclude that the choice of distribution is unlikely to have a significant impact on model predictions. However, Benton and Grant (1996) found that, in highly variable environments, different sampling distributions can have marked effects on the range of vital rates produced, and this was particularly true of truncated distributions. Thus the distributions selected for the model were those with the most favourable characteristics: for survival the beta distribution, as this can take a range of shapes while still being constrained to lie between 0 and 1; and for fecundities the lognormal distribution.

Modelling vital rate covariance

Covariance is incorporated in each year's demographic rates following the method of Gross et al (1998), employing modified versions of functions provided by Dan Doak (doak@biology.ucsc.edu). Correlation coefficients defining the relationship between each of the demographic rates are entered into the upper right triangle of a 12*12 matrix (12 = no. of demographic rates). This is transformed into a symmetrical matrix (about the diagonal), and then singular value decomposition is used to turn this matrix into a covariance matrix. In each year of a simulation a set of twelve standard normal random numbers are multiplied by the

covariance matrix to produce twelve correlated random normal numbers. These normally distributed values are transformed into uniformly distributed values, which are used to pick a set of demographic rates from their respective cumulative distributions. Todd and Ng (2001) have shown that under some circumstances the transformation process can alter the correlation coefficients of the final values. However comparison of the vital rates generated using this method with the original correlation matrix indicated that the changes were sufficiently small (less than 10%) to be of minor concern.

There is little available information on the degree of covariance which exists between the vital rates of wild populations. In two studies where such relationships were analysed (red deer, *Cervus elephas*, (Benton, et al, 1995) and desert tortoise, *Gopherus agassizii*, (Doak, et al, 1994)) general trends were found for survival rates to be positively correlated with each other, while survival and reproduction (deer) and survival and growth (tortoise) were negatively correlated. Although no consistent trends could be identified for the wren population data, since variations in demographic rates from year to year are likely to be correlated, with potentially important consequences for the population dynamics (Tuljapurkar, 1990), a background low level of covariance between the vital rates was incorporated into the model. This was based on the assumption that a 'good' year for survival will be good for all age classes (positive correlation between survival rates in any one year = 0.33), and likewise for fecundity rates (positive correlation of 0.33). However, fecundity and survival are expected to be traded off against one another, and are negatively correlated by -0.33 . In this way rate covariance was incorporated into the model without large assumptions being made about either its direction or strength. When density dependent survival is applied only to juveniles there can be a conflict with the positive survival correlation between juveniles and adults as described

here. This could arise because in a good year for survival less territories become available and so we would expect lower juvenile survival. However this does not have any affect on the overall population size, since non-territory holders do not contribute to the production of the next generation.

Modelling density dependent survival

Density dependent survival was modelled using a flexible, two parameter function (Maynard Smith and Slatkin, 1973), chosen to enable comparisons to be made not only of linear and non-linear models, but also of different forms of density dependent feedback. The function takes the form:

$$f(N) = (1 + (aN)^b)^{-1} \quad [5]$$

where $f(N)$ is a function of population density which acts to modify the P_i survival rates, a and b are the density dependent control parameters and N is the total population size. The scaling parameter, a , determines the population size at which proportional mortality reaches a fixed level, while parameter b determines the strength of the density dependence. Bellows (1981) conducted a comparison of the descriptive properties of seven different density dependent functions and recommended this one based on its combination of flexibility and good descriptive properties. The population dynamics produced by different response curves can be investigated (by independent adjustment of parameters a and b), and thus the role of density dependent survival in population regulation can be more fully explored. Male and female survival can be treated either independently or together.

Density dependence, acting through survival rates, may affect subsets of real populations differentially (Coulson et al, 2001; Clutton-Brock et al, 2002). Over winter survival of wrens is greatly affected by weather conditions, as obtaining sufficient invertebrate food during periods of severe weather is critical for survival. It is possible, therefore, that during these periods territory holders (i.e. age classes 2 and 3) have an advantage over non-territory holders (i.e. juveniles, age class 1) through exclusive access to the resources on their territories. This could offer older individuals a degree of protection from the density mediated resource competition to which juveniles are more prone. Thus the density dependent function can be applied in one of two ways, either to all survival rates equally or, to mimic this scenario, just to juvenile survival. Although it is unlikely that density dependent survival would apply across age classes in such a strict ‘on-off’ manner, this format permits exploration of how differentially regulated survival may affect population dynamics.

Modelling density dependent reproduction

It was not possible to establish the upper limit of available territories on the study site from the counts of territorial male numbers, but it was assumed to be not much greater than the observed maximum number of 19 and thus a limit was set on the number of territories at a baseline value of 25. Wren territories are defined by the suitability of the vegetation for building nests and supporting breeding attempts. The vegetational characteristics which determine wren territories are not static, but change through time, partly in response to environmental conditions. It is reasonable to suppose that such changes will normally occur gradually and that the number of available territories will change progressively rather than taking big steps between years. If we simulate variation in the number of territories as a

random number using the observed mean and variance values this could lead to frequent sequential occurrences of territory numbers at the upper and lower ends of the defined distribution. In order to limit this possibility and introduce a degree of positive autocorrelation in territory availability, the number of territories in any one year is found as the previous year's

$$\text{territory no}_t = \text{territory no}_{t-1} + \varepsilon$$

value plus a small random number:

[6]

where ε is a normal random deviate with a standard deviation of 1 and a mean equal to:

$$\text{mean}(\varepsilon) = 1 - \frac{\text{territoryno}_{t-1}}{\text{baselineterritoryno.}}$$

[7]

thus the mean varies around 0, and is negative when the previous territory number was greater than the baseline and positive when it was less. This promotes both a central tendency in territory number and also a 'stepped' progression in territory number over time, reducing the incidence of consecutive high and low values. This mechanism was adopted to mimic the way changes (affecting the number of wren territories) are expected to occur in the vegetation structure.

Estimating density independent vital rate means and variances

It is assumed that the mean survival rates obtained from the study population were recorded in the presence of density dependence. To avoid the situation where density dependence is applied twice during simulations (the 'implicit' density dependence in the observed rates, and that added by the model), the input mean rates need to be increased, ideally to their density

independent levels. Increasing the input mean rates has a negligible effect on the output mean rates because of the action of density dependence, and therefore comparing input and output rates is ineffective in this regard. However, since the probability of extinction is strongly influenced by change in the mean survival rates this was used as a means to identify an appropriate amount by which to increase the observed mean values prior to simulation. The target for mean survival rate increases was the minimum amount which would deliver an approximate extinction probability of 10% in 250 years. This was chosen as a conservative probability of extinction for a small, isolated wren population. Prior to simulation all survival rate means were multiplied by a small value (in the range 0.9-1.5) and the subsequent extinction probability recorded.

The variance in vital rates recorded for field populations is the product of both demographic and environmental stochasticity (Saether, et al, 2002). The variances required as model inputs are those which would be obtained in the absence of demographic stochasticity, so it was necessary to decompose the rate variances in order to isolate the environmental component. To do this, incremental percentage reductions were made to the input variances and model was run with both environmental and demographic stochasticity. The resulting model output variances were compared to the observed field variances, using a least squares method, and the appropriate level of adjustment to make to account for demographic variation was identified as that which gave the closest match.

Calculation of extinction probability

A quasi-extinction threshold of 5 individuals was set for all simulations. Extinction risk was estimated both as the proportion of simulations in which the population falls below the

threshold (simulation extinction risk) and also as an analytical rate (analytical extinction risk), calculated as follows. Assuming the population size over time conforms to a normal distribution, the probability (p) of falling below a threshold level per unit time can be estimated from the area under the tail of the cumulative distribution function (specified by the long run population mean and standard deviation), and we can calculate the risk of extinction (E) within

$$E = 1 - (1 - p)^t$$

a specific time period (t) as:

[8]

4.3 Results

Density dependent survival in the study population

In a multiple regression analysis both the previous year's proportion of occupied territories and the number of winter snowdays were found to be marginally significant at the 5% level in explaining change in the proportion of occupied territories (previous occupation: $F = 7.64$, $P = 0.051$; snowdays: $F = 8.03$, $P = 0.047$). Fig. 6 plots the observed data and the fitted lines taking into account low, average and high numbers of snowdays, as recorded over the study period. Because of the chance that the proportional measure used in this analysis would not be normally distributed a Kolomogorov-Smirnov normality test was performed on the residual values, which returned a non-significant result ($P > 0.15$). We therefore have some evidence that once winter weather is accounted for, the survival of the wrens in the study population is a function of the previous year's population density.

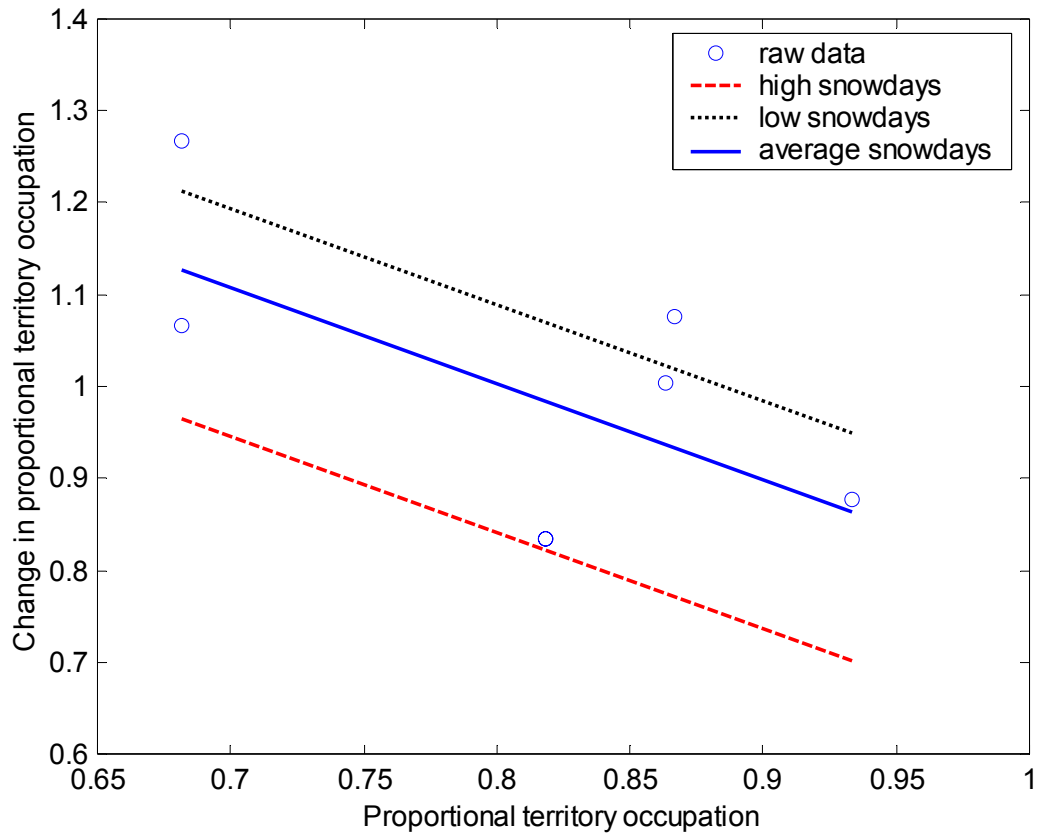


Fig. 6. Change seen in proportional territory occupation (proportion occupied in year t / proportion occupied in year $t-1$) in relation to the proportion of territories occupied in the previous breeding season (proportion occupied in year $t-1$), taking into account the number of days of snow lying during the intervening winter. The multiple regression equation is: change in proportion = $1.93 - 1.05$ (occupation proportion) - 0.0103 (snowdays); p (occupation proportion) = 0.051 ; p (snowdays) = 0.047 . The points are the observed data, the middle (blue) line the change expected with average snowdays (9.3), the upper (dotted black) and lower (dashed red) lines show the expected change after respectively a low (1) snowday winter and a high (25) snowday winter.

Estimates of extinction probability

The simulation extinction risk was calculated using the total population size, while the analytical extinction probability was calculated using the total population mean and variance and also the male and female population means and variances separately (fig. 7). The extinction risks found using each method show the same marked increase as the total population size falls below 100 individuals. Due to differences between the mean and variance of each of these sub-classes of the population at any particular total population size, the estimates of analytical extinction risk for each are slightly different. Clearly, however, if either males or females becomes extinct then the population becomes extinct, and estimates of the simulation extinction probability based on either sex would be identical. The fact that the analytical rate for females is higher than for males is an indication that low female numbers are more likely to trigger population extinction than low male numbers. Since the analytical extinction rate derived using female numbers closely matches the numerical simulation extinction probability, it was used for the descriptions of the relationship between extinction risk and density dependent survival. This reduced the need to perform large numbers of model simulations in order to obtain robust estimates of the extinction probability under a range of possible model settings.

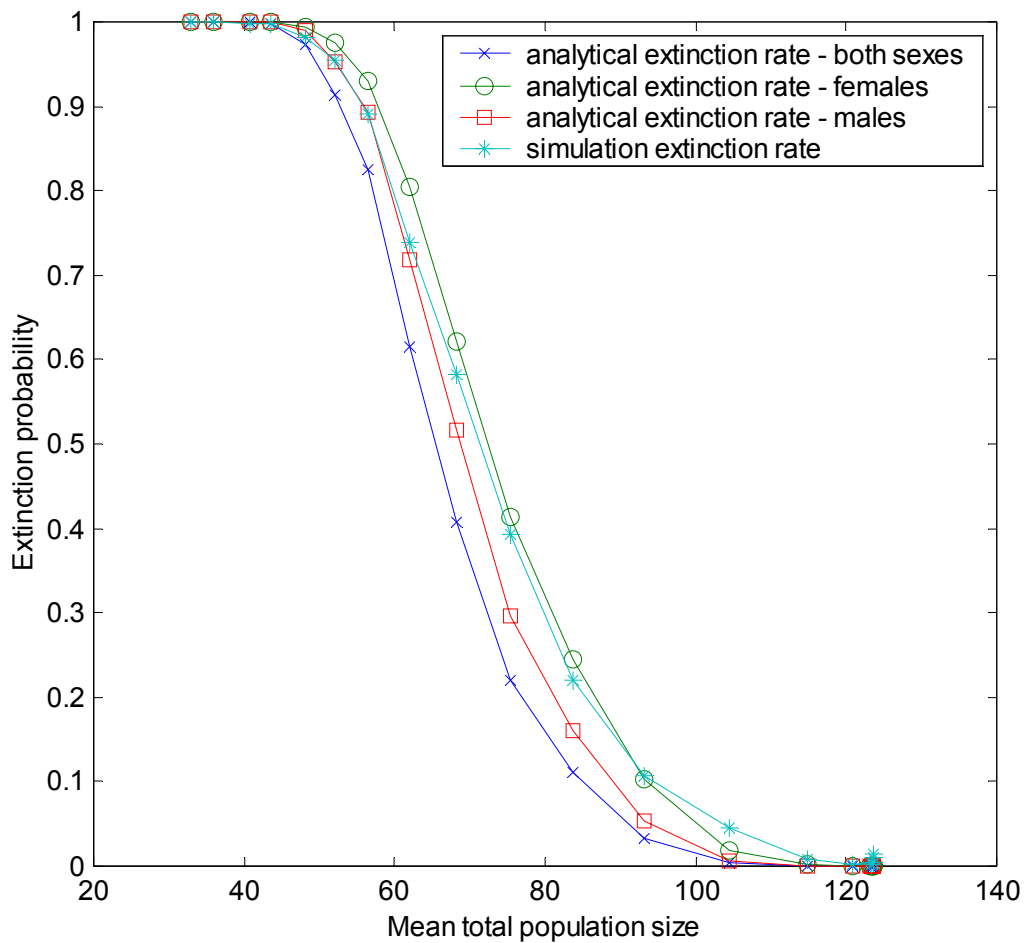


Fig. 7. The effect of the mean population size on the extinction risk, calculated both analytically (using the long run mean and variance and the cumulative normal probability distribution) and numerically ‘simulation extinction’ (from the observed probability of extinction within 250 years, repeated 500 times). An extinction threshold of 5 individuals was used in each case (either sex for the numerical rate and combined analytical rate, specifically male or female numbers for the other analytical rates). The mean population size is determined by the density dependent survival scaling parameter a , with the mean population size decreasing as a increases.

Demographic rate adjustment

Vital rate variances

The probability of extinction obtained from the model using the observed vital rate variances indicates that these values are likely to be overestimates of the actual variances (fig. 8). In the presence of demographic stochasticity the observed (i.e. unmodified) vital rate variances yield probabilities of population extinction within 250 years of 72-84%. Decreasing the variance in vital rates reduces the risk of extinction, although even with the variances set to 10% of their observed values extinction can still occur (without demographic stochasticity the risk of extinction is significantly reduced at all levels of variance adjustment, and falls immediately to zero when the variances are reduced below their observed values). It is thus evident that the variances need to be reduced prior to use in model simulations. To identify the appropriate amount by which to reduce the observed variances, the coefficients of variation (for all demographic rates) obtained from the field values were compared to those taken from simulations with incrementally adjusted variances, using a least squares method (fig. 9a: plot of coefficients of variation, fig 9b: least squares comparison of observed and adjusted coefficients of variation). The best-fit model corresponds to a reduction in the variances to 60% of their observed values. This adjustment was adopted in all subsequent simulations.

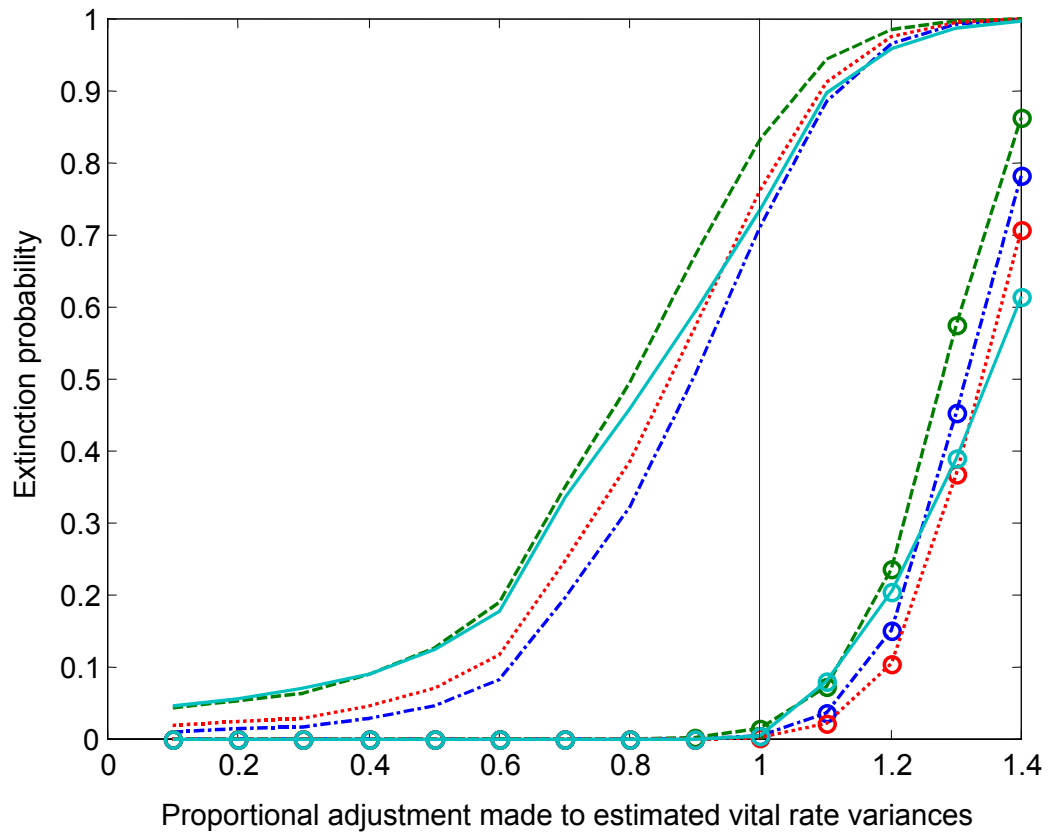


Figure 8. Sensitivity of extinction risk to estimated variance in vital rates. Extinction probability within 250 years plotted against proportional adjustment made to demographic rate variances. The vertical line at 1 indicates the results when no adjustment to the recorded demographic rate variances was made (actual rate coefficients of variation in range: 0.2-0.56). Lines with no markers were found with demographic stochasticity present, lines with circle markers with demographic stochasticity absent. The solid lines (—) are the simulation extinction rate, the dashed lines (--) are the female analytical extinction rate, the dotted lines (···) are the male analytical extinction rate and the dot-dash lines (._.) are the analytical extinction rate for both sexes combined.

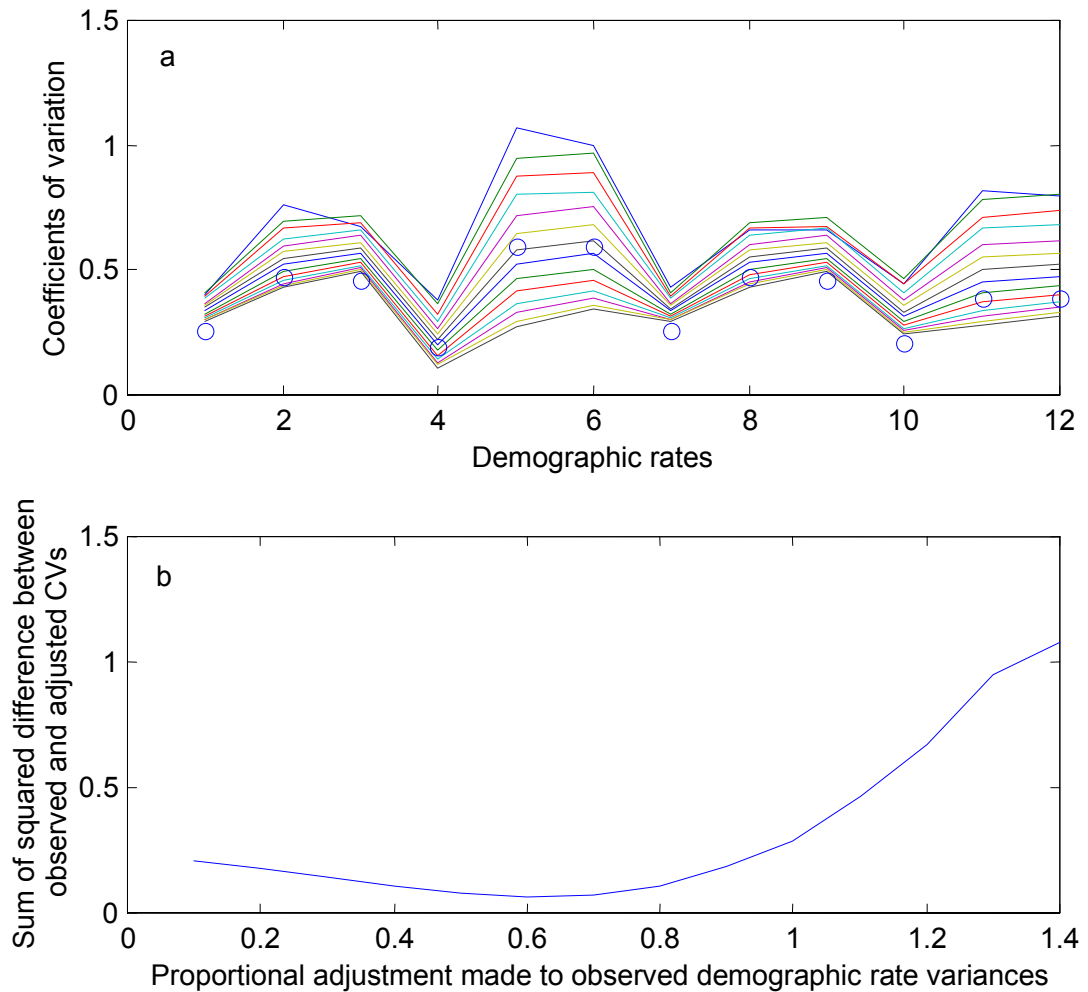


Fig. 9

(a) Coefficients of variation for each of the 12 demographic rates (1-3: Female survival, 4-6: female reproduction, 7-9: male survival, 10-12: male reproduction). Blue circles are the observed CVs from the study population. Each line represents the CV's from one of 14 simulations in which the input demographic rate variances were multiplied prior to simulation by 0.1 – 1.4 (increments of 0.1).

(b) Sum of squared difference between the observed CVs (blue circles in fig 9a) and the CVs obtained from each adjusted simulation (lines, fig 9a), summed across all demographic rates, plotted against the adjustment made to the rate variances. The least squares was obtained when the observed variances were multiplied by 0.6.

Vital rate means

If the observed mean survival rates are used unmodified in the model, all population projections become extinct within 250 years (fig. 10). In order to account for the implicit density dependence in the observed survival rates, simulations were conducted with the mean survival rates increased incrementally. These increases produce a rapid decline in the extinction probability, for example an increase of 20% in the mean survival rates reduces the extinction probability within 250 years from 1.0 to approximately 0.1 (fig. 10). Although further increases in the mean values bring further reductions in extinction, 20% was chosen as a conservative level of adjustment, and this was applied in all subsequent simulations.

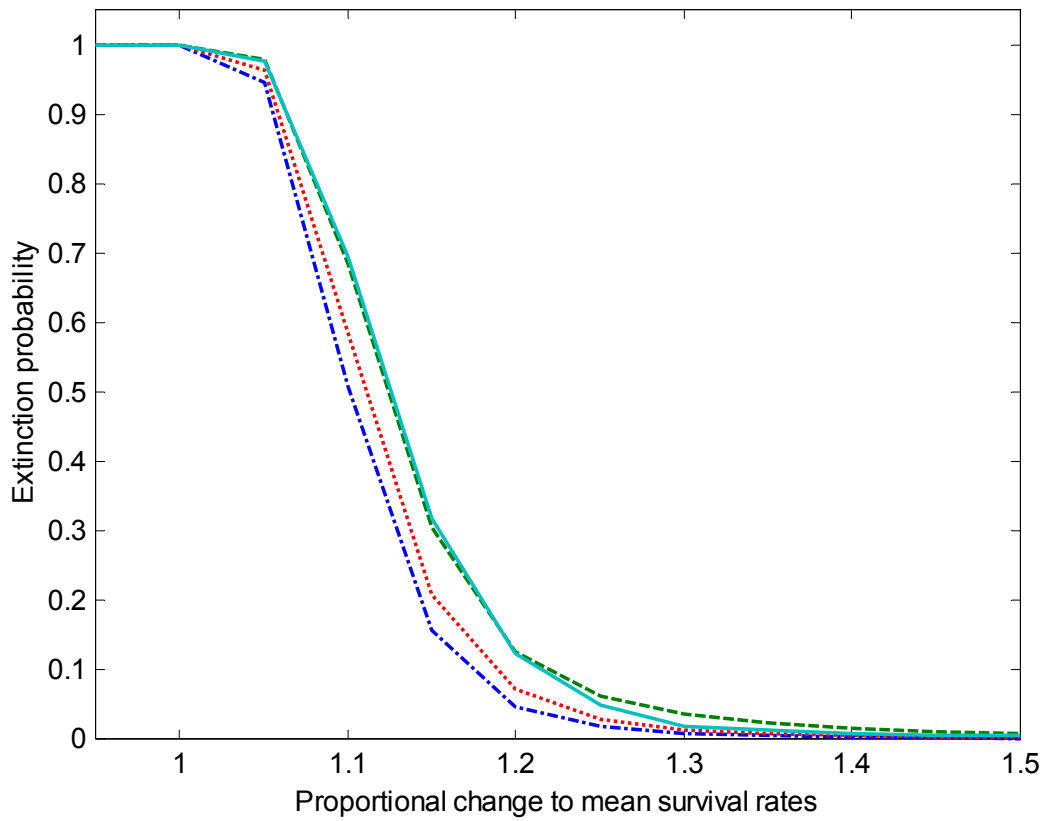


Figure 10. The change in extinction probability (simulation and analytical) against proportional increase made to observed mean survival rates prior to simulation. Simulations of 250 years, 500 repeats. Solid light blue line: simulated extinction; dashed green line: female analytical extinction; dotted red line: male analytical extinction; dash-dot dark blue line: combined analytical extinction.

Influence of stochasticity on population dynamics

An initial comparison of population trajectories produced with and without either demographic or environmental stochasticity does not suggest there are big differences in their population dynamics, since both types of stochasticity appear to be capable of producing large year to year variations (fig 11 simulation runs 2 and 3; see also table 2). However, in the absence of either form of stochasticity, the population size increases and the variance decreases. Demographic stochasticity can only be either on or off, but environmental stochasticity can be more finely controlled through adjustment of vital rate variances. As we have already seen, as the rate variances are reduced the extinction risk falls (fig. 8). However, even though the extinction rate can be reduced to very low levels by this means, as long as demographic stochasticity is operating the possibility of extinction remains.

The addition of a low level of covariance between vital rates has no discernible effect on the mean population size and variability and there is no difference in the extinction probability of model runs with and without co-varying vital rates (fig. 11, simulation run 4). Partial auto-correlation tests of populations projected with and without rate covariance exhibit similar lag structures. While this could be interpreted as evidence that vital rate covariance plays a minor role in wren population dynamics, as modelled here, and is an unnecessary extra complexity in the model, it is more likely that there is a low level of rate covariance present, rather than none at all. Thus the covariance routine was used in all subsequent simulation.

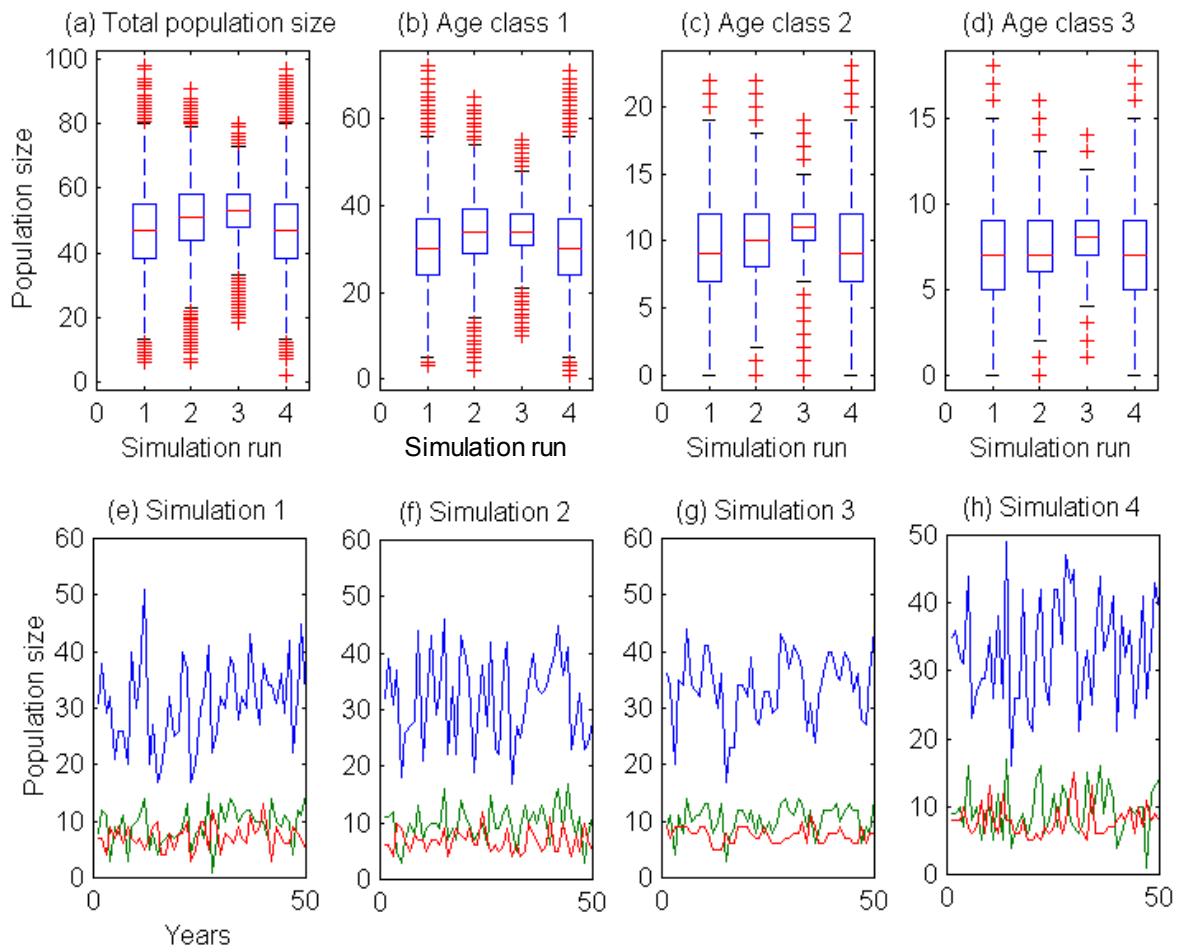


Fig 11. Model outputs under a range of stochastic settings. a-d are box plots of total population size and individual age classes for 4 different simulations. e-h are representative population projections for 4 different simulations, showing female age classes: 1 (blue lines), 2 (green lines), 3 (red lines). Run 1 = baseline (all stochastic routines on); run 2 = environmental stochasticity off, mean demographic rates used; run 3 = demographic stochasticity off, numbers of survivors and offspring found by rounding to nearest integer; run 4 = rate covariance off. Absence of either environmental or demographic stochasticity raises means and reduces variances. Comparison of runs 2 and 3 indicates that demographic stochasticity is the majority contributor to the modelled population variance. The low level of rate covariance employed has little impact on the population dynamics, backed up by non-significant PACF tests (not shown).

For tabulated data see table 2.

Table 2. Female population data for 4 different stochastic simulations, with both density dependent survival and breeding operating. Simulation runs: (1) full model, including environmental and demographic stochasticity and vital rate covariance; (2) environmental stochasticity off, mean demographic rates used throughout; (3) demographic stochasticity off (numbers of survivors and offspring found as product of individuals and vital rates, rounded to the nearest integer); (4) no within year covariance between vital rates. Absence of either environmental or demographic stochasticity raises the means and reduces variances. Comparison of runs 2 and 3 indicates that demographic stochasticity contributes the majority of the population variance under these model conditions. For graphical representation of this data see fig. 11.

	Simulation run			
	1	2	3	4

Total population				
Max	98	91	80	97
Uppr quartile	55	58	58	55
Median	47	51	53	47
Lwr quartile	38	44	48	38
Min	6	6	18	2
Mean	46.75	51.06	52.38	46.81
S.d.	12.69	10.48	7.71	12.92
s.e.	0.0005	0.0004	0.0003	0.0005

Age class 1				
Max	72	65	55	71
Uppr quartile	37	39	38	37
Median	30	34	34	30
Lwr quartile	24	29	31	24
Min	3	2	10	1
Mean	30.53	33.72	34.06	30.65
S.d.	9.23	7.71	5.62	9.48
s.e.	0.0003	0.0003	0.0002	0.0002

Age class 2				
Max	22	22	19	23
Uppr quartile	12	12	12	12
Median	9	10	11	9
Lwr quartile	7	8	10	7
Min	0	0	0	0
Mean	9.06	10.05	10.78	9.04
S.d.	3.59	2.98	2.33	3.61
s.e.	0.0001	0.0001	0.00009	0.0001

Age class 3				
Max	18	16	14	18
Uppr quartile	9	9	9	9
Median	7	7	8	7
Lwr quartile	5	6	7	5
Min	0	0	1	0
Mean	7.16	7.29	7.54	7.12
S.d.	2.51	2.09	1.52	2.39
s.e.	0.0001	0.00008	0.00006	0.0001

Density dependence

Baseline population dynamics

The influence of the two density dependent regulators, density dependent survival and breeding territory limitation, on model population dynamics depends on their relative strengths. For example, there is little difference in the population dynamics of simulations run with either limited or unlimited numbers of territories, when density dependent survival parameters a and b equal 0.0025 and 4 respectively (fig 12 simulations 1 and 3; table 3). In this case density dependent survival is exerting a greater degree of regulation than territory limitation. Further evidence for this is obtained when survival rates are unaffected by density (simulation 2) and all the population size increases to a level determined by the availability of territories. When density dependent survival is applied only to the first survival transition (fig 12, simulation 4), the second age class declines (the age group immediately following the density regulated transition), the oldest age class increases (containing all individuals aged 2 years and older) and the youngest age group increases slightly since overall there is a greater breeding population.

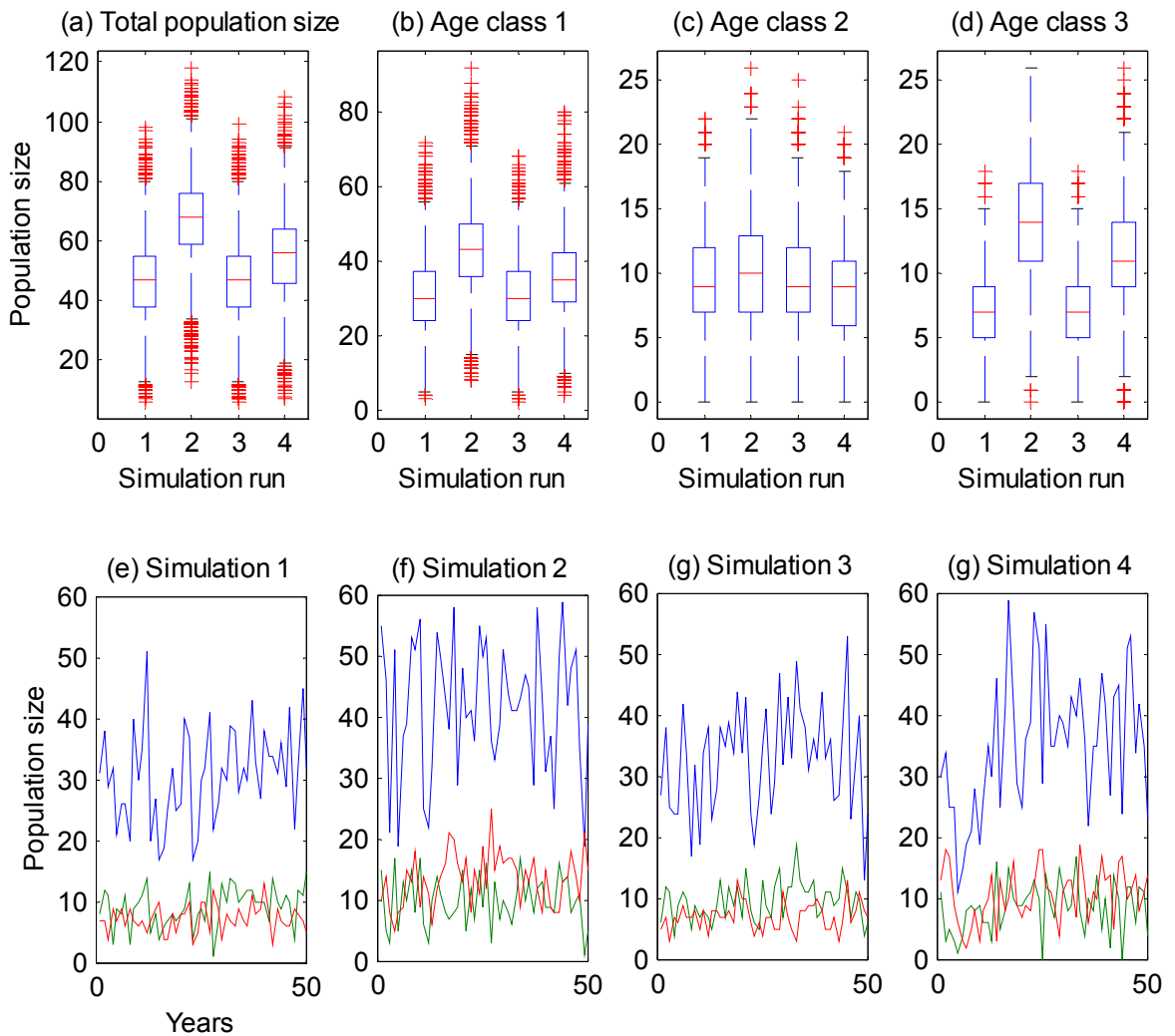


Fig 12. Model output under a range of density dependent settings. a-d, box plots of total population size and individual age classes for 4 different simulations. e-h, representative population projections for the 4 different simulations, showing female age classes: 1 (blue lines), 2 (green lines), 3 (red lines). Run 1 = baseline (density dependent survival and territory limit operating), run 2 = survival of all age classes unregulated by population density, run 3 = unrestricted number of breeding territories, run 4 = density dependent survival for juveniles only, adult survival unaffected by population density. With the level of density dependent survival at an intermediate value and a mean limit to the number of territories of 25, runs 1-3 demonstrate that the survival function is exercising the main population regulation. Run 4 indicates that approximately half of this is due to regulation of adult survival. For tabulated data see table 3.

Table 3. Population data for females derived from 4 different density dependent simulations (with environmental and demographic stochasticity and vital rate covariance operating). Simulation runs: (1) full model, including density dependent survival and breeding territory regulation; (2) density independent survival for all age classes, only breeding territory operating; (3) unrestricted number of breeding territories, only density dependent survival operating; (4) density dependent survival for juveniles only, adult survival unaffected by population density. With an intermediate strength of density dependent survival and a mean limit to the number of territories of 25, runs 1-3 demonstrate that the survival function is the main population regulator. Run 4 indicates that approximately half of this is due to regulation of adult survival. For graphical representation of this data see fig. 12

	Simulation run			
	1	2	3	4

Total population				
Max	98	118	99	108
Uppr quartile	55	76	55	64
Median	47	68	47	56
Lwr quartile	38	59	38	46
Min	6	13	6	7
Mean	46.76	67.43	46.83	55.24
S.d.	12.68	12.82	12.71	13.06
s.e.	0.0005	0.0005	0.0005	0.0005

Age class 1				
Max	72	92	68	80
Uppr quartile	37	50	37	42
Median	30	43	30	35
Lwr quartile	24	36	24	29
Min	3	8	2	4
Mean	30.53	43.43	30.56	35.53
S.d.	9.22	10.66	9.21	9.75
s.e.	0.0003	0.0004	0.0003	0.0004

Age class 2				
Max	22	26	25	21
Uppr quartile	12	13	12	11
Median	9	10	9	9
Lwr quartile	7	7	7	6
Min	0	0	0	0
Mean	9.07	10.08	9.10	8.30
S.d.	3.59	4.27	3.62	3.70
s.e.	0.0001	0.0001	0.0001	0.0001

Age class 3				
Max	18	26	18	26
Uppr quartile	9	17	9	14
Median	7	14	7	11
Lwr quartile	5	11	5	9
Min	0	0	0	0
Mean	7.16	13.92	7.16	11.42
S.d.	2.51	3.82	2.51	3.75
s.e.	0.0001	0.0001	0.0001	0.0001

Influence of parameter a on extinction risk

The scaling parameter a determines the threshold population size at which the reduction in density dependent survival (for a given value of parameter b) reaches a fixed value. Raising a lowers the threshold and so increases the extinction probability (fig 13a). The extinction risk increases through decreased survival rates, which reduce the mean population size, leading to a greater likelihood of population decline below a threshold level. The rate of increase of extinction risk with increasing a and the level of risk at any particular value of a depends also on other model settings.

Influence of parameter b on extinction risk and population dynamics

Parameter b determines the severity of the density dependent reduction in survival. The relationship between extinction risk and the magnitude of parameter b is not as straightforward as that for parameter a (fig. 13b). Although it is highly unlikely that values of b in the wild will reach the higher values shown, they are included here in order to confirm the fact that extinction risk is at its lowest when b is at an intermediate level and rises with either an increase or decrease. It also serves to illustrate the contrast between the symmetrical pattern of extinction risk seen at intermediate and high values of parameter a , with that when a is low, or density dependent survival is applied to juveniles only.

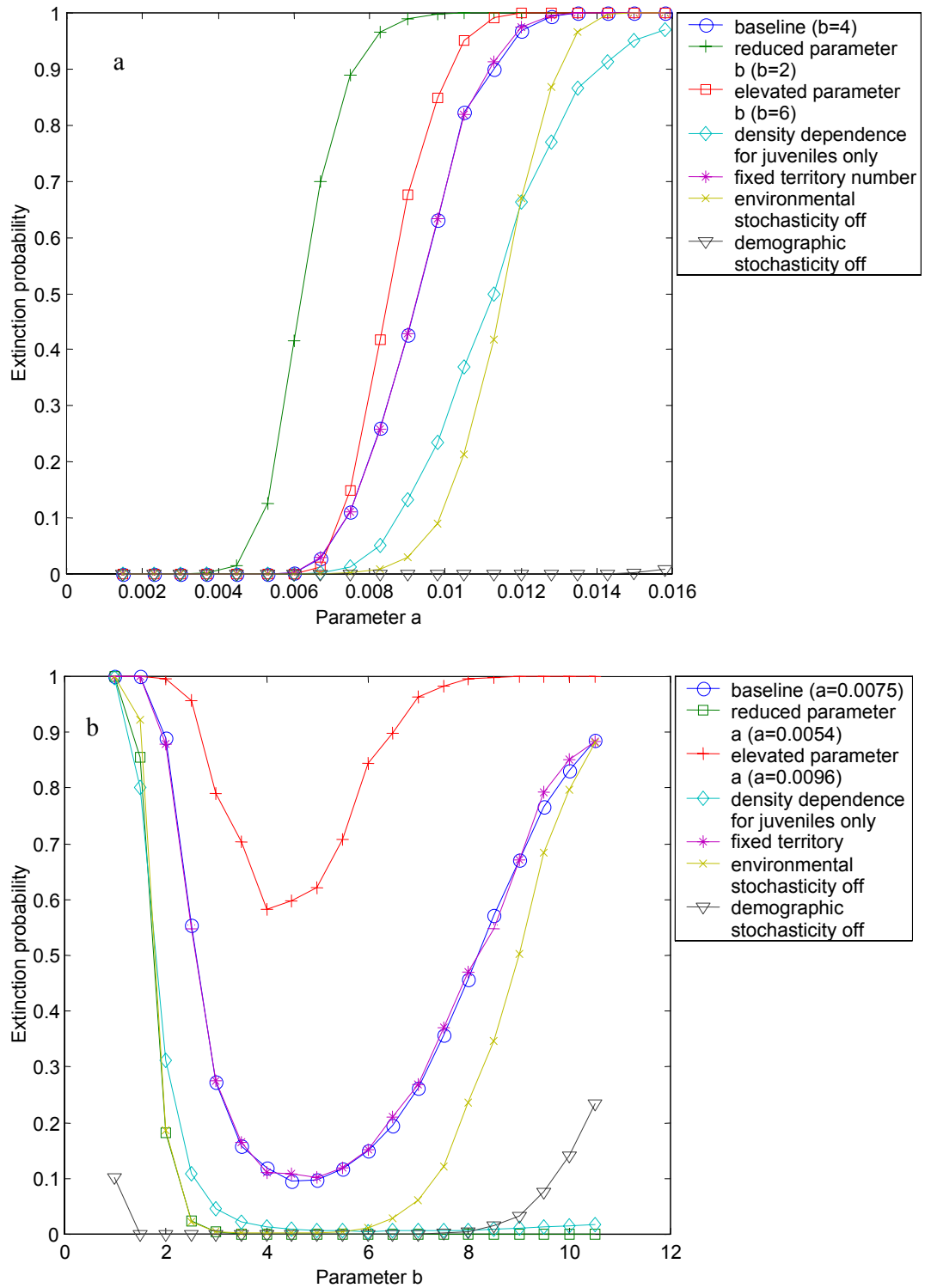


Fig. 13. Influence of (a) parameter a (scaling constant) and (b) parameter b (strength of density dependence) on extinction risk calculated using female data. At any particular level of either parameter the extinction probability is also determined by the value of the other density dependent parameter, as well as the stochastic settings (environmental/demographic only) and whether density dependent survival is applied to all equally to all age classes or only to juveniles.

Further insight into the operation of parameter b can be gained from examination of deterministic model behaviour. Figures 14a-c display bifurcation plots of the deterministic total population size against changing levels of parameter b , at three values of parameter a . At low levels of a (fig. 14a) the population maintains a stable equilibrium across all levels of b presented here, but at intermediate (fig 14b) and high (fig 14c) levels of a , increasing b leads first to two-point cycles, followed by four-point cycles and then increasingly complex periodic patterns. These changes occur as the density dependent regulation moves from compensatory, to increasingly over-compensatory. At intermediate values of a the territory limit also plays a role in the dynamics at values of b exceeding 8. Breeding regulation prevents the population from achieving the maximum which density dependent survival alone would permit. Thus the worst extremes of over compensatory density dependence are avoided (and a three point cycle ensues). This is not seen at the higher level of a as the population is maintained below a level at which the territory limit becomes important.

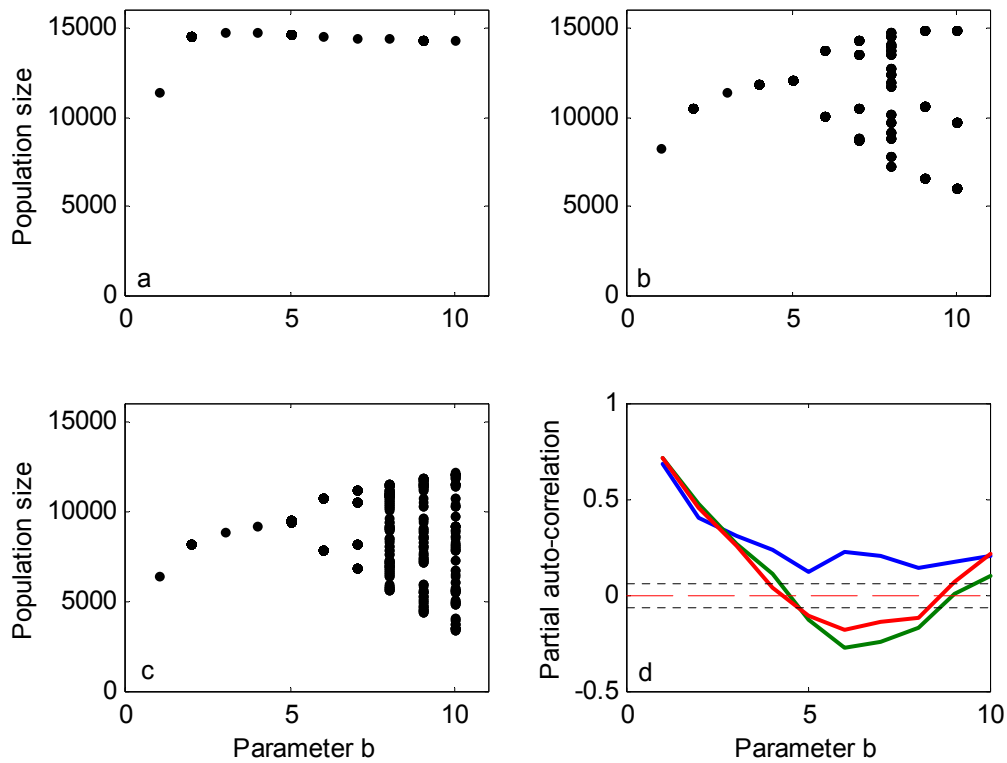


Figure 14. Panels a-c are bifurcation plots of the deterministic total population size against increasing parameter b (strength of density dependence) at different levels of density dependent scaling parameter a : (a) low parameter a ($=0.0054$); (b) intermediate parameter a ($=0.0075$); and (c) high parameter a ($=0.0096$). Panel (d) shows the values of the first order partial auto-correlation coefficients of the logged total population size against parameter b . Data from stochastic simulations of 10000 time steps. Dashed (blue) line: low parameter a ; solid (green) line: intermediate parameter a ; dotted (red) line: high parameter a . The horizontal lines are at 0 and the approx. 95% confidence intervals.

It is not possible to detect such clear patterns in the presence of stochasticity, however analysis of model time series using a partial auto-correlation function of the logged total population size provides evidence of the action of parameter b for stochastic populations. When a is at intermediate to high levels, the first order partial auto-correlation values (only first order correlations were significant) show a trend from significantly positive to significantly negative as increasing values of b shift the population from stability to instability ($b = 1$ to 7). This indicates a change in the density dependence from compensatory to over-compensatory. As b continues to rise the strongly negative auto-correlations, which might be expected, become diluted by the positive ones occurring during the periods of population growth following crashes.

There is also evidence that density dependence and stochasticity are interacting in their influence on the population dynamics, as has been demonstrated previously (Higgins et al, 1997; Leirs et al, 1997; Grenfell et al, 1998; Coulson et al., 2001). The first significantly negative PAC values (implying over-compensatory dynamics) occur under stochastic conditions when $b = 5$, but when there is no environmental noise the transition to fluctuating population dynamics occurs when $b > 5$. Similarly, the extinction probability at high levels of a (fig 13b), is lowest when $b = 4$, indicating the population size is both at its highest and least variable. However, the deterministic population reaches its stable maximum when $b = 5$ (fig. 14c). Thus there is evidence that noise induced oscillations are being maintained in the population dynamics at a strength of density dependence which, in the absence of noise, produces a stable equilibrium. In other words, population cycles induced by over-compensatory density dependence occur at a lower absolute strength of density dependence in the presence of environmental noise. Greenman and Benton (2003) have demonstrated that this

effect is a feature of the dynamics of structured population model outputs when they are close to a threshold from stability to instability.

Influence of territory number on extinction risk

Fig. 15 illustrates the poor match between the analytical and simulation estimates of extinction risk when population regulation occurs solely through breeding territory restriction. This contrasts with the close match between the simulation and female analytical estimates when density dependent survival is the sole or dominant regulator (fig. 7). This is due to a reduction in the size of the population variance when the number of territories is reduced, compared to that observed when the threshold for density dependent survival is decreased (i.e. by increasing scaling parameter a). This can be illustrated if we consider two populations fluctuating around the same mean size, the first regulated by the number of breeding territories, the second by density dependent survival. In the first case the maximum reproductive output will be lower than that possible in the second, since the breeding limit acts to cap the maximum number of offspring produced. Thus, restricted breeding reduces the variation in the size of age class one, and thus also the total population variance as most of the overall variance is accounted for by the first age class. Since the population variance is a determinant of the analytical extinction probability this causes the observed difference between the analytical and simulation extinction risk. In contrast, when territories are unlimited and the population size is regulated by density dependent survival, the average survival of all age classes is lower than before, and consequently in most years the level of reproduction is similar to the first case. However, because there are now surplus territories available, years of higher reproduction can occur when, by chance, survival is high leading to an overall larger population variance (fig. 16).

This leads to a closer match between the analytical rate and the simulation extinction rate when density dependent survival is the chief population regulator. It is also of note that the extinction rates are lower for any given population size when the dominant regulator is territory number rather than density dependent survival, regardless of the method of calculation (simulation or analytical). This is due to density dependent survival reducing all age classes, whereas the effects of limited territory numbers are more concentrated in age class one.

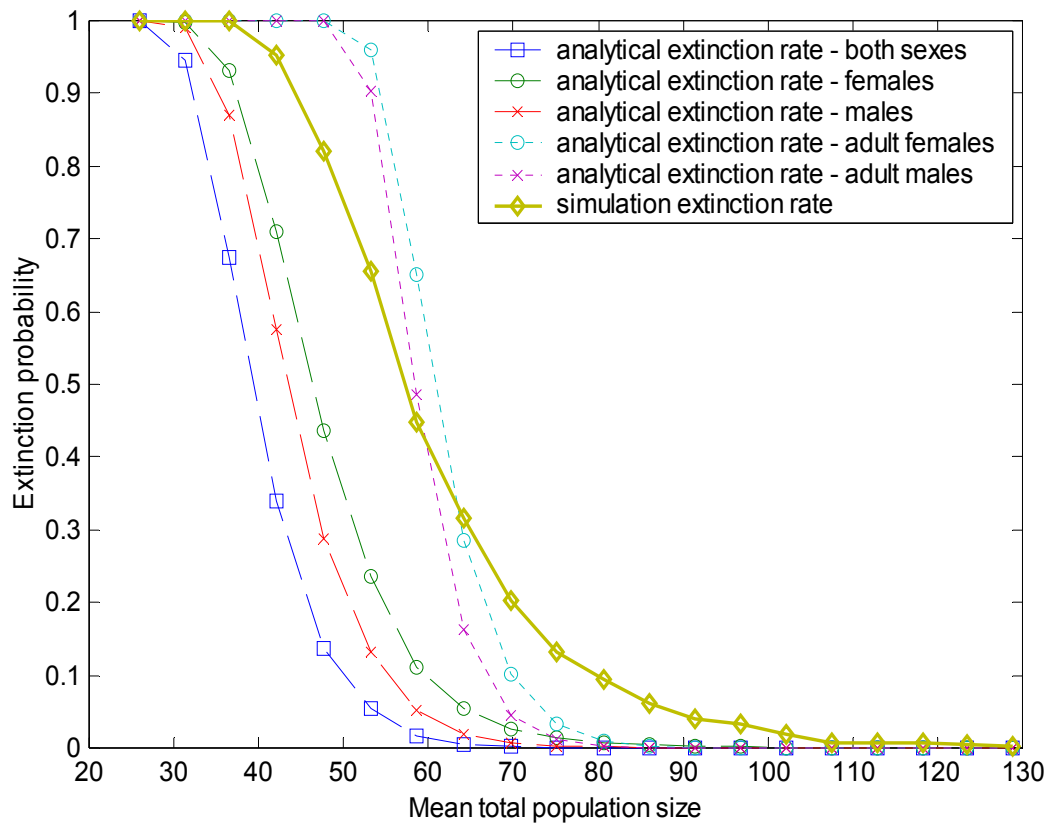


Fig. 15. The effects of mean population size on extinction probability, with the population size regulated by reduced territory availability. Extinction estimated using a quasi extinction threshold of 5 individuals. Error bars for the plotted lines are omitted for clarity, but in all cases are comparable in size, or smaller than, the points symbols used. The simulation extinction rate is the percentage of population simulations which fall below the extinction threshold. The analytical rates are found from the cumulative normal distribution specified by the long term population mean and variance, using the total population or subsets (all males, all females, adult males, adult females). The differences between the analytical rates for each category of the population indicate contrasts between the subclasses in their means and variances.

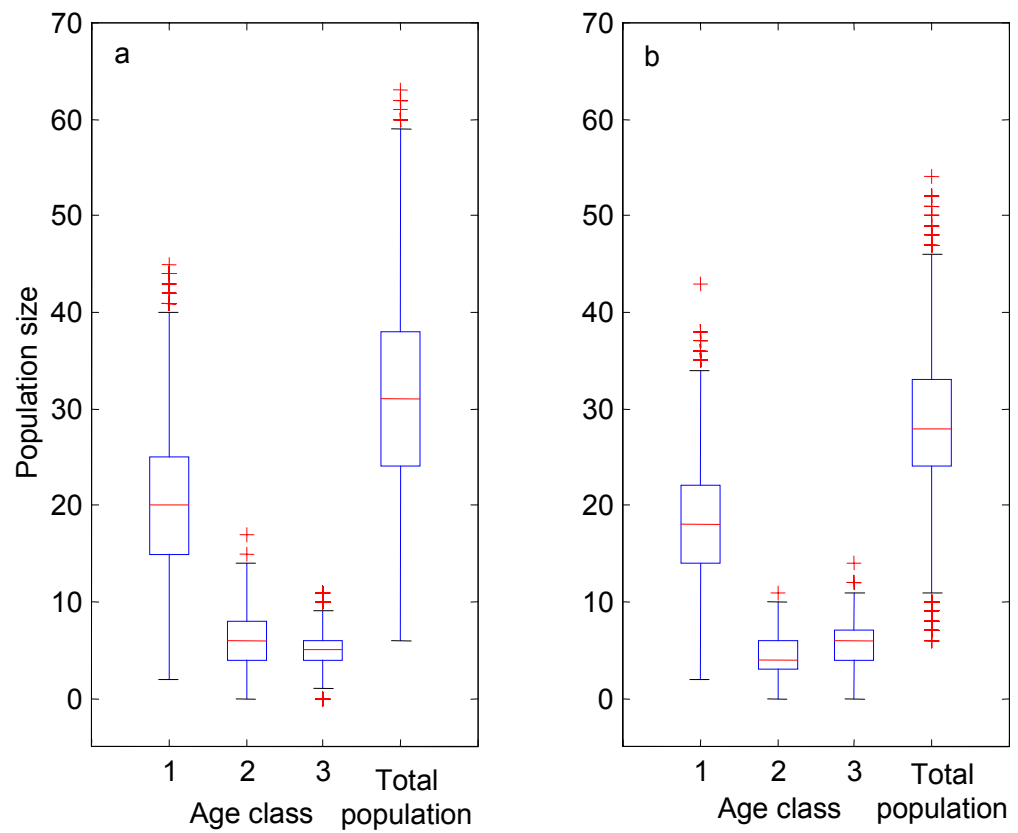


Fig. 16. Comparison of population variation within each age class of females and for the total female population, when the population is regulated by (a) density dependence in survival, and (b) limited availability of territories. The mean total population sizes are comparable for the two data sets: (a) 30.9; (b) 28.2, but when density dependent survival is the population regulator the upper limit of the variance is greater than when territories are restricted, thus the equivalent total population variances are: (a) 9.6 and (b) 7.0.

4.4 Discussion

Models produced for wildlife management can be viewed in one of two ways: as ‘true’ representations of a particular system, or as problem solving tools to address specific questions (Starfield, 1997). It might be considered that the model described here is an example of the former, due to the detailed approach taken to simulating the wren life-cycle. Viewed from this perspective a model will often be found wanting since it will inevitably be a compromise between capturing the complexities of a natural system and the need to produce a manageable model. However, I would argue that this model is a problem solving tool, and the questions to be addressed (are stochasticity and density dependence important for population models? how critical is it to investigate them together?) are the reason the life-cycle is treated in such detail. This led to the production of a model which could be run under a range of possible density dependent and stochastic scenarios.

Wrens were chosen for this study because previous work has found both considerable variation in their demographic rates between years, and evidence for density dependent population regulation. Wrens are amongst the species of passerine in the UK which are most affected by severe weather during the winter (Armstrong, 1955). Over winter survival rates vary extremely widely between years in response to cold temperatures and snowfall (Peach, et al, 1995). Less is known about variation in breeding performance between years, but there was a noticeable difference in nesting success in two consecutive years of this study and it seems reasonable to suppose that this is not unusual. While there are plenty of anecdotal reports of wren numbers dwindling after occasional extremely harsh winters (i.e. 1962-3), there are none which claim wren numbers of excessive proportions following sequences of favourable winters. So, what

prevents wren population explosions? It is apparent from the range of variability in survival, and the ability of wren populations to recover from severe reductions, that there must be regulatory mechanisms which keep populations in check. Williamson (1969) monitored the expansion of wren populations over several years in England in the aftermath of the severe winter of 1962-3. He noted that as the population recovered from the low level caused by the high mortality rate experienced in that winter, the most favourable breeding habitats were occupied first (e.g. woodland) and that in subsequent years, with the best sites already taken, less productive habitats became increasingly re-colonised (e.g. hedgerows, gardens, etc.). These observations are in line with the observations made for other passerine populations (Brown, 1969; Krebs, 1971) which led to the formulation of the 'buffer theory' for population regulation through breeding (Brown, 1969). This theory proposes that for species which maintain breeding territories the population's overall reproductive output will decline in stages as the population size increases. During the first stage, when there are more territories in the best quality habitat than breeding individuals, reproduction increases in line with the population. When all the best habitat has been filled the remaining individuals of breeding age are forced to occupy lower quality sites and consequently contribute less to the overall reproduction in the population, which subsequently increases at a decreasing rate. At some further point of population increase there are no more locally available territories remaining, at which time any excess individuals either emigrate or become non-breeding 'floaters'. By this mechanism reproduction is limited and population regulation occurs. However, with a species that maintains a degree of territoriality throughout the year, such as the wren, this also presents a means by which the population density may influence survival. It is not unreasonable to suppose that a territory which is better for reproductive success is also one which has better resources for winter survival. Space limitations may simultaneously regulated both

reproduction and survival. Thus we have a basis to state that modelling wren population dynamics with a density independent, deterministic matrix model is *a priori* inappropriate. Since we have no information detailing how reproduction might decline with territory quality the model makes the simplifying assumption that the whole study site is of equal quality and once all territories are filled excess individuals are treated as emigrants.

Environmental stochasticity is relatively straightforward to model, and is achieved by simply using the observed variation in vital rates. However, there is a need to decompose this variance to account for that imposed by the environment and that due to chance demographic factors (Saether et al, 2002). An approximation of this process was performed using the model itself, and this highlights the adaptive nature of the modelling approach employed here. Detecting and measuring the effects of population density in wild populations is notoriously difficult, but for wrens there is evidence that both breeding (Wesolowski, 1983), and survival (Greenwood and Baillie, 1991; Peach et al, 1995; Newton et al, 1998) are regulated by density. Two of the studies comprised over 20 years of continuous population monitoring (Greenwood and Baillie, 1991; Newton et. al, 1998), yet the authors do not present any information about the form of the density dependent survival response. It is not clear whether this was due to limitations in the data or if it was simply not investigated. However, in combination with the lack of sufficient data from this study (a feature shared with many population studies), this meant it was not possible to parameterise the response of the vital rates to the population density. One of two courses of action can be taken when workers are faced with this difficulty, either assume density dependence plays a sufficiently minor role that its absence from a population model will not be critical (e.g. Cuthbert et al, 2001; Weiglus et al, 2001), or use the available information and apply density dependence to vital rates using a realistic, and flexible,

approximation of its form (e.g. Saether et al, 2000). As we have shown here this latter, pragmatic approach led to the incorporation of density dependent routines which can produce a range of population dynamics. This greatly enhanced the likelihood of identifying the appropriate density dependent response, while also permitting the potential consequences of misidentification to be tested.

Through adjustment of the density dependent control parameters we have shown how the strength of density dependent survival plays a key role in determining the frequency and amplitude of population fluctuations, which in turn are critical factors in determining extinction probabilities. In the absence of stochasticity, regular population fluctuations only occur when the strength of the density dependence operating on survival is high. But with the same strength of density dependence in the presence of stochasticity, the moderately high levels of extinction risk experienced by the population suggest this probably overestimates its natural level. This is an example of environmental noise acting to amplify the deterministic population fluctuations, as described by Greenman and Benton (2003), and this may have important implications for estimating extinction probabilities. If adding environmental noise to a deterministic, density dependent model with stable dynamics can induce instability, intuitively it follows that adding density dependence to a stochastic model will also enhance the amplitude of population fluctuations, leading to an elevated extinction probability. This has implications for applications of PVA which omit density dependent regulation (e.g. Wielgus et al. 2001; Brook et al, 2000).

There is growing evidence that stochastic and density dependent processes interact to produce observed population dynamics (Higgins et al, 1997; Leirs et al, 1997; Grenfell et al, 1998;

Coulson et al, 2001), and it is becoming increasingly apparent that for a full appreciation of population fluctuations it is necessary to analyse them in combination (Saether, 1997; Milner et al, 1999). There are indications that wren survival during the winter conforms to this pattern, with both this study and two previous ones (Peach et al, 1995; Newton et al, 1998) finding greater support for density dependent survival when winter weather variables were included in analyses. It appears therefore that this system is an example of one in which linear and non-linear effects combine to produce observed population dynamics which are greater than the sum of their parts. Using either a stochastic model or a density dependent one in isolation will fail to capture the full range of dynamics displayed by the combined model. The model described here was developed primarily with elasticity analysis in mind, rather than as a form of PVA, however there are some important features of this model which apply to investigations of extinction risk. PVA models are designed to provide information about population persistence. While absolute estimates of extinction risk are highly sensitive to parameter values (Ludwig, 1999) and should therefore be treated with a large degree of caution (Beissinger and Westphal, 1998), comparison of the change in relative extinction probability obtained under alternative management regimes can provide useful guidance for management (Reed et al, 2001). If such comparisons are to be made, the results presented here indicate that models which lack any, or all, of density dependence, environmental stochasticity and demographic stochasticity, may fail to provide a sufficient degree of accuracy for their outputs to be useful. Since extinction is a chance event, environmental and demographic stochasticity obviously play central roles. What is striking however, is their relative importance for a small population, as modelled here. Either form of stochasticity in isolation can produce population fluctuations of a broadly similar nature to those seen when both are operating together (fig. 11). Yet the probabilities of extinction obtained when either is absent are much lower than when both are

present (fig. 13b). This is particularly evident in the absence of demographic stochasticity. While acknowledgement of demographic stochasticity's influence on extinction rates is not new (e.g. Soule, 1987), it is still not universally incorporated into models of small and endangered populations (e.g. Reed et al, 1998; Cuthbert et al, 2001; Gerber and VanBlaricom, 2001; Wielgus et al, 2001). By failing to include demographic stochasticity these analyses run a very real risk of underestimating the likelihood of population decline and extinction. While it is possible that comparisons of relative extinction risk may retain the same relationships with or without demographic stochasticity, its incorporation into a population model requires a trivial amount of additional programming. Thus, compared to the effort employed in obtaining demographic rates in the first place, its inclusion should be standard for all models of small populations.

Restrictions on space also are an important part of wren population dynamics, since possession of a breeding territory is essential for reproduction. If the availability of territories in the model is limited, we obtain deterministic population cycles of a simple nature even when overcompensation is strong, whereas with unlimited territories the dynamics become extremely complex. The territory restriction controls the population by preventing numbers from reaching the extreme peaks they would otherwise, which in turn limits the severity of population crashes. This stabilising effect is likely to be retained in the presence of stochasticity, and therefore density dependent survival and territory limitation probably act together in their effects on the population dynamics. Population regulation through the availability of breeding sites is probably an important factor for many species of bird, and possibly also for other species which congregate to breed (e.g. pinniped breeding colonies). For example, modelling of red-cockaded woodpecker populations by Heppell et al (1994) suggested that one of the

largest restrictions on population growth was limited numbers of nest cavities, and subsequent experiments have shown how provision of extra cavities can help population recovery (Walters et al, 2002).

It might be argued that density dependent regulation will play a secondary role to environmental variation in regulating the numbers of a species such as the wren, since they appear to be so prone to harsh conditions. However, the result of reducing the strength of over-compensatory density dependence is to increase the likelihood of population extinction. This is due to the relationship between density dependent survival and extinction probability being bimodal, with a minimum extinction risk at intermediate strengths of density dependence ($b = 4$) and peaks to either side. Thus, the fact that extinction risk is minimised at medium strengths of density dependent survival rather than low levels, is further support for the role density dependent survival plays in this system. While it is quite likely that we will never know exactly how density dependent survival operates for the wrens in the study population, through exploration of regulatory mechanisms in a flexible modelling framework we have been able to identify its probable characteristics. We can't discount the possibility that individual wren populations do undergo frequent extinction and recolonisation events, but it is more likely that density dependence operates in real populations in a similar manner to that described here.

The work here is an example of the type of model that can be produced using a limited dataset. Many of the short-comings commonly seen with data for rare species (short duration, missing years, etc.) are shared by this study, limitations which can be used to justify the omission of density dependence and stochasticity from population models. For such reasons the inclusion of these features into matrix models specifically developed to assist the management of rare

populations is still uncommon. This, in spite of general acknowledgement that environmental variation, chance events and density dependent regulation are key components of natural population processes. While there is evidence for the presence of density dependence in the study population we have little information as to how it operates – in common with most species. By making sensible inferences, guided by the biology of the study population, we have demonstrated here that this need not be a hindrance to successful model development.

Chapter 5

Elasticity analysis of density dependent, stochastic model

5.1 Introduction

Sensitivity analysis is a generic term which describes a range of techniques used in many different disciplines to analyse the relationship between a model's structure and its outputs. In the context of a traditional, deterministic, linear matrix population model, the output is λ , the population growth rate, and the structure is derived from a species demographic rates (survival, growth and fecundity). Sensitivity analysis apportions the contribution of each of the demographic rates to the rate of population growth (Caswell, 1978). Proportional sensitivity analysis (elasticity analysis) was introduced by Caswell et al. (1984), and developed by de Kroon et al. (1986). The use of elasticity analysis for the study of wild populations has become very popular, particularly for species of conservation concern (Heppell et al, 2000; Benton and Grant, 1999). The reasons are obvious if we imagine a common scenario. A species' numbers are in decline and a conservation body wishes to reverse this trend. Mean demographic data for the species are entered into a matrix, and after a few simple calculations estimates of λ and the elasticities of λ can be obtained. The demographic rates with the largest corresponding elasticities are those which contribute most to λ . Thus, the most effective management, either in terms of cost or the biggest increase in λ , can be identified.

Typically, sensitivities and elasticities are calculated analytically from a population matrix containing a species' average vital rates. Both forms of analysis estimate the change in λ resulting from a change in one vital rate (all others held constant) and thus ranking vital rates by their contribution to λ is possible. The difference between the two techniques is in the form of change made to the vital rates: for sensitivity analysis the

changes are absolute, while for elasticity analysis the changes are proportional. The analytical method for calculating sensitivities can lead to the estimation of values for entries in the population matrix with a value of 0. These may be transitions which do not currently occur but, under different circumstances could (e.g. precocious maturation), or they may be biologically impossible (e.g. reversion from adult to juvenile). Despite debate about the value of such results (Mesterton-Gibbons, 2000; Caswell et al., 2000) they may provide insights into alternative life history strategies, and indicate transitions (e.g. early maturity) which might occur if extra resources became available (Benton and Grant, 2000). Elasticities avoid such issues, since a proportional change in a demographic rate with a zero value remains zero.

Elasticity analysis is a predictive (or prospective: Caswell, 1989) technique which estimates the change expected in λ resulting from a proportional change in a vital rate. All else being equal, changing the matrix element with the largest corresponding elasticity value will produce the greatest change in λ . This correspondence between demographic rates and population growth, and the relative ease of calculation and interpretation, has led to the popularity of elasticity analysis in conservation management. However, there are some important questions concerning the general applicability of elasticity analysis to population management. Central to the technique is the concept of population growth, since analytical elasticities are a measure of how the rate of population growth will change as a result of proportional change in each matrix element. However, populations in the real world are constrained by resources and rarely, if ever, exhibit unrestricted growth. We need to know how well analytical

elasticities, calculated with reference to λ , perform for populations constrained by density dependence. In addition to intrinsic controls on population dynamics, environmental variation causes demographic rates to change over time. While Benton and Grant (1996) have shown that the elasticities derived from density independent models with small to moderate stochastic variation in vital rates are typically not significantly different from those obtained for λ , if data are available on the variation in demographic rates it is clearly sensible to employ it.

Examples of elasticity analysis

The following section briefly describes a few of the published examples (listed in table 1) of elasticity analysis of matrix models, covering a range of model formulations and levels of complexity, from simple, deterministic, linear models to simulations incorporating stochasticity or density dependence or, occasionally, both. This list is not exhaustive, but represents the type of studies typically conducted in order to gain an understanding of the cause(s) of a particular species' decline, and thereby assist in the identification of methods to reverse such trends. Although 12 of the 16 studies incorporated stochasticity into their elasticity analysis, all but two calculated elasticities of λ , albeit in some cases a range of the possible values which λ might take. The exceptions were Cuthbert et al. (2001, example 8), who calculated the elasticities of the stochastic equivalent of λ , and Yearsley et al. (2003, example 16) who calculated the elasticities of the deterministic equilibrium population size. In the majority of the remaining, stochastic elasticity examples, a form of regression analysis was used,

following broadly similar methods to those described by Wisdom and Mills (1997; example 14). Typically this involved the repeated generation of a complete set of random vital rates, calculation of λ for each set, and subsequent regression of the vital rate values against their associated λ value, to identify how change in each of the vital rates affected the value of λ obtained. Such analyses are an improvement over a deterministic elasticity assessment based on a single set of mean vital rates since they incorporate environmental variation, but they still take no account of population regulation through density dependent processes. To address this issue, two of the studies claim to calculate deterministic, density dependent elasticities. However, in the first of these, Escos et al. (1994, example 2) in fact calculate a selection of elasticities of λ . The only difference between their approach and an elasticity analysis using mean vital rates is that, prior to each set of elasticity calculations the fecundity rates were adjusted across a range of (fixed) values derived using a density dependent parameter. Thus, despite the inclusion of a feedback process which would promote population regulation (and an expected long term mean λ value ≈ 1), the elasticities were calculated from time-invariant matrices with reference to an (effectively) density independent value of λ . In the second case, Yearsley et al (2003, example 16) used the characteristic equations of the deterministic model developed by Hunter et al, (2000, example 15) to calculate density dependent, analytical elasticities of the equilibrium population size (N_e). Based on their findings they conclude that the results of a density dependent elasticity analysis, evaluated at N_e , are directly proportional to those derived from a density independent analysis (i.e. the elasticities of λ), a result supported by the work of Takada and Nakashizuka (1996) and Caswell (2001). This prompted Yearsley et al

(2003) to suggest that the inclusion of density dependence is therefore not critical for a successful elasticity analysis. However, Grant and Benton (2000) used a numerical elasticity technique applied to simulation models of simplified density dependent life histories to demonstrate that this equivalence can break down when populations experience non-equilibrium, density dependent dynamics or if the density dependence is determined not by the total population size, but from a subset of the population.

Interactions between density dependence and stochasticity

Since it has recently been demonstrated that environmental variation and density dependence can interact in their effects on population dynamics (Higgins et. al, 1997; Grenfell et. al, 1998; Leirs et. al, 1997; Coulson et al, 2001; Milner, 1999) elasticities calculated either for λ , or for its density independent stochastic equivalent, or for equilibrium density dependent models may all omit vital parts of natural population processes. To investigate the likelihood of conservation actions being based on potentially misleading results, elasticity analysis needs to be performed using models which incorporate both environmental stochasticity and density dependence, so that an understanding can be developed of when to expect the equivalence of elasticity techniques to break down.

Grant and Benton (2000; 2003) have shown how the elasticities of λ can differ from those for density dependent, non-equilibrium (deterministic and stochastic) populations using both generic models and ones parameterised using data from laboratory populations. However, there is an urgent need to extend these results to models of

populations in natural systems. The central questions are: can the inclusion of ubiquitous features of natural systems alter the results of a traditional elasticity analysis sufficiently that management recommendations based on their results are misleading? And can we calculate elasticities using metrics other than λ , which are more appropriate to the goals of population management?

This chapter will present the elasticities of λ , its stochastic density independent equivalent (α), and its density dependent equivalent (Θ). This last measure will also be applied to stochastic, density dependent situations, as will two further elasticity methods which are based on alternative population measures (mean population size, extinction risk). All the elasticities will be calculated using a model based on a wild population of wrens (*Troglodytes troglodytes*), and the results compared. Two of the density dependent, stochastic methods used here have been demonstrated previously (Grant, 1997; Grant and Benton, 2000; Grant and Benton, 2003). The first calculates elasticities of fitness (the density dependent equivalent of the elasticities of λ) by estimation of an invasion exponent (Θ) and are known as invasion elasticities. The second calculates elasticities of the mean population size. A third method, introduced here, uses the probability of extinction (either simulated or analytical: for details of analytical extinction risk calculation see chapter 4) as the comparative measure, and these will be referred to as elasticities of extinction risk (E). Despite the development of Population Viability Analysis (PVA) packages in recent years with the specific role of guiding management aimed at minimising extinction risk, use of estimates of the probability of

extinction has received only limited attention with regard to the calculation of elasticities.

5.2 Methods

Matrix model framework

The matrix population model used for the following elasticity calculations is described in detail in chapter four (the model code is provided in appendix 1). This is a stochastic, density dependent simulation model, written in Matlab (Mathworks), developed using data collected and analysed for a small population of wrens (*Troglodytes troglodytes*) as part of this study (see chapters 2 and 3). The model readily permits manipulation of environmental and demographic stochasticity, vital rate covariance and density dependent survival and breeding. The density dependent survival function selected was first described by Maynard Smith and Slatkin (1973), and subsequently recommended by Bellows (1981) for its combination of flexibility and good descriptive properties.

The function takes the form:

$$f(N) = (1 + (aN)^b)^{-1} \quad [1]$$

where $f(N)$ is a function of population density which acts to modify the survival rates, a is the scaling parameter, b determines the strength of the density dependence and N is the total population size. For all density dependent simulations the survival function is calculated using the total population size, but it is applied in one of two ways: either to all age classes equally, or to just the first survival transition (i.e. for juveniles surviving from fledging to one year of age). In the latter instance the older age class survival rates

are left unmodified by population density and take either the mean observed values (deterministic models), or random values (stochastic models) as drawn from appropriate distributions (see chapter 4 for details). This division of density dependent survival by age enables the contrast between equal and unequal competition for resources, and the implications for elasticity analysis, to be investigated. Density dependence can also be applied to reproduction by limiting the availability of breeding territories, and thus only individuals in possession of a territory (and a breeding partner) contribute to the overall production of offspring.

Linear, deterministic elasticity analysis

The formula for calculating analytical sensitivities is given by:

$$s_{ij} = \frac{\partial \lambda}{\partial c_{ij}} \quad [2]$$

Where s is the sensitivity value for matrix element c in row i and column j of the population matrix and λ is the population growth rate. The sensitivities can then be used to calculate the elasticity values for λ thus:

$$e_{\lambda ij} = \left(\frac{\partial c_{ij}}{\lambda} \right) \left(\frac{\partial \lambda}{\partial c_{ij}} \right) \quad [3]$$

Or alternatively elasticities may be calculated directly as:

$$e_{\lambda ij} = \frac{\partial \ln \lambda}{\partial \ln c_{ij}}$$

[4]

Where $e_{\lambda ij}$ is the elasticity value for matrix element c_{ij} . Only non-zero matrix elements have elasticities and because they measure proportional change in λ they sum to one. The remainder of the work presented here will be on elasticities.

Elasticities of λ were calculated from two different sets of mean demographic rates. The first uses the mean survival and fecundity rates as measured from the study population (see table 1, chapter 4), and the second uses these same rates after being ‘re-sampled’ by the model during simulation. To calculate the elasticities for both sets of mean values, they were entered into a 6*6 population matrix, which incorporates the vital rates for both sexes. The upper left quarter of the matrix contains the female rates, the lower right quarter the male rates and elasticity analysis of this matrix is straightforward (after adjustments to accommodate the two sex format). However, there is an important extra consideration to be made regarding the composite nature of the fecundity rates. The vital rates to be entered into the matrix were derived from a series of annual ‘post-breeding’ censuses. The period from one census to the next is made up of a survival period followed by breeding. Thus the matrix elements for fecundity are products of the age class breeding rate (specifically the mean number of same sex offspring produced by each age class, assuming a fledgling sex ratio of 50:50) and the age class survival rate, since only surviving individuals breed. Analytical elasticity analysis is carried out by perturbation of each matrix element in isolation, so for example perturbing the matrix element for first year female survival has no effect on any other matrix element.

However, if we were to perturb the *actual* survival of first year females in the study population then the fecundity rate of first year females (the product of survival and breeding) would be perturbed by the same amount. Similarly, when rates are perturbed during model simulations it mimics this latter form, thus perturbing a survival rate also perturbs that age class's fecundity rate. Consequently the elasticity values for lower level rates derived from simulations are not directly comparable to analytical elasticities of λ (Wisdom and Mills, 1997). We can, however, calculate elasticities of λ for the lower level vital rates either analytically or numerically (e.g. Crowder et al, 1994; Heppell et al 1994) and these are equivalent to simulation elasticities. Since simulation elasticities are calculated numerically, for consistency the lower level λ elasticities were also calculated numerically. Each of the underlying vital rates (either mean or time-averaged) is perturbed in turn by a small proportion (e.g. *1.05) and the elasticity for the lower rate (x) is calculated using the observed change in λ :

$$e_{\lambda x} = \frac{\lambda_{(1.05x)} - \lambda_{(x)}}{0.05 * \lambda_{(x)}} \quad [5]$$

It should be noted that elasticities of underlying rates do not have the property of summing to one, because λ is not a homogenous function of lower-level rates (Caswell, 2001).

Linear stochastic elasticity analysis

To find density independent, stochastic elasticities the stochastic population growth rate, a (Tuljapurkar, 1990) is calculated from a stochastic time series:

$$a = \frac{1}{t} \mathbf{E} \log[N_t - N_0]$$
[6]

Where E is the expected value, N_0 is the starting population size and N_t is the population size after a period of time t . Elasticities are calculated by replacing the deterministic population growth rate, λ , in eq. [3] with a , thus:

$$e_{a ij} = \frac{\partial a}{\partial \ln c_{ij}}$$
[7]

Non-linear elasticity analysis

As previously stated, populations which experience density dependent regulation can be considered as having a long-term growth rate of zero (i.e. $\lambda \approx 1$). Manipulation of vital rates for population management can have only a transient effect on the population growth rate since density dependent regulation will promote population stability in the long term. Thus elasticity analysis performed with respect to λ may not provide accurate predictions of population responses for populations regulated by density dependence. Alternative measures to λ are required for a non-linear elasticity analysis. Three different population measures were used to calculate elasticities in this study: invasion exponent, population size and extinction risk. The method for implementing each will

be described in more detail below. In each case vital rates were perturbed by 5%. This is larger than ideal, since the relationship between increment size and change in the model output metric need not be linear (Grant and Benton, 2000). However, larger changes maximise the precision of estimates obtained from stochastic simulations.

Invasion elasticities

Elasticities of invasion are calculated by measuring the rate of growth of a small population of a mutant (invader) type, with one vital rate perturbed, into a larger resident population at equilibrium (whether stable or fluctuating). The rate of invader population growth (i.e. the rate of invasion) is the average slope of the regression line fitted through replicated invader population time series (log transformed), and is known as the invasion exponent (ϑ). In a stochastic model the likelihood of success or failure of each invasion event is highly variable. A mean invasion rate is obtained from multiple, short duration invasions (e.g. 2000 invasion events of 50 time steps each). The elasticities of ϑ are calculated as the log change in ϑ (compared to an unperturbed, baseline invasion rate, expected to be 0) divided by the log change in each vital rate:

$$e_{\vartheta ij} = \frac{\partial \ln \vartheta}{\partial \ln c_{ij}} \quad [8]$$

In the previous applications of this technique (Grant, 1997; Grant and Benton, 2000, Grant and Benton, 2003) the strength of density dependent regulation, applied to both residents and invaders, is a function of the resident population size. Invasion elasticities

calculated in this way are the stochastic, density dependent equivalent to elasticities of λ .

When density dependent regulation also operates through restricted territories, modifications to the invasion elasticity technique are required, since in this case the invaders and residents must compete for the limited number of available territories. In this modified form, the density dependent survival function is calculated using the combined population size of the residents and invaders, and the two types compete for breeding territories as follows. First year birds of the two types are assigned territories in proportion to their respective population sizes, either deterministically or stochastically (using a binomial routine). As described in chapter 4, once in possession of a territory a bird remains there until it dies, thus it is only first years which compete. The θ of the modified technique is a measure of the rate of replacement of residents by invaders. The elasticities of invasion calculated using either technique do not sum to 1, for the same reason that elasticities of λ calculated from lower-level vital rates do not sum to 1: the vital rates perturbed during simulation are not equivalent to matrix elements. A comparison of the results from both the original method and the new one will be presented. To distinguish between the two, the original method will be referred to as 'ghost' invasions, the modified one as 'real' invasions.

Population size elasticities

Population size elasticities are calculated as the change in the mean population size with the change in each vital rate, using a baseline, unperturbed run for comparison. To minimise the influence of large population fluctuations the average of the logged population size is used:

$$e_{Nij} = \frac{\partial(\overline{\ln N})}{\partial \ln c_{ij}} \quad [9]$$

where N is the total population size. Elasticities of population size provide an intuitively direct connection between the results of model analysis and a common aim of species conservation, since management goals are often stated in terms of population targets. Any subset of the population can be used to calculate elasticities (by sex, age, etc.), although the results presented here are for the total population size.

Extinction risk elasticities

Estimation of the time to extinction has become a common feature in the assessment of populations of conservation concern, through the use of PVA packages (Beissinger and Westphal, 1998). The relative risk of, and estimated time to, extinction under current conditions can be found and then the change in this resulting from alternative management strategies or environmental scenarios can be compared in order to gain an understanding of the relationship between extinction risk and management or environmental conditions. A method to formalise this approach was developed here,

using the estimate of extinction risk to calculate elasticities. Extinction probability (E) is calculated both from the number of simulations dropping below an extinction threshold (simulation extinction) and also analytically (analytical extinction) from the mean and standard deviation population size (as described in chapter 4). The elasticities of E are then calculated as the change in E (within a specific time period) seen with change in the vital rates, using the value of E derived from a baseline (unperturbed) state for comparison:

$$e_{E ij} = \frac{\partial E}{\partial \ln c_{ij}} \quad [10]$$

It could be argued that elasticities of E provide limited additional information beyond that obtained from elasticities of population size, since the former is an assessment of how best to avoid extinction, and the latter how best to maximise population size. However, it is possible to envisage a situation where the two elasticity analyses might not indicate the same management prescriptions. Consider a population which under normal circumstances is subject to large fluctuations of population size, perhaps in response to a highly variable environment. Elasticity analysis of population size might suggest that manipulation of vital rate 'x' will promote the highest mean population size. However, while the mean population size may be increased by manipulating rate 'x', the magnitude and/or frequency of population fluctuations could also be increased, if for example, the elevated mean population size is accounted for by an increase in a life stage which is highly sensitive to environmental conditions. The probability of extinction, rather than being reduced could in fact be elevated by the larger fluctuations

in population size due to the increased risk posed by chance catastrophes or sequences of 'poor' years. Thus the largest extinction elasticities will be for those parameters which increase the mean population size and also those which reduce the magnitude of population fluctuations. An analysis based on mean population size alone could overlook the latter characteristic.

5.3 Results

Density independent models

Elasticities of λ and stochastic growth rate ' a '

The elasticities of λ , derived from both the time averaged mean matrix and the study population's mean vital rates, and the elasticities of a from multiple (5000) simulations provide broadly similar results (fig. 1). The different techniques produce small variations in their elasticity estimates, but these do not change the overall pattern. It is not surprising that the elasticities of λ and a are close to each other since it has been shown that adding small to moderate levels of stochastic variation to demographic parameters typically makes only a small difference to the overall pattern of elasticities (Benton and Grant, 1996). The order of elasticities remains the same for each method of calculation: elasticities for both survival and fecundity decline with age, and within each age class, survival has a slightly greater elasticity than fecundity. The vital rates which contribute most to both λ and a are first year survival and breeding at age one. In a conservation setting, these analyses would recommend management efforts targeted at

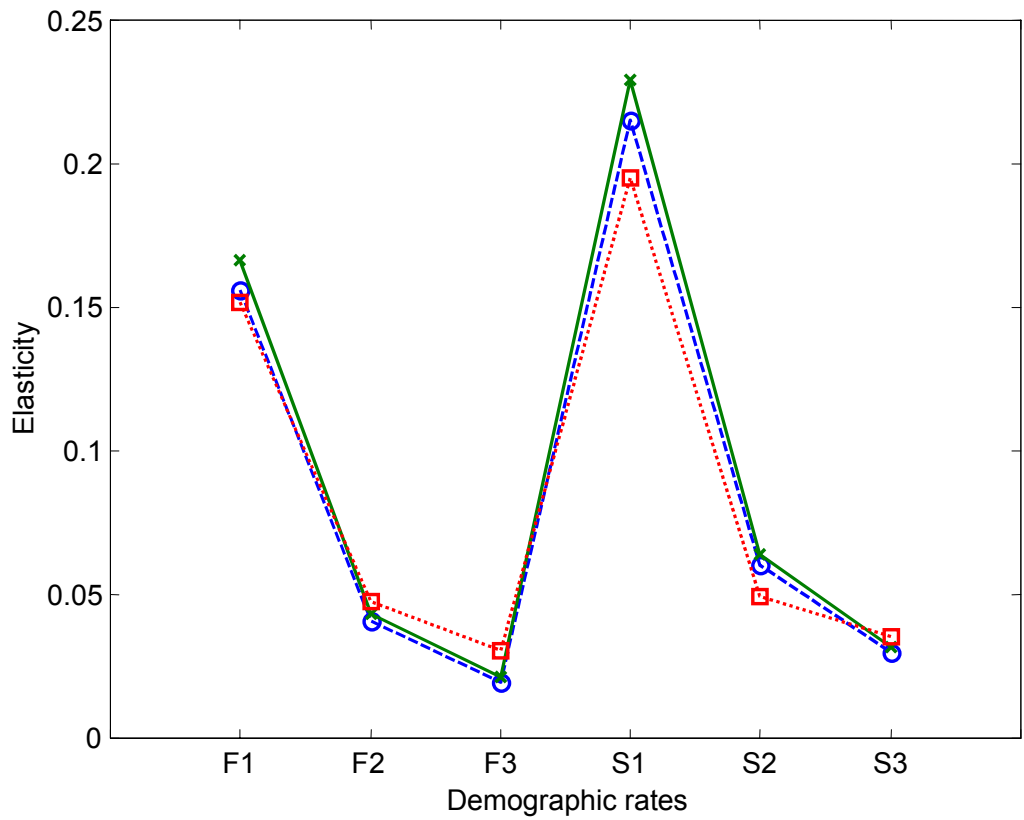


Fig 1. Comparison of density independent elasticities for female demographic rates. Red dotted line ('o' symbols): elasticities of population growth rate, λ , using mean vital rates from field data; green solid line ('x' symbols): elasticities of λ , using time-averaged mean vital rates from 10000 simulations; blue dashed line ('□' symbols): elasticities of stochastic growth rate, a from 5000 simulations (errorbars excluded for clarity, however the errors are smaller than the symbols used). All elasticities scaled to sum to one, including male rates, but only female rates shown. Demographic rates: F – Fecundity; S – survival; 1 –3 age classes

the 1st year rates. These elasticities are equivalent to many of those quoted in the literature and applied in conservation situations.

Density dependent, deterministic models

Elasticities of ϑ , ghost invasion – unlimited territories

Elasticities of ϑ were estimated from 2000 simulated invasions, of 50 time steps each. When breeding territories are unrestricted, increasing the strength of over-compensatory density dependence shifts the population dynamics from stable equilibria, through 2 point cycles, into more complex periodic behaviour (fig 2a). In common with the results of other workers (Takada and Nakashizuka 1996; Yearsley et al, 2003), the elasticities of λ and ϑ when the population is at a stable equilibrium are nearly identical (density dependent parameter $b \leq 5$, fig. 2b-d, f-h). Investigation of the elasticities of non-equilibrium populations by Grant and Benton (2000; 2003) have demonstrated that, if density dependence operates on fecundity, this situation can change considerably as populations move from stable to oscillating dynamics due to changes in selection pressures occurring with the transition from a stable population to a two-point cycle. Unlike their results, here the onset of population bifurcations does not give rise to a changes in the elasticities and the equivalence of λ and ϑ is maintained even at high levels of over-compensation. This is due to the density dependence in the model operating equally on the survival of all age classes, and under these circumstances individual fitness is always maximised by increasing early survival and breeding.

Elasticities of ϑ , real invasions – limited territories

If density dependence operates through restricted availability of territories as well as the survival function, the population dynamics move from stable equilibria through simple oscillations to more complex dynamics as before (fig. 2e). However, this is followed by a return to simpler dynamics caused by the territory limit capping the population. Under these conditions the elasticities of λ are no longer a good guide to those of ϑ (fig 2b-d, f-h). While the ghost invasion elasticities of ϑ match those for λ , with elasticities for survival having higher values than fecundity (at any particular age), the real invasion elasticities are reversed, with fecundity elasticities higher than survival. This occurs because survival rate perturbation is applied to only one sex, and without an accompanying increase in the other sex, the extra surviving individuals cannot breed. Therefore increasing survival of first years has no effect on the rate of invasion because the extra survivors are surplus to the availability of either territories or breeding partners (or both). However, an increase in fecundity increases the number of offspring of *both* sexes, there is no subsequent imbalance in the sexes, and a higher rate of invasion results, since the invaders are able to out compete residents for territories. At weak strengths of density dependence the final survival transition has an elasticity of zero because, under these particular conditions the increase in age class three, and the corresponding decrease in age class one lead to identical levels of offspring production. However, for values of b greater than three (i.e. from mild to high overcompensation), increasing older age class survival exacerbates the imbalance in the sexes by further reducing the availability of territories and partners for first years. Since first year breeders are the most productive age class this puts the invaders at a disadvantage

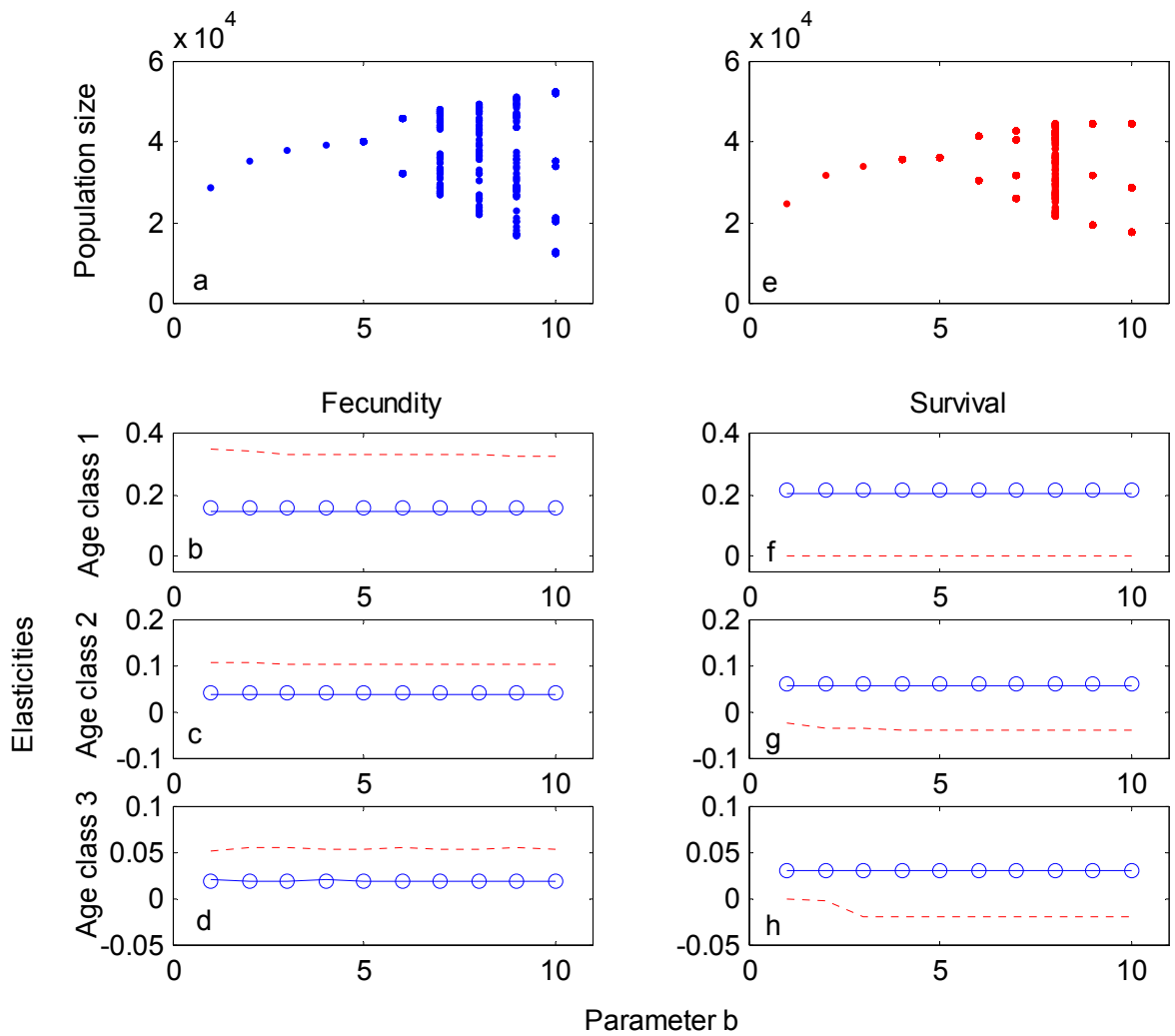


Fig 2. Population bifurcation and elasticity plots for density dependent, deterministic simulations for female demographic rates. Elasticities of λ (time averaged mean values) and θ , plotted against density dependent control parameter b (increasing b increases the strength of overcompensation). Panel (a) bifurcation plot of total population size, with unlimited breeding territories. Panel (e) bifurcation plot of total population size, with restricted number of territories. Panels (b-d, f-h) female elasticities of: λ (open circles); θ ghost* invasion method (solid blue lines); θ real** invasion method (dotted red lines). Elasticities scaled to sum to unity for comparison, including male values but only female ones shown.

*Ghost invasions: unlimited breeding territories

**real invasion: restricted number of breeding territories.

relative to the residents, the invader population fails to increase in number, and negative elasticities result. Negative elasticities signify that *positive* rate perturbation is having a *negative* effect on the rate of invasion, indicating that an individual's fitness may actually be reduced by elevated survival rates after the age of first breeding.

Elasticities of ρ , ghost invasion – unlimited territories, density dependent survival applied to juveniles only

When territories are unlimited, and all age classes contribute to the strength of density dependence but only juvenile survival regulated by it, the population declines as the density dependent function increases (fig. 3a). This is because the effect of increasing the strength of density dependence (parameter b) from low to intermediate levels depends on the size of the population, relative to the reciprocal of the scaling parameter, a . This is the value at which the density dependence survival rate is reduced by 50% (Bellows, 1981). When the population size is smaller than $1/a$, increasing b from low to intermediate values increases the mean population size (fig 2a), while for a population greater than $1/a$, the reverse occurs and the population falls (fig 3a).

With density dependent survival restricted to juveniles, this is effectively regulation of breeding, albeit in a delayed sense, and the population undergoes a single bifurcation to a two-point cycle. The elasticities for fecundity at age 1 and 2 now do follow the pattern described by Grant and Benton (2000) after the bifurcation point: the elasticity for fecundity at age 1 begins to fall, whilst that for fecundity at age 2 corresponding

increases, so that when $b = 10$, the elasticity for fecundity at age two exceeds that for age one (fig. 3b-c). This is explained by considering the following. Birds born in a year with a low population will have higher first year survival than those born at a peak, and once past the only density regulated survival transition they are subsequently unaffected by the population density. While the offspring this generation produce in their first breeding season are born at a population peak and experience reduced survival, the breeding birds themselves have unaffected survival and the offspring they produce in their second breeding season will have a higher survival rate. Thus increased breeding at age two, despite the smaller proportion of two year olds in the population, becomes a successful alternative strategy to increased breeding at age one. For the same reasons the elasticities for survival to one and two show the same (but smaller) trend.

Elasticities of 9, real invasion – limited territories

With a limited number of breeding territories and density dependent survival applied only to juveniles, the population initially increases with increasing b and only develops two point cycles when b reaches a value of ten (fig 3e). As before, when territories are limited the fecundity elasticities are higher than the survival ones (figs. 3b-d and f-h). Because the difference between ‘good’ and ‘bad’ years when the population is fluctuating is now smaller, the relative change in the fecundities of ages one and two, although still present, is much less pronounced. The survival elasticities are largely unaffected by the application of density dependent survival only to juveniles, and their values remain the same as those in fig. 2.

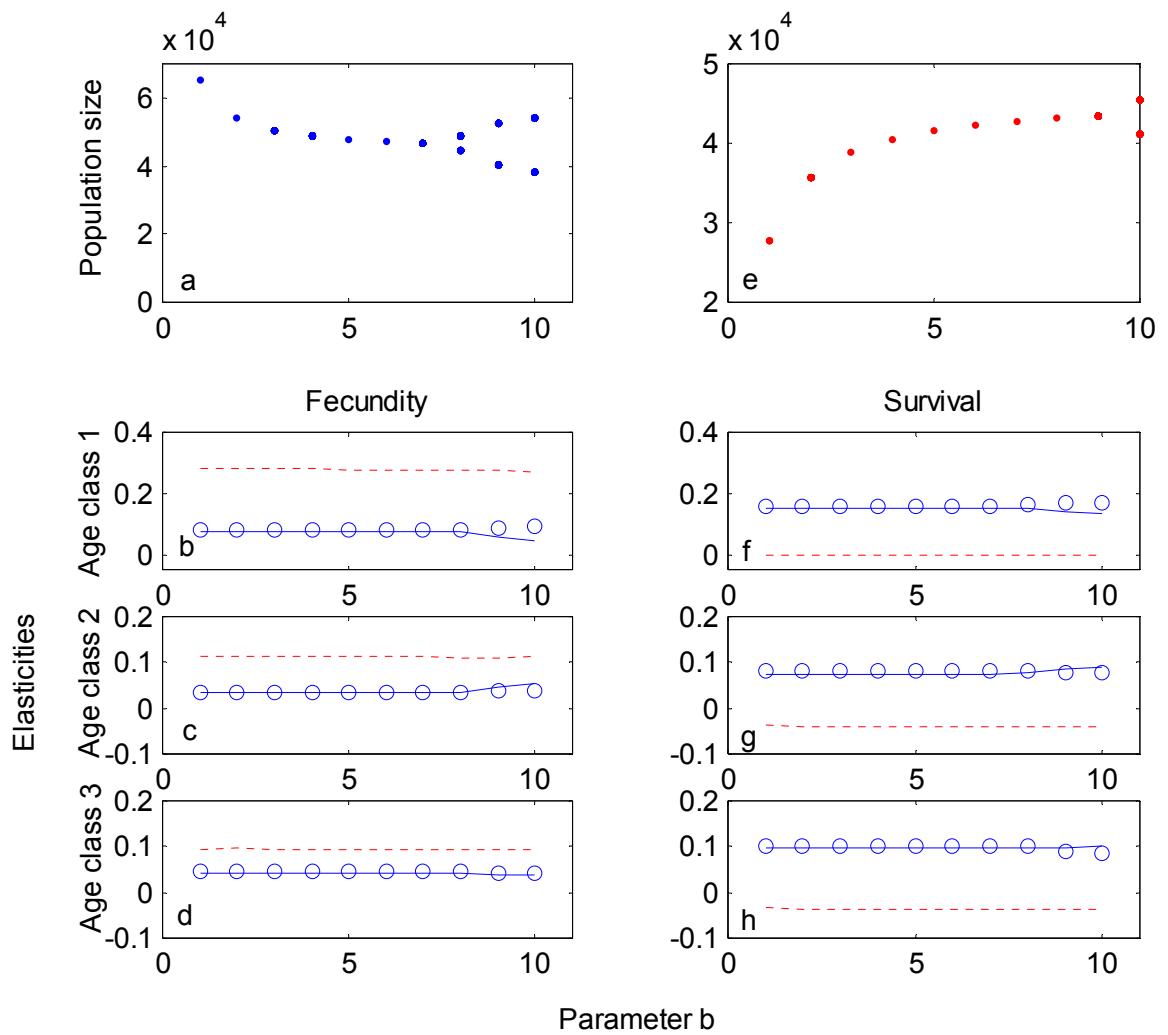


Fig 3. Population bifurcation and elasticity plots for density dependent, deterministic simulations for female demographic rates. Elasticities of λ (time averaged mean values) and ϑ , plotted against density dependent control parameter b . Only juvenile survival is modified by the density dependent function. Panel (a) bifurcation plot of total population size, with unlimited breeding territories. Panel (e) bifurcation plot of total population size, with restricted number of territories. Panels (b-d, f-h) female elasticities of: λ (open circles); ϑ ghost* invasion method (solid blue lines); ϑ real** invasion method (dotted red lines). Elasticities scaled to sum to unity for comparison, including male values but only female ones shown.

*Ghost invasions: unlimited breeding territories

**real invasion: restricted number of breeding territories

Elasticities of population size

As described previously, if only density dependent survival regulates the population size, the population dynamics, after initial two-point cycles become extremely complicated (fig. 2a). When the population is at a stable equilibrium ($b \leq 5$) the elasticities are almost identical to those for λ (fig. 4a, $b=2$). As the strength of density dependence increases further, the population first bifurcates to a two-point cycle ($b = 6$) and all the elasticities become negative, while maintaining the same values relative to one another. This occurs because although all rate perturbations increase the peak population size, they consequently also lower the subsequent trough by a greater amount, and the mean population size falls. The same occurs when b is ten, but for values of b between seven and nine the elasticity responses do not follow any particular pattern apart from being predominantly negative (fig. 4b). This is a reflection of the complex periodic dynamics present at these strengths of density dependence (fig. 2a), which, in combination with the size of vital rate increment, make for unpredictable population responses to rate perturbation.

As we have already seen, when the number of breeding territories is limited, population bifurcations return to simple dynamics at high levels of density dependence (fig. 3). The elasticities of total population size under such conditions are strongly influenced by the strength of over-compensatory density dependence (fig. 5). The elasticities for fecundity are the same as those when territories are unlimited (see fig. 4a), but those for survival are quite different. First year survival has an elasticity of, or near to, zero for all strengths of density dependence. Again, this is a result of the competition for breeding

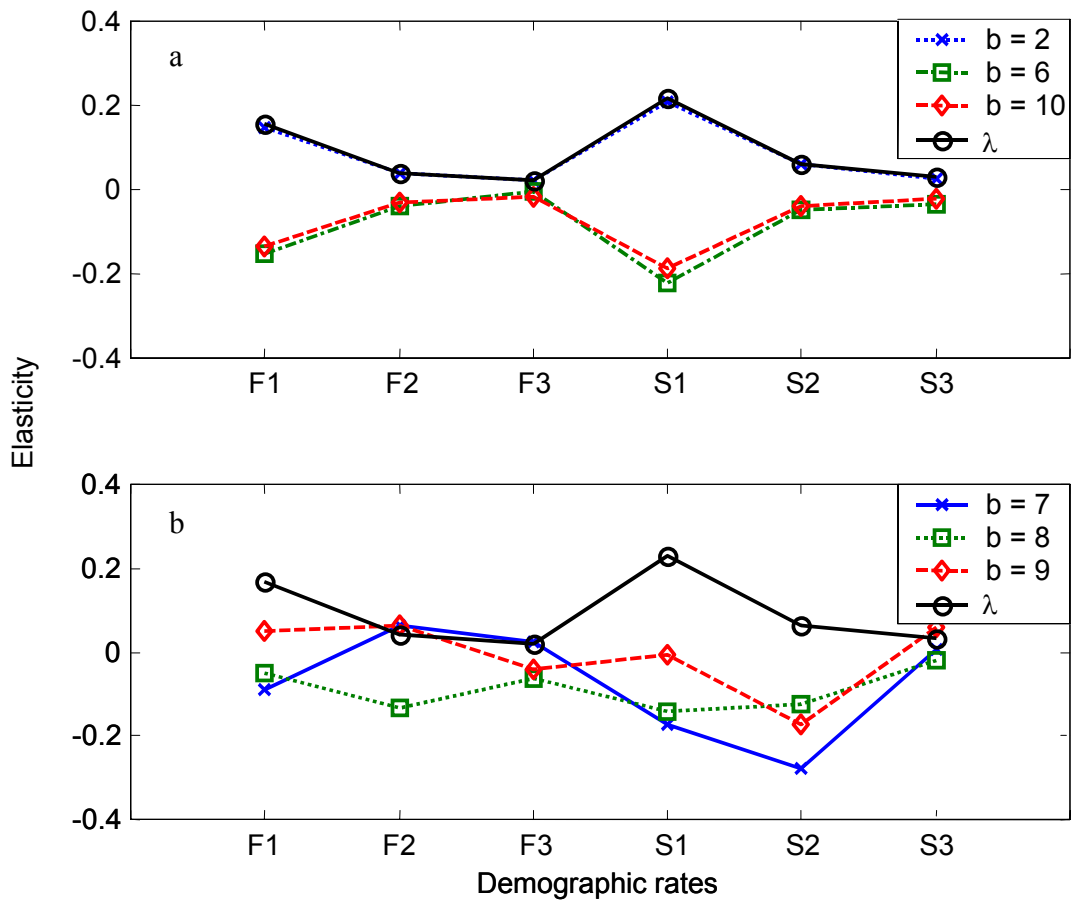


Fig. 4. Comparison of deterministic female elasticities of λ from time averaged mean matrix and population size, for different strengths of density dependent control parameter b . There is no restriction on the number of territories. Population dynamics as in fig. 2a. Panel (a): elasticities of: λ , solid black line ('o'); population size, for $b=2$ blue line (stable equilibrium), 6 green line (two-point cycles) and 10 red line (four point cycles). Panel (b) elasticities of: λ , solid black line ('o'); population size for $b=7$ blue line, 8 green line and 9 red line (all multiple point cycles). Errorbars are omitted for clarity, as in all but one case they are smaller than the marker symbols used. The exception is when $b = 6$ (graph a), reflecting the small absolute elasticity values obtained, and the consequent inflation of the values (by a factor of approx. 6) also increases the relative size of the errors. All elasticities (male and female) scaled to sum to one, but only female elasticities shown. Demographic rates: F – Fecundity; S – survival; 1 – 3 age classes. Population size elasticities calculated when the population has a stable equilibrium ($b = 2$) match the elasticities of λ from the time averaged matrix (graph a). When the population exhibits simple cycles ($b = 6$ and 10), the elasticities retain the same relative positions but become negative, due to enhanced cycling and a lowered mean population size. When the dynamics are complex, interactions between the density dependence and perturbation size lead to a high degree of variability in the population size elasticities (graph b), corresponding to greater imprecision.

territories and indicates that there are already surplus first years in the population, so increasing their survival has no effect on the breeding population size. Increasing older age class survival when b is below six has a small negative effect, through greater exclusion of first years (as described above for real invasions). However at higher strengths of density dependence ($b > 6$), the same elasticities are positive, (with the exception of when b equals eight (not shown): this is the only strength of density dependence which produces complex periodic dynamics when territories are limited, and as a result the elasticities do not follow a simple pattern, as with those in fig. 5b). These positive survival elasticities for age classes two and three occur for the following reasons. Increasing the proportion of older territory holders at the expense of first time breeders, limits the overall production of offspring, since first year birds have the highest fecundity rates and are the most numerous age class. Thus, in combination with the territory restriction, this reduces the peak of the population cycles by a small amount, but more importantly raises the subsequent trough by a larger quantity, leading overall to a higher mean population size. The end result is an almost complete reversal in the rank order of population size elasticities as we move from weak to strong, over-compensatory density dependence.

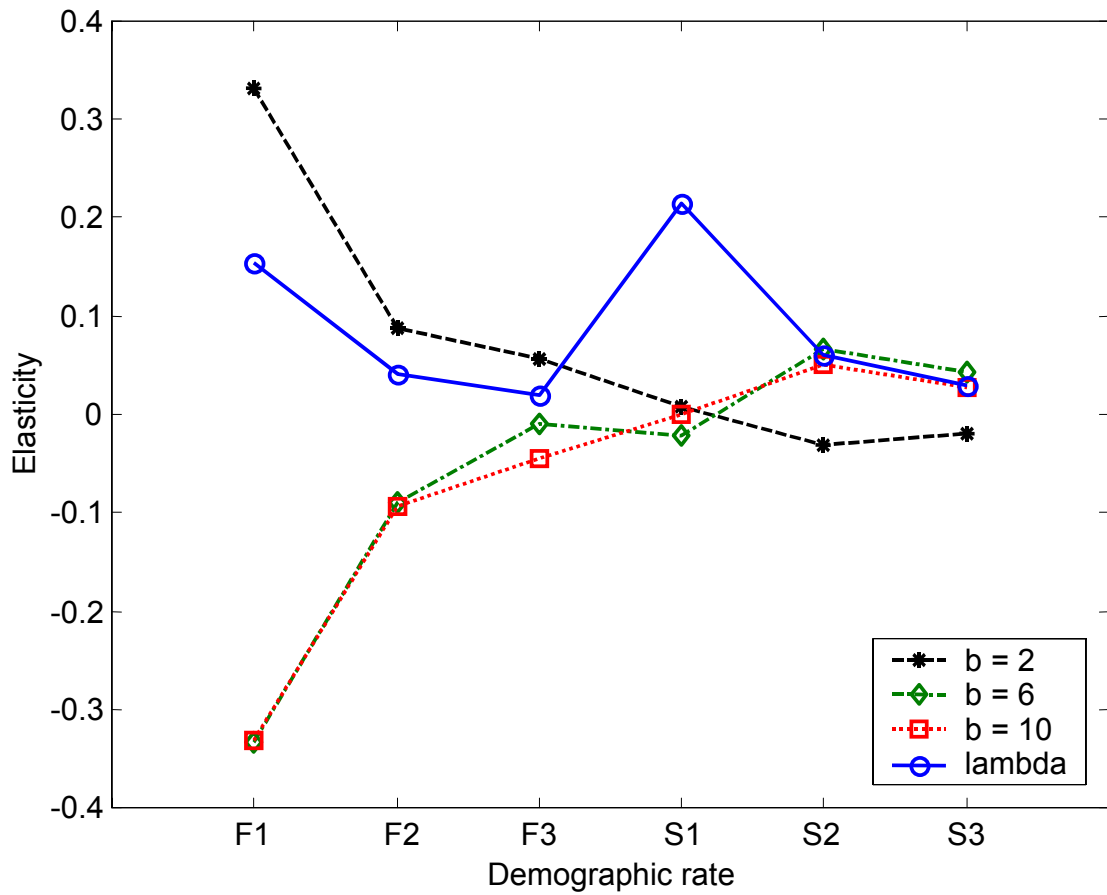


Fig 5. Comparison of deterministic female elasticities of λ from time averaged mean matrix and population size, at low, medium and high values of density dependent parameter b . Population dynamics as in fig. 2e. There is a limited number of breeding territories. Elasticities of: λ solid blue line ('o'); population size, $b = 2$ black line (stable equilibrium), 6 green line (two point cycles) and 10 red line (three point cycles). When $b = 8$ the elasticities are unpredictable as in fig 4b. All elasticities (male and female) scaled to sum to one, but only female elasticities shown. Actual value for elasticity F1 at $b = 10$: -1.14. Demographic rates: F – Fecundity; S – survival; 1 –3 age classes

Density dependent, stochastic models

Elasticities of ϑ

The effect of adding stochasticity (environmental and demographic) to the estimation of elasticities of ϑ can be seen in fig. 6. The elasticities change by only negligible amounts across values of b from 1 to 10, so the data plotted in fig. 6 all come from simulations with the same strength of density dependence ($b = 4$). The ghost invasion elasticities are not significantly different from those for λ (fig. 2). Surprisingly however, while the deterministic survival elasticities from *real* invasions were either zero or negative (fig. 2), their stochastic equivalents are large and positive: comparable to the elasticities from both the ghost invasion method and for λ (from the time averaged mean matrix). Thus the addition of noise changes the survival elasticities from negative (i.e. an increase in 2nd year survival *decreases* the rate of invasion) to positive (i.e. an increase in 2nd year survival *increases* the rate of invasion), indicating that constant environments and stochastic environments can elicit alternative approaches for maximising individual fitness. In this case the mechanism for the difference is as follows. In the presence of stochasticity (unlike the situation in a constant environment), there is sufficient variation between the survival rates and the number of territories from one breeding season to the next, to allow increased numbers of first years to obtain territories and breeding partners in most years. For example, under deterministic conditions the numbers of each sex in age classes two and three are identical at each time step. This is extremely unlikely to occur under stochastic conditions, and the imbalance in the sexes means there will usually be older birds available as breeding partners for first years. In the deterministic models when density dependent survival affected only the first transition there was a

decrease in first year fecundity and survival elasticities matched by an equivalent increase in the rates for age class two (fig. 3), but again the presence of stochasticity minimises this effect.

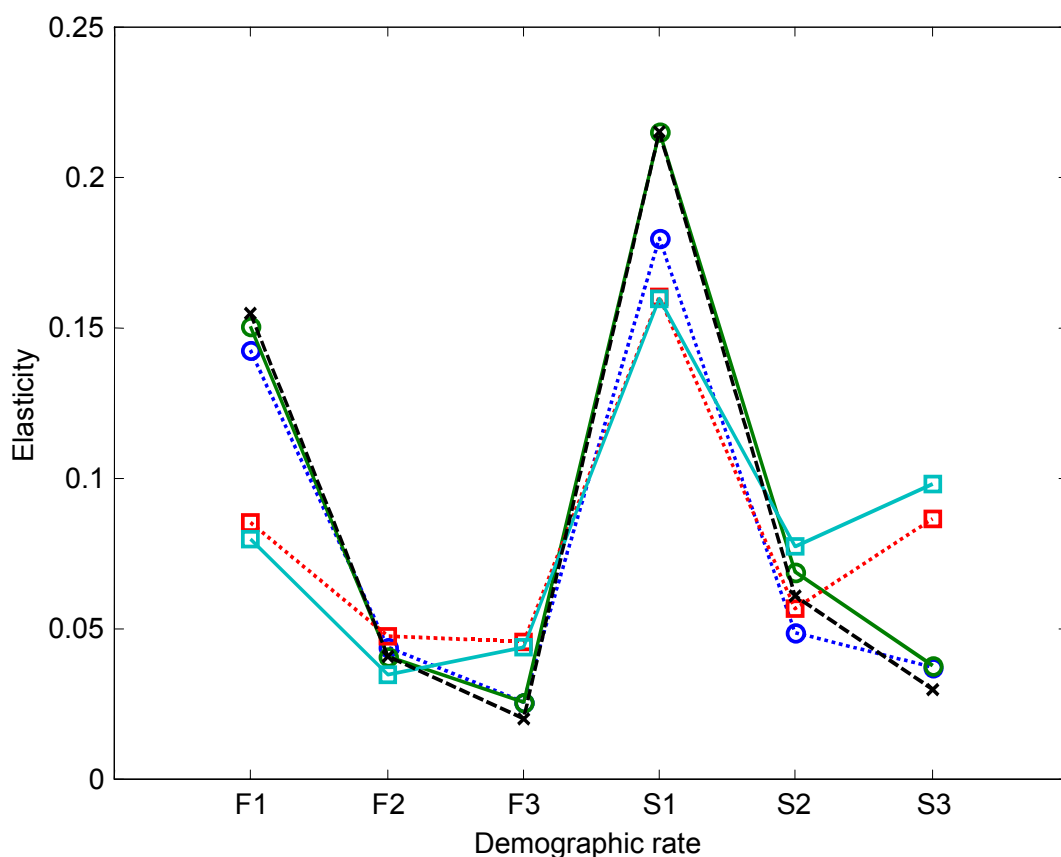


Fig. 6. Comparison of density dependent, stochastic elasticities of ϑ for female demographic rates, and elasticities of λ from time averaged matrix. Solid lines are ghost* invasions, dotted lines real** invasions. Lines with circle ('o') symbols are from simulations with density dependent survival applied to all age classes, lines with square ('□') symbols are simulations with only juvenile survival modified by the density dependent survival function. Invasions were for 50 time steps, repeated 2000 times, values shown are the means, confidence intervals are smaller than the point symbols. For comparison the elasticities of λ from the time averaged matrix are added. The strength of density dependence did not significantly alter the elasticity values. Lines shown came from an intermediate strength of density dependence. Elasticities are scaled to sum to one, including the male elasticities (not shown). Confining density dependent survival to juveniles increases selection on late survival and breeding and decreases selection on juvenile rates. Demographic rates: F – Fecundity; S – survival; 1 – 3 age classes

*ghost invasions: unlimited breeding territories

**real invasion: restricted number of breeding territories

Elasticities of population size and extinction risk

In the previous elasticity plots the female and male elasticities followed the same patterns, and the male rates were omitted for clarity. However, that is not the case for the elasticities presented here, so the male rates are included. When density dependence is weakly over-compensatory the stochastic elasticities of extinction and population size are in reasonable agreement, both with each other (figs. 7 and 8) and also with λ (fig. 1). As the strength of over-compensation increases, the elasticities of population size remain similar to those for λ until b has a high value (> 8), but the extinction risk ones change much earlier. By the time b has a value of six only the male survival elasticities are still positive. The elasticities of population size are positive for rate perturbations which increase the mean population size, and this will also tend to be true for extinction elasticities. However, the latter also take into account changes in the variance in the population size. In the example here, when b has a value of six, increasing the first year female survival rate by 5% raises the mean population size by 0.5%, while the same rate increase for first year male survival produces a rise of 0.9%. The population size elasticities for the two rates are 0.1 and 0.28 respectively. However, at the same time as the mean population size increases, the variance also changes, only in opposite directions: for first year female fecundity it increases by 5.7%; for first year male survival it decreases by 5.2%. Hence the respective extinction elasticities are -0.8 and $+0.22$. The same pattern is repeated to a lesser extent for all the survival rates. The cause of this difference lies in a combination of each sex's stable age structure and age related contribution to the total reproductive output, and how these respond to perturbations at high levels of over-compensation. Average female offspring production

is split 2.67 : 1 in favour of first years over older ages, while the male equivalent is 1.68 : 1. When first year female survival is increased, their proportion of the breeding population rises and consequently there is a large increase in offspring production. This raises the population to a level which triggers a severe density dependent response, causing the population to crash. Repetition of this pattern leads to wide population fluctuations, and subsequently a large population variance. The same does not occur with elevated first year male survival because, although the total offspring number still rises, the increase is insufficient to prompt the same degree of density dependent regulation. The elasticities for the older survival rates have the same signs, but are closer to zero, since in the female case older individuals produce less young and the increase in the variance is smaller, while for the males, reproductive output increases with age and the variance increase is higher. This is an example of a situation in which conservation management prescriptions, guided by elasticities of population size would be at odds with those from elasticities of extinction risk.

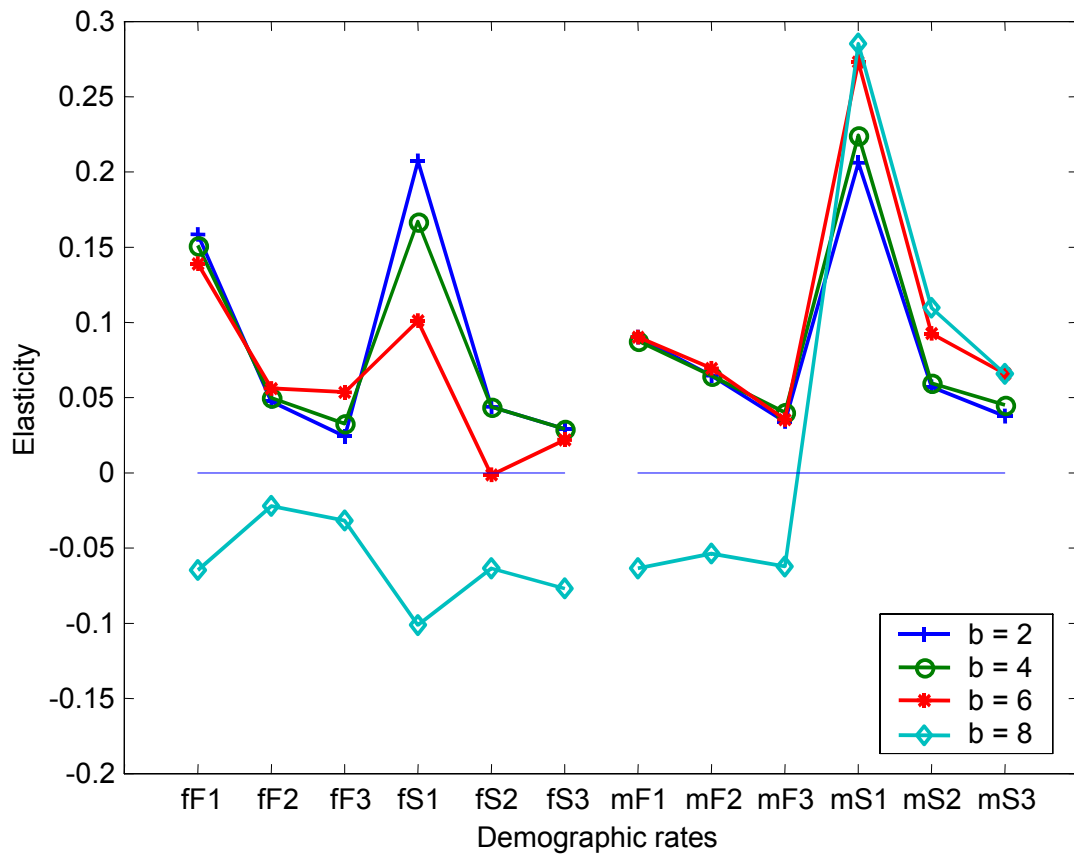


Fig. 7. Comparison of density dependent, stochastic elasticities of population size for both sexes at different strengths of density dependence. Simulations were of 200,000 time steps, with a 5% increment in vital rates. Horizontal lines indicates zero. All elasticities scaled to sum to one. Demographic rates: f – female, m – male; F – Fecundity; S – survival; 1 – 3 age classes.

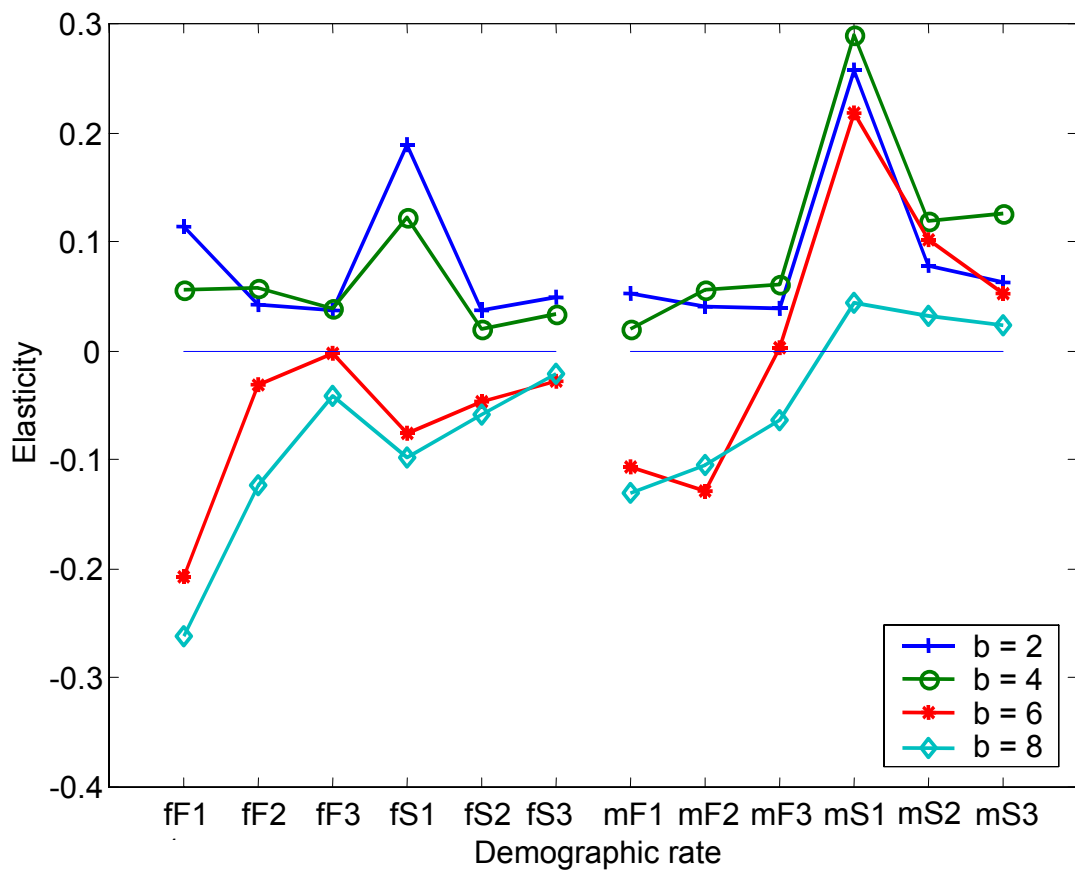


Fig. 8. Comparison of density dependent, stochastic extinction risk elasticities at different strengths of dependence. Simulations were of 250 years, with a 5% increment in vital rates. Extinction probability was calculated analytically using the mean and variance of the population size from 5000 simulations. Horizontal lines indicates zero. All elasticities scaled to sum to one. Demographic rates: f – female, m – male; F – Fecundity; S – survival; 1 – 3 age classes

5.4 Discussion

The work presented here demonstrates how a pragmatic approach to population modelling, coupled with recently developed methods for performing elasticity analysis (Grant, 1997; Benton and Grant, 1999), can provide valuable guidance for conservation managers and allow an insight into the evolutionary pressures underpinning population processes. By using a simulation model to compare the deterministic, linear elasticities of λ with those derived from stochastic and density dependent populations, we can begin to appreciate the conditions under which disagreements arise between the elasticity methods, and perhaps more importantly, why. Grant and Benton (2000; 2003) have used models of both simplified life histories and also the 'LPA' model for *Tribolium* populations (Dennis et al, 1995), to demonstrate that the elasticities for population growth and population size need not be in accordance when density dependence and stochasticity are operating in a realistic manner. The results here extend this work to a density dependent, stochastic model developed for a wild population and find similar differences between the elasticities of λ and population size, and also show how elasticities for alternative metrics (e.g. extinction risk) may present further alternative management recommendations.

In the field of conservation management elasticity analysis has become a useful guide, and this is symptomatic of a welcome and widespread expansion in the use of scientific methods in conservation (Reed et al, 2002). However, the analysis presented here, and the work on which it builds, indicate that great care is needed in both the application of elasticity techniques, and the interpretation of their results (Benton and Grant 1999;

Mills et al, 1999). As we have shown, for a range of plausible circumstances the elasticities of λ are a useful guide to the levels of selection acting on demographic rates. However the goals of a conservation management programme, and the direction in which selection acting on individuals may be operating need not coincide (Grant and Benton, 2003). This should not be a surprising conclusion, as it seems unreasonable to expect that any one method of calculating elasticities will provide useful (or accurate) answers in all the situations where elasticities may be used (a 'one size fits all' philosophy). As we have shown here the elasticities of fitness, population size and extinction risk calculated for the same population can all be different. For example, if we consider the female elasticities for a stochastic population with all age classes experiencing an intermediate level of over compensatory density dependent survival, first year fecundity can have a (scaled) value of: 0.15 (population size), 0.08 (real invasion) or -0.2 (extinction risk), while its respective rank order changes from 1st to 2nd to 6th (in terms of positive value). Thus under these conditions a positive perturbation applied to the first year female fecundity rate will be expected to raise the mean population size, but at the same time the increase is combined with an elevation in the population variance around the mean, putting a small population at an enhanced risk of extinction. This difference between the elasticities for population size and extinction risk will be of greatest concern to conservation managers, since management goals for rare species are frequently expressed in terms of either population size or extinction probability.

When density dependence operates through the survival rates of all age classes equally we find that the elasticities of θ and λ are in general agreement, and thus a simple analysis of a matrix of mean values will provide a good guide to the selection pressures acting on demographic rates. This concordance does not appear to be affected by either the presence or absence of realistic levels of environmental stochasticity, nor by the strength of density dependent regulation, whether it is stabilising or strongly destabilising. Therefore, under these circumstances, an understanding of the evolutionary processes will be gained from a simple elasticity analysis of a matrix of mean values, and little extra information will be gained through analysis of a fully density dependent, stochastic model. However, the same may not be true if density dependence operates unequally on subsets of the population (Grant and Benton, 2000). The example used in this account, of juvenile birds being subject to density dependent survival while older individuals are not, represents an extreme case but highlights some possible outcomes. It is not unreasonable to suppose that for a species which maintains a degree of territorial behaviour all year round, birds not in possession of a territory may be disadvantaged during critical survival periods, through elevated resource competition among similarly afflicted conspecifics. So it is not a trivial result that in such circumstances the elasticity which was previously the largest (first year survival of either sex), now has a value of zero. This indicates that the selection pressure in a system where space is at a premium may be focused on elevated levels of fecundity instead of survival. It is true that a time averaged matrix of mean values derived from a simulation which incorporates this form of density dependent survival structure will produce comparable elasticities. However, once such a model has been developed there

is little additional extra work required to calculate fully density dependent elasticities, and it would seem unwise in such circumstances to assume that the result presented here (of elasticity equivalence) was always the norm. It should also be noted that in this instance, elasticity analysis of a matrix of mean *observed* values (as often reported) makes no provision for questions of space and may produce results of limited value. Heppell et al (2000), performed comparative λ elasticity analyses to see if was possible for species to be categorised using common life history patterns, thus assisting the management of species with minimal demographic data. They report success in this aim using a generalised model, however the result described above demonstrates that the absence of density dependent considerations in their analyses calls such generalisations based only on life histories into question. If we consider a hypothetical example of two species with the same pattern of λ elasticities, but in which the effects of density dependence on survival rates for one are felt by all ages equally and in the other are concentrated on a specific age group, it is highly likely that the density dependent elasticities for the two species will be different.

Analysis of change in the mean population size and extinction probability provide two directly applicable and easily understandable measures on which to base elasticities for the management of rare species and populations. They should not be considered as competitors for the title of ‘best’ elasticity method, any more than the elasticities of λ should be dismissed as too simplistic. The two methods offer alternative approaches to investigate the closely related problems of small and declining population sizes. Small populations are confronted by much higher risks of extinction than larger ones simply

through the enhanced impact of chance events. Estimation of a projected time to extinction using simulation modelling techniques has become a popular means with which to assign conservation priorities (Brook et al, 2000), although the validity of absolute predictions has been called into question (Coulson et al., 2001; Ludwig, 1999; Ellner et al, 2002). Beissinger and Westphal (1998) in their review of PVA state that, “in our opinion the optimal use of PVA is to evaluate relative differences among model outcomes”. By comparing the relative extinction probabilities resulting from different management regimes an appreciation of the factors contributing to the level of extinction probability can be gained (e.g. Lindenmayer and Possingham, 1996). Calculation of the elasticities of extinction risk (or population size) is simply a formalisation of this process and represents a prime example of this approach.

Since the extinction risk can be considered as a product of a population's size and variance, the elasticities of extinction risk will identify the vital rates which combine increases in the population size and reductions in year to year variability. Instances when extinction elasticities may be of less value would be for species or populations not in imminent danger of extinction, but rather showing the early signs of decline. Such examples might include harvested species or populations, such as marine fish. In these cases the population size will be sufficiently large, and the risks of imminent extinction sufficiently small, that the dangers associated with chance events can largely be ignored. Such a population is likely to be little affected in the long term by relatively large year to year variations, and elasticities of the mean population size will be a more useful guide for long term management aimed at maintaining a healthy population size. Thus,

just as the elasticities of λ may be inappropriate in certain density dependent situations, so the elasticities of extinction risk or population size can also be of limited value, depending on the circumstances and goals of management. Before performing an elasticity analysis it is important that the purpose for which the results are sought has been carefully considered and clearly stated, in order that the most appropriate elasticities are employed. The metrics used here are not exclusive, and other systems may warrant alternatives, indeed conservation managers should be encouraged to consider alternative elasticity measures which may suit their needs better, since this will also assist them in refining management goals.

Chapter 6

General discussion

The pressures on the natural environment resulting from the expansion of the human population have created a situation in which many species are facing an extinction risk far greater than that which might otherwise be expected. Conservation science as a discipline has grown out of a need to effectively target limited resources in order to maximise results. Quantitative approaches have been applied at many scales, from the study and modelling of climate patterns, through to species specific population research. Within the field of species conservation the term population viability analysis (PVA) has come to be applied to models which are used both to quantify the risks faced by populations, and to select the best means to ameliorate such risks. While many of the commercially available PVA model packages have become quite sophisticated, with population projections explicitly incorporating density dependent processes and realistic means for simulating environmental and demographic stochasticity, their chief purpose has remained the provision of estimates of population growth rates and extinction risk. It is somewhat surprising, given the availability of such models, that the identification of management targets by means of elasticity analysis is nearly always still conducted with reference to a deterministic, density independent estimate of the population growth rate (λ). The work presented in this thesis forms part of a growing body of evidence that elasticity analysis which fails to incorporate ubiquitous natural processes may produce misleading results. By providing an example of how natural processes may influence a species' population dynamics, and demonstrating how such effects can have important implications for conservation planning it is hoped that species conservation efforts will be enhanced.

Population models are a useful tool to aid the conservation of rare species. Their development can promote greater understanding of the factors underlying a species' population dynamics and their outputs can be used both to guide further research efforts and to identify optimum courses of action to slow, stop and reverse population declines. Most population models have at their core estimates of a species' rates of survival and reproduction. Using these it is possible to make a calculation of probable future trends in the population size. For most species, demographic rates will not be constant throughout an individual's lifetime but will vary as, for example, experience is gained (affecting e.g. reproductive success) and the risk of predation changes (affecting e.g. survival rates). A model which uses single survival or reproductive rates for all ages or stages will inevitably be a compromise under such circumstances. However, it is possible to accommodate age (or stage) structure within the lifecycle by entering demographic rates appropriate to each age into specific locations in a matrix. The subdivisions of the life-cycle can be based simply on age or alternatively on size classes (e.g. carapace length in turtles) or developmental stage (e.g. arthropod instars). Common to all forms of matrix model, however, is the requirement for a certain threshold level of demographic data to permit accurate estimation of vital rate parameters, and the quality and quantity of the available data will determine the degree of uncertainty which will be associated with the estimates obtained. Unfortunately, it is often the case that the amount of data available with which to estimate demographic parameters for endangered species is limited. The wren population data collected during the course of this study is typical of this intermediate level of data quality. Since the outputs obtained from a population model are very dependent on the quality of the data

used for parameter estimation care must be exercised during the interpretation of results. However, by adopting a pragmatic approach to parameter estimation and model development the risk of prescribing misguided management based on erroneous model outputs can be minimised (Starfield, 1997). For example, the estimate of juvenile wren survival (from fledging to one year) derived during this study was estimated from two summers (June – September) and one winter (October – February) of radio tracking data, combined with inferences based on older age class survival and first year return rates for the periods outside the radio tracking study. While this is a limited amount of data on which to base a parameter estimate, the amount of effort required and the availability of suitable technology (i.e. sufficiently small radiotags) mean that this represents a typical level of data quality. One way we can gain extra confidence in our estimated value is to make comparisons with ecologically similar species, since such species are likely to share common traits. In this case we can consider both short-term radio tracking studies of other small passerine species of temperate forests (e.g. coal and great tits: Naef-Daenzer et al, 2001), and also longer term studies of passerine populations for which dispersal and death can be distinguished with reasonable accuracy (e.g. great tit: Perrins, 1965). Comparison of our juvenile wren survival rate with these other data sources suggests that our estimate is likely to be reasonably accurate. Thus, while this survival rate should receive further attention in the field in order to improve the confidence we have in its value, we can still use the data we have to begin the process of parameter refinement. Indeed, this highlights the second proviso with an analysis based on limited data such as this, which is that modelling results are not final, but can and should be updated as further periods of study are carried out. As

more data becomes available we can refine our models and so gain further confidence in them. The model itself can assist this process by identifying parameters which require further research.

If a species or population exhibits fluctuations in numbers and there is reason to suppose that density dependent regulation is also present, a linear, deterministic model clearly leaves out a great deal of potentially relevant information. Omitting ubiquitous features of natural systems because of a lack of empirical data may thus prevent the level of insight into population processes that an open-minded, experimental attitude may yield. Since the means with which to develop stochastic and density dependent population simulations are now readily available there is little excuse for not doing so, and indeed more and more published population models are both stochastic and density dependent. Incorporating routines to calculate the elasticities of such stochastic, density dependent models requires little extra work (e.g. elasticities of population size or extinction risk). It is surprising therefore, that elasticities are so often still calculated with reference to λ , when stochastic and density dependent population simulation models have been produced for many years.

One of the key aims of the modelling and elasticity analyses presented here is to highlight the fact that neglecting to take account of density dependent population regulation can have major implications for the results obtained. Omitting density dependence from population models has sometimes been excused because researchers have no information about how population density may effect demographic processes

(e.g. Wielgus et al, 2001). This is not surprising since few species have sufficiently long datasets for its presence to be unequivocally identified, and even less for estimation of its form. In addition it is occasionally asserted that an endangered species will, by definition, be present in sufficiently low numbers that density dependence processes may be ignored. However, this argument may seldom be justified. For example, it is reasonable to suppose that small populations of social species will actually maintain similar local densities to those found in larger populations, in order to facilitate their normal activities (e.g. feeding, reproduction, predator detection). If we also consider the fact that one of the chief causes of population declines is habitat loss it becomes increasingly clear that density dependence is almost certainly not confined to large populations. For the population studied here there is some evidence for density dependent survival, but we can also draw on the results of other workers who have found evidence for density effects in wren populations of a similar size (Newton et al, 1998; Peach et al, 1995). The datasets available in these cases covered over 20 years, yet even with such time series we still have no information on the form of the density dependent regulation. This led to the adoption of a flexible density dependent survival function, which enabled investigation of the effects of changing the strength and form of the feedback. By doing this, a range of possible density dependent scenarios could be modelled and the implications of each could be investigated. This approach permitted questions regarding the form and strength of density dependence to be addressed through analysis of the model by making sensible guesses about its probable characteristics within a modelling framework. By such methods a greater understanding of its probable function in the study population can be obtained, and improved means to

identify its action in the field may be suggested. The results of the stochastic, density dependent elasticity analysis presented here indicate that at relatively modest strengths of density dependent survival the elasticities of λ and the elasticities for population size or extinction probability can be markedly different, even to the extent of having opposite signs. This suggests that the management of a small population with the aim of maximising the population size or minimising the risk of extinction, based on recommendations derived from the deterministic, density independent elasticities of λ , may at best fail to have the desired effect and at worst actually be detrimental to the population's status. This result is extremely concerning given the number and range of studies which have reported the elasticities of λ . If reducing extinction risk is a management goal, it seems logical that estimates of the rate of extinction are used directly to guide management, rather than estimates of other population characteristics which may provide only indirect measures of the population health. It is hoped that this result will lead other workers to recognise that omitting density dependence and stochasticity from elasticity analysis may have serious implications for the results obtained.

There are a range of possible directions in which the modelling research presented here could be extended. For example, all of the work here deals with a single population in isolation, so an obvious development would be to link up one or more replicate populations to create a meta-population model. This could be used to ask questions about topics such as the degree of dispersal between populations and the potential impacts of source-sink dynamics could be investigated. It would also be instructive to

parameterise the model with data for other species, particularly ones with different life-cycles (e.g. longer lived, slower breeding species). This might indicate the presence of more general rules regarding the dynamics of density dependent, stochastic simulations and elasticity analyses. Allee effects were not incorporated as part of the density dependence in the model since it was felt that considering the wren's highly mobile and vocal nature, along with the size of population and study site modelled here, their effects would be minimal, but this assumption (as with all assumptions) is worth testing.

The use of a matrix model formulation for this study was driven by the goal of improving a technique which is already commonplace, rather than to develop a novel approach to demographic modelling which might better represent wren population dynamics. All models by their nature have inherent advantages and disadvantages with regards to their ability to capture the salient features of a chosen system and provide insights into their workings. It is hoped that the work presented here addresses some of the limitations of traditional elasticity analysis and thus improves the value of matrix modelling to the task of endangered species conservation.

References

Adams, A. A. Y., Skagen, S. K. & Adams, R. D. 2001 Movements and survival of Lark Bunting fledglings. *Condor* **103**, 643-647.

Akande, M. 1972 The food of feral mink *Mustela vison* in Scotland. *Journal of Zoology* **167**, 475-479.

Akcakaya, H. R. 1991 A Method For Simulating Demographic Stochasticity. *Ecological Modelling* **54**, 133-136.

Akcakaya, H. R., Burgman, M. A. & Ginzburg, L. R. 1999 *Applied Population Ecology*. Sunderland, Massachusetts: Sinauer Associates, Inc.

Anders, A. D., Dearborn, D. C., Faaborg, J. & Thompson, F. R. 1997 Juvenile survival in a population of neotropical migrant birds. *Conservation Biology* **11**, 698-707.

Anders, A. D., Faaborg, J. & Thompson, F. R. 1998 Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk* **115**, 349-358.

Armstrong, E. A. 1955 *The Wren*. London: Collins.

Beissinger, S. R. & Westphal, M. I. 1998 On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* **62**, 821-841.

Bellows, T. S. 1981 The descriptive properties of some models for density dependence. *Journal of Animal Ecology* **50**, 139-156.

Benton, T. G. & Grant, A. 1996 How to keep fit in the real world: Elasticity analyses and selection pressures on life histories in a variable environment. *American Naturalist* **147**, 115-139.

Benton, T. G. & Grant, A. 1999 Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology and Evolution* **14**, 467-471.

Benton, T. G. & Grant, A. 1999 Optimal reproductive effort in stochastic, density-dependent environments. *Evolution* **53**, 677-688.

Benton, T. G. & Grant, A. 2000 Reply to comment by Mesterton-Gibbons, M. *Trends in Ecology and Evolution* **15**, 116.

Benton, T. G., Grant, A. & Clutton-Brock, T. H. 1995 Does environmental stochasticity matter - analysis of red deer life-histories on Rum. *Evolutionary Ecology* **9**, 559-574.

Block, G., L. & Allen, J. S. 2000 Population extinction and Quasi-stationary behaviour in stochastic density-dependent structured models. *Bulletin of Mathematical Biology* **62**, 199-228.

Brook, B. W., O'Grady, J. J., Chapman, A. P., Burgman, M. A., Akcakaya, H. R. & R. & Frankham, R. 2000 Predictive accuracy of population viability analysis in conservation biology. *Nature* **404**, 385-387.

Brooks, E. N. & Lebreton, J. 2001 Optimizing removals to control a metapopulation: application to the yellow legged herring gull (*Larus cachinnans*). *Ecological Modelling* **136**, 269-284.

Brown, J.L. 1969 The buffer effect and productivity in tit populations. *The American Naturalist* **103**, 347-354.

Buckland, S. T. B., K.P.; Augustin, N.H. 1997 Model selection: an integral part of inference. *Biometrics* **53**, 603-618.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* **5**, 437 pp.

Caccamise, D. F. & Hedin, R. S. 1985 An aerodynamic basis for selecting transmitter loads in birds. *The Wilson Bulletin* **97**, 306-318.

Caswell, H. 1978 A general formula for the sensitivity of population growth rate to changes in the life history parameters. *Theoretical Population Biology* **14**, 215-230.

Caswell, H. 1989 *Matrix Population Models*. Sunderland, Massachusetts: Sinauer Associates, Inc.

Caswell, H. 2000 No inconsistencies in sensitivity analysis. *Trends in Ecology and Evolution* **15**, 204.

Caswell, H. 2001 *Matrix Population Models, Construction Analysis and Interpretation, 2nd Ed.* Sunderland, Massachusetts: Sinauer Associates, Inc.

Caswell, H., Naiman, R. & Morin, R. 1984 Evaluating the consequences of reproduction in complex salmonid life cycles. *Aquaculture* **43**, 123-143.

Cawthorne, R. A. & Marchant, J. H. 1980 The effects of the 1978/79 winter on British bird populations. *Bird Study* **27**, 163-172.

Chaloupka, M. 2002 Stochastic simulation modelling of southern great barrier reef turtle population dynamics. *Ecological Modelling* **148**, 79-109.

Chapin, F., Zavaleta, E., Eviner, V., Naylor, R., Vitousek, P., Reynolds, H., Hooper, D., Lavorel, S., Sala, O., Hobbie, S., Mack, M. & Diaz, S. 2000 Consequences of changing biodiversity. *Nature* **405**, 234-242.

Citta, J. J. & Mills, L. S. 1999 What do demographic sensitivity analyses tell us about controlling brown-headed cowbirds? *Studies in Avian Biology* **18**, 121-134.

Clutton-Brock, T. H. (ed.) 1988 *Reproductive Success: Studies of individual variation in contrasting breeding seasons*. Chicago: University of Chicago Press.

Clutton-Brock, T. H., Coulson, T. N., Milner-Gulland, E. J., Thomson, D. & Armstrong, H. M. 2002 Sex differences in emigration and mortality affect optimal management of deer populations. *Nature* **415**, 633-637.

Cochran, W. W. 1980 Wildlife Telemetry. In *Wildlife Management Techniques Manual* (ed. S. D. Scemnitz), pp. 507-520. Washington, D.C.: The Wildlife Society.

Cooch, E., White, G.C. 1998 Program MARK: a gentle introduction.

<http://www.phidot.org/software/mark/docs/book/>

Coulson, T. M., G.M.; Hudson E.; Possingham H. 2001 The use and abuse of population viability analysis. *Trends in Ecology and Evolution* **16**, 219-221.

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. & Grenfell, B. T. 2001 Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**, 1528-1531.

Crooks, K. R., Sanjayan, M. A. & Doak, D. F. 1998 New insights on cheetah conservation through demographic modeling. *Conservation Biology* **12**, 889-895.

Crouse, D. T., Crowder, L. B. & Caswell, H. 1987 A stage based population model for loggerhead sea turtles and implications for conservation. *Ecology* **68**, 1412-1423.

Crowder, L. B., Crouse, D. T., Heppell, S. S. & Martin, T. H. 1994 Predicting the Impact of Turtle Excluder Devices On Loggerhead Sea-Turtle Populations. *Ecological Applications* **4**, 437-445.

Cuthbert, R., Fletcher, D., Davis, L.S. 2001 A sensitivity analysis of Hutton's shearwater: prioritising conservation research and management. *Biological Conservation* **100**, 163-172.

de Kroon, H., Plaisier, A., van Groenendael, J. & Caswell, H. 1986 Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**, 1427-1431.

de Kroon, H., van Groenendael, J. & Ehrlén, J. 2000 Elasticities: A review of methods and model limitations. *Ecology* **81**, 607-618.

Dennis, B., Desharnais, R. A., Cushing, J. M. & Costantino, R. F. 1995 Nonlinear demographic dynamics - mathematical models, statistical methods and biological experiments. *Ecological Monographs* **65**, 261-281.

Doak, D., Kareiva, P. & Kleptetka, B. 1994 Modeling Population Viability For the Desert Tortoise in the Western Mojave Desert. *Ecological Applications* **4**, 446-460.

Dobson, A. P. 1987 A comparison of seasonal and annual mortality for both sexes of common British birds. *Ornis Scandinavica* **18**, 122-128.

Ellner, S. P., Fieberg, J., Ludwig, D. & Wilcox, C. 2002 Precision of population viability analysis. *Conservation Biology* **16**, 258-261.

Escos, J., Alados, C. L. & Emlen, J. M. 1994 Application of the Stage-Projection Model With Density- Dependent Fecundity to the Population-Dynamics of Spanish Ibex. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **72**, 731-737.

Evans, M. R. & Burn, J. L. 1996 An experimental analysis of mate choice in the wren: a monomorphic, polygynous passerine. *Behavioural Ecology* **7**, 101-108.

Evans, M., R. 1997 Nest building signals male condition rather than age in wrens. *Animal Behaviour* **53**, 749-755.

Ferrer, M. & Harte, M. 1997 Habitat selection by immature Spanish imperial eagles during the dispersal period. *Journal of Applied Ecology* **34**, 1359-1364.

Fieberg, J. & Ellner, S. P. 2001 Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters* **4**, 244-266.

Frankham, R. 2000 Predictive accuracy of population viability analysis in conservation biology. *Nature* **404**, 385-387.

Gerber, L. R., VanBlaricom, G.R. 2001 Implications of three viability models for the conservation status of the western population of Steller sea lions (*Eumetopias jubatus*). *Biological Conservation* **102**, 261-269.

Gould, W. R. N. J. D. 1998 Estimation of temporal variability of survival in animal populations. *Ecology* **79**, 2531-2538.

Grant, A. & Benton, T. G. 2000 Elasticity analysis for density-dependent populations in stochastic environments. *Ecology* **81**, 680-693.

Grant, A. & Benton, T. G. 2003 Density dependent populations require density dependent elasticity analysis: an illustration using the LPA model of *Tribolium*. *Journal of Animal Ecology* **72**, 94-105.

Grant, A. 1997 Selection pressures on vital rates in density dependent populations. *Proceedings of the Royal Society, series B* **264**, 303-306.

Greenman, J. V. & Benton, T. G. 2003 The amplification of environmental noise in population models: causes and consequences. *The American Naturalist* **161**, 225-239.

Greenwood, J. J. D. B., S.R. 1991 Effects of density-dependence and weather on population changes of English passerines using a non-experimental paradigm. *Ibis* **133**, 121-133.

Greenwood, P. J. 1980 Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**, 1140-1162.

Grenfell, B. T., Wilson, K., Finkenstadt, B. F., Coulson, T. N., Murray, S., Albon, S. D., Pemberton, J. M., Clutton-Brock, T. H. & Crawley, M. J. 1998 Noise and determinism in synchronized sheep dynamics. *Nature* **394**, 674-677.

Gross, K., Lockwood, J. R., Frost, C. C. & Morris, W. F. 1998 Modelling controlled burning and trampling reduction for conservation of *Hudsonia montana*. *Conservation Biology* **12**, 1291-1301.

Hamilton, S., Moller, H. 1995 Can PVA models using computer packages offer useful conservation advice? Sooty shearwaters (*Puffinus griseus*) in New Zealand as a case study. *Biological Conservation* **73**, 107-117.

Hawthorn, I. & Mead, C. J. 1975 Wren movements and survival. *British Birds* **68**, 349-358.

Heppell, S. S., Caswell, H. & Crowder, L. B. 2000 Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology* **81**, 654-665.

Heppell, S. S., Crowder, L. B. & Crouse, D. T. 1996 Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications* **6**, 556-565.

Heppell, S. S., Walters, J. R. & Crowder, L. B. 1994 Evaluating Management Alternatives For Red-Cockaded Woodpeckers - a Modeling Approach. *Journal of Wildlife Management* **58**, 479-487.

Heppell, S., Pfister, C. & de Kroon, H. 2000 Elasticity analysis in population biology: Methods and applications. *Ecology* **81**, 605-606.

Higgins, K., Hastings, A., Sarvela, J. N. & Botsford, L. W. 1997 Stochastic dynamics and deterministic skeletons: Population behaviour of Dungeness crab. *Science* **276**, 1431-1435.

Hill, I. F., Cresswell, B. H. & Kenward, R. E. 1999 Field-testing the suitability of a new back-pack harness for radio-tagging passerines. *Journal of Avian Biology* **30**, 135-142.

Inchausti, P., Weimerskirch, H. 2001 Risks of decline and extinction of the endangered Amsterdam albatross and the projected impact of long-line fisheries. *Biological Conservation* **100**, 377-386.

Jensen, A. L. 1995 Simple density dependent matrix model for population projection. *Ecological Modelling* **77**, 43-48.

Johnson, G. D., Peabworth, J. L. & Krueger, H. O. 1991 Retention of Transmitters Attached to Passerines Using a Glue- On Technique. *Journal of Field Ornithology* **62**, 486-491.

Jones, C. 2002 A model for the conservation management of a 'secondary' prey: sooty shearwater (*Puffinus griseus*) colonies on mainland New Zealand as a case study. *Biological Conservation* **108**, 1-12.

King, C. M. 1980 The weasel (*Mustela nivalis*) and its prey in an English woodland. *Journal of Animal Ecology* **49**, 127-159.

King, R. A. & Belthoff, J. R. 2001 Post-fledging dispersal of burrowing owls in southwestern Idaho: Characterization of movements and use of satellite burrows. *Condor* **103**, 118-126.

Kluijver, H. N. L., J.; van den Ouwelant, C. & Zegwaard, F. 1940 De levenswijze van der Winter-koning, *Troglodytes troglodytes* (L.). *Limosa* **13**, 1-51.

Korschgen, C. E., Kenow, K. P., Green, W. L., Johnson, D. H., Samuel, M. D. & Sileo, L. 1996 Survival of radiomarked canvasback ducklings in northwest Minnesota. *Journal of Wildlife Management* **60**, 121-132.

Krebs, J.R. 1971 Territory and breeding density in the Great tit, *Parus major* L. *Ecology* **52**, 2-22.

Krementz, D. G., Nichols, J. D. & Hines, J. E. 1989 Postfledging Survival of European Starlings. *Ecology* **70**, 646-655.

Lebreton, J. B., K.P.; Clobert, J.; Anderson, D.R. 1992 Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67-118.

Leirs, H., Stenseth, N. C., Nichols, J. D., Hines, J. E., Verhagen, R. & Verheyen, W.

1997 Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature* **389**, 176-180.

Leslie, P. H. 1945 On the use of matrices in certain population mathematics. *Biometrika* **33**, 183-212.

Lindenmayer, D. B. & Possingham, H. P. 1996 Ranking conservation and timber management options for Leadbetter's possum in southeastern Australia using population viability analysis. *Conservation Biology* **10**, 235-251.

Ludwig, D. 1999 Is it meaningful to estimate a probability of extinction? *Ecology* **80**, 298-310.

Magrath, R. D. 1991 Nestling Weight and Juvenile Survival in the Blackbird, *Turdus-Merula*. *Journal of Animal Ecology* **60**, 335-351.

Marchant, J. H. H., R.; Carter, S.P.; Whittington, P. 1990 Population trends in breeding birds. Tring: British Trust for Ornithology/Nature Conservancy Council.

Martien, K. K., Taylor, B. L., Slooten, E. & Dawson, S. 1999 A sensitivity analysis to guide research and management for Hector's dolphin. *Biological Conservation* **90**, 183-191.

Martin, K. 1995 Patterns and mechanisms for age-dependent reproduction and survival in birds. *American Zoologist* **35**, 340-348.

Maynard Smith, J. & Slatkin, M. 1973 The stability of predator prey systems. *Ecology* **54**, 384-391.

McCarthy, M. A., Possingham, H. P., Day, J. R. & Tyre, A. J. 2001 Testing the accuracy of population viability. *Conservation Biology* **15**, 1030-1038.

McDonald, R. A., Webbon, C. & S., H. 2000 The diet of stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) in Great Britain. *Journal of Zoology* **252**, 363-371.

Mesterton-Gibbons, M. 2000 A consistent equation for ecological sensitivity in matrix population analysis. *Trends in Ecology and Evolution* **15**, 115.

Mills, L. S., Doak, D. F. & Wisdom, M. J. 1999 Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* **13**, 815-829.

Mills, L. S., Hayes, S. G., Baldwin, C., Wisdom, M. J., Citta, J., Mattson, D. J. &

Murphy, K. 1996 Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* **10**, 863-873.

Milner, J. M., Elston, D. A. & Albon, S. D. 1999 Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *Journal of Animal Ecology* **68**, 1235-1247.

Morris, W., Doak, D., Groom, M., Kareiva, P., Fieberg, J., Gerber, L. & Thomson, D. 1999 A practical handbook for population viability analysis. The Nature Conservancy, 88pp

Myers, R. A. & Worm, B. 2003 Rapid worldwide depletion of predatory fish communities. *Nature* **423**, 280-283.

Naef-Daenzer, B., Widmer, F. & Nuber, M. 2001 Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* **70**, 730-738.

Nations, C. S. B., M.S. 1996 Stochastic demography for conservation biology. In *Structured population models in marine, terrestrial and freshwater systems* (ed. S. C. Tuljapurkar, H.), pp. 451-469: Chapman and Hall.

Newton, I., Rothery, P. & Dale, L. C. 1998 Density dependence in the bird populations of an oak wood over 22 years. *Ibis* **140**, 131-136.

Opdam, P. & Wiens, J. A. 2002 Fragmentation, habitat loss and landscape management. In *Conserving Bird Biodiversity: General principles and their application* (ed. K. Norris & D. Pain). Cambridge: Cambridge University Press.

Owens, I. P. F. B., P.M. 1994 Mortality costs of parental care and sexual dimorphism in birds. *Proceedings of the Royal Society of London, Series B* **257**, 1-8.

Pauly, D., Christensen, V., Guenette, S., Pitcher, T. J., Sumaila, R., Walters, C. J., Watson, R. & Zeller, D. 2002 Towards sustainability in world fisheries. *Nature* **418**, 689-695.

Peach, W. J., Du Feu, C. & McMeeking, J. 1995 Site tenacity and survival rates of wrens *Troglodytes troglodytes* and treecreepers *Certhia familiaris* in a Nottinghamshire wood. *Ibis* **137**, 497-507.

Perrins, C. M. 1965 Population fluctuations and clutch size in the great tit, *Parus major* L. *Journal of Animal Ecology* **34**, 601-647.

Pollock, K. H., Winterstein, S. R., Bunck, C. M. & Curtis, P. D. 1989 Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* **53**, 7-14.

Reed, J. M., Elphick, C. S. & Oring, L. W. 1998 Life history and viability analysis of the endangered Hawaiian Stilt. *Biological Conservation* **84**, 35-45.

Reed, J. M., Mills, L. S., Dunning Jr, J. B., Menges, E. S., McKelvey, K. S., Frye, R., Beissinger, S. R., Anstett, M. & Miller, P. 2002 Emerging issues in population viability analysis. *Conservation Biology* **16**, 7-19.

Saether, B. 1997 Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology and Evolution* **12**, 143-149.

Saether, B. E., Engen, S., Lande, R., Arcese, P. & Smith, J. N. M. 2000 Estimating the time to extinction in an island population of song sparrows. *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**, 621-626.

Saether, B. E., Engen, S., Lande, R., Both, C. & Visser, M. E. 2002 Density dependence and stochastic variation in a newly established population of a small songbird. *Oikos* **99**, 331-337.

Silvertown, J., Franco, M. & Menges, E. 1996 Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* **10**, 591-597.

Soule, M. E. (ed.) 1987 *Viable populations for conservation*. Cambridge, United Kingdom: Cambridge University Press.

- Starfield, A. M. 1997 A pragmatic approach to modelling for wildlife management. *Journal of Wildlife Management* **61**, 261-270.
- Sullivan, K. A. 1989 Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeotus*). *Journal of Animal Ecology* **58**, 275-286.
- Sutherland, G. D., Harestad, A. S., Price, K. & Lertzman, K. P. 2000 Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* **4**, Article 16. [online].
- Svensson, L. 1984 *Identification guide to European passerines*. Stockholm: Svensson
- Sweeney, J. J. & Tatner, P. 1996 Sexing wrens *Troglodytes troglodytes indigenus* using morphological measurements and discriminant analysis. *Bird Study* **43**, 342-350.
- Sykes, P. W., Carpenter, J. W., Holzman, S. & Geissler, P. H. 1990 Evaluation of 3 Miniature Radio Transmitter Attachment Methods For Small Passerines. *Wildlife Society Bulletin* **18**, 41-48.
- Takada, T. & Nakashizuka, T. 1996 Density dependent demography in a Japanese temperate broad leaved forest. *Vegetatio* **124**, 211-221.
- Tinbergen, L. 1946 Sperver als Roofvijand van Zangvogels. *Ardea* **34**, 1-123.

Todd, C. R. & Ng, M. P. 2001 Generating unbiased correlated random survival rates for stochastic population models. *Ecological Modelling* **144**, 1-11.

Tuljapurkar, S. 1990 *Population dynamics in variable environments*. New York, USA: Springer-Verlag, New York.

van Tienderen, P. H. 2000 Elasticities and the link between demographic and evolutionary dynamics. *Ecology* **81**, 666-679.

Velando, A. & Freire, J. 2002 Population Modelling of European shags (*Phalacrocorax aristotelis*) at their southern limit: conservation implications. *Biological Conservation* **107**, 59-69.

Walls, S. S. & Kenward, R. E. 1998 Movements of radio-tagged buzzards *Buteo buteo* in early life. *Ibis* **140**, 561-568.

Walters, J. R., Crowder, L.B., Priddy, J.A. 2002 Population viability analysis for red-cockaded woodpeckers using an individual based model. *Ecological Applications* **12**, 249-260.

Wesolowski, T. 1981 Population restoration after removal of wren (*Troglodytes troglodytes*) breeding in primeval forest. *Journal of Animal Ecology* **50**, 809-814.

Wesolowski, T. 1983 The Breeding Ecology and Behavior of Wrens Troglodytes-Troglodytes Under Primeval and Secondary Conditions. *Ibis* **125**, 499-515.

White, G. C. & Burnham, K. P. 1999 Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46**, 120-138.

White, G. C. B., K.P.; Anderson, D.R. 2000 Advanced features of program MARK
<http://www.cnr.colostate.edu/~gwhite/mark/Hungary/Advanced.PDF>

Wielgus, R. B., Sarrazin, F., Ferriere, R. & Clobert, J. 2001 Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation* **98**, 293-303.

Williamson, K. 1969 Habitat preferences of the wren on English farmland. *Bird Study* **16**, 53-59.

Wisdom, M. J. & Mills, L. S. 1997 Sensitivity analysis to guide population recovery: Prairie- chickens as an example. *Journal of Wildlife Management* **61**, 302-312.

Wisdom, M. J., Mills, L. S. & Doak, D. F. 2000 Life stage simulation analysis: Estimating vital-rate effects on population growth for conservation. *Ecology* **81**, 628-641.

Yearsley, J. M., Fletcher, D. & Hunter, C. 2003 Sensitivity analysis of equilibrium population size in a density-dependent model for Short-tailed Shearwaters. *Ecological Modelling* **163**, 119-129.

Zann, R. & Runciman, D. 1994 Survivorship, dispersal and sex ratios of Zebra finches *Taeniopygia guttata* in south east Australia. *Ibis* **136**, 136-146.

Appendix 1

Model code
(written in Matlab, The Mathworks Inc.)

```

%Mark Trinder, 2003.
%Density dependent, stochastic simulation model of a Wren population
%Based on data collected in Mine Wood, Brideg of Allan, Stirling.

clear all
runno=1; %runno defines number of repeat simulations
for runloop=1:runno;
    runloop

    %clears file stores
    [fid,msg]=fopen('pop1','w'); %population vector for all time steps
    fclose(fid);
    [fid,msg]=fopen('pop13','w'); %population vector excluding 0 entries
    fclose(fid);
    [fid,msg]=fopen('pop14','w'); %population vector excluding extinct runs
    fclose(fid);
    [fid,msg]=fopen('ssbdm','w'); %density dependent vital rate storage
    fclose(fid);
    [fid,msg]=fopen('ssibdm','w'); %density independent vital rate storage
    fclose(fid);
    [fid,msg]=fopen('finvad','w'); %female invader population storage
    fclose(fid);
    [fid,msg]=fopen('minvad','w'); %male invader population storage
    fclose(fid);
    [fid,msg]=fopen('fresid','w'); %female resident population storage
    fclose(fid);
    [fid,msg]=fopen('mresid','w'); %male resident population storage
    fclose(fid);
    [fid,msg]=fopen('spare','w'); %excess resident and invader numbers store
    fclose(fid);
    [fid,msg]=fopen('gendat','w'); %general breeding data store
    fclose(fid);

    %-----model run info-----
    %the following section contains 'switches' for different
    %subroutines in the model

    invpopext=0; %takes a value of 0,1,2:
    %switches between:
    %(1) invasion elasticities
    %(0) population elasticities
    %(2) extinction elas

    allrand=1; %turns all random routines on (1) or off (0)
    density=1; %turns d.d. survival on (1) or off (0)
    terrlimit=1; %breeding territory density dependence on (1) or off (0)
    juvdd=0; %d.d. survival for all ages (0) or just juveniles (1)
    mfext=1; %quasi-extinction level sum of both sexes (0) or just lower (1)

    %individual random routine switches: 0-off, 1-on
    env=1; %environmental stochasticity
    demog1=1; %survival demographic stochasticity - for residents
    demog2=0; %survival demog stoch - for invaders
    demog3=1; %demographic stochasticity in birth sex ratio
    covar=1; %vital rate covariance
    randterr=1; %number of male breeding territories fixed/random
    randterr2=0; %female breeding territories: (1) random and different from
        %male number, (0) same as male (whether random or fixed)
    binoterrm=0; %territory sharing between male residents and invaders,
        %binomial or rounded to nearest integer
    binoterrf=0; %territory sharing between female residents and invaders
    breedattempts=1; %number of breeding attempts per individual
    breedratio=1; %random ratio of female territories to male territories

    %switches for breeding routines
    mixedpairs=1; %excess res and inv breed together (1) or don't (0)
    dominant=0; %excess res and inv mate and offspring all inv(1) or equal(0)
    binomix=0; %offspring of mixed prs split res and inv by rounding (0) or binomially (1)

```

```

switch allrand
case 0; %randomness switches all off (0)
    env=0;
    demog1=0;
    demog2=0;
    demog3=0;
    covar=0;
    randterr=0;
    randterr2=0;
    binoterrm=0;
    binoterrf=0;
    breedratio=0;
    breedattempts=0;
    dominant=0;
    mixedpairs=0;
    binomix=0;
    breedratio=0;
end

quasiextmain=5; %sets extinction threshold
redvar=0.6; %reduces the size of the inpur vital rate variances

%popsizer is used to increase the simulated population size actual to any
%size range to reduce rounding errors and prevent population extinction
if invpopext==2; %extinction run
    popsizer1=1;
else
    popsizer1=1000; %popsizer1 applies to residents
    popsizer2=10; %popsizer2 applies to invaders
end

%-----invader format-----
%sets parameters to determine invasion format (if appropriate)
%number of time steps for each invasion, invaders only present
%for 1st half of time, the 2nd half is a recovery period for residents
invp=200;

%number of time steps at beginning of invasion not used for
%invasion rate calculations
cut=15;

invdelay=50; %time period before first invasion
invprop1=0.2; %proprn. of res turned into inv at beginning of invasion
rateindexstart=1; %counter used to record data

%-----displays run type and prompts for input data-----
if invpopext==1; out='invasion run';
elseif invpopext==0; out='population size run';
else out='extinction risk run';
end
disp(out)
switch invpopext
case 0 %population run
    if runno==1;
        years=input('how many years to simulate? ');
        sim=input('how many simulation runs? ');
        inc=input('perturbation value (range 0-0.05)? ');
        pert=1;
        ratepert1=2; %runloop+X
    elseif runno>1;
        years=500;
        sim=13;
        inc=0.01;
        pert=1;
        ratepert1=2; %runloop+X
    end
case 1 %invasion run

```

```

if runno==1;
years=input('how many years to simulate? ');
sim=input('how many simulation runs? ');
inc=input('perturbation value (range 0-0.05)? ');
pert=1;
ratepert1=2; %runloop+X
elseif runno>1;
years=160050; %160100
sim=13;
inc=0.05;
pert=1;
ratepert1=2; %runloop+X
end
case 2
if runno==1;
years=input('how many years to simulate? ');
sim=input('how many simulation runs? ');
inc=input('perturbation value (range 0-0.05)? ');
pert=input('how many repeats runs? ');
ratepert1=2; %runloop+X
elseif runno>1;
years=250;
sim=10; %repeat runs of the same perturbed parameter
inc=0.05;
pert=500;
ratepert1=1; %runloop+X
end
end

%bigrun reduces the size of files stored to aid in managing space
switch invpopext
case 0
if years>=100000; bigrun=1;
else bigrun=0;
end
case 1
if ((years-invdelay)/invp)>=100; bigrun=1;
else bigrun=0;
end
case 2
if pert>=1; bigrun=1;
else bigrun=0;
end
end

%if no d.d. routines operating, stochastic growth rates are calculated
if density==0 | terrlimit==0; stocha=1; else stocha=0; end

%d1main determines strength of density dependent survival parameter 'a'
d1main=0.0025; %0.0018 - 0.0036 (low to high values)
fred=1; %fred adjusts strength of female d.d. survival relative to males
%d2main determines strength of density dependent survival parameter 'b'
d2main=4; %2 - 10 (weak to strong)

cov=0.33; %degree of covariance between vital rates

%raise/raise2 adjust mean vital rate values to take account of d.d. in
%the recorded values
raise=1.2;
raise2=1.2;

%potir can be used to apply a rate of immigration into the population
potir=0; %usually set to 0
terrnomain=25; %sets the mean number of male breeding territories

%switch on (1) or off (0) file stores
saverates=1; %vital rates
savef=1; %general stuff (e.g. territory number etc)
savepop=1; %population data
%-----

```

```

%if inv elasticities: creates storage matrices (slope,slopedat)
switch invpopext;
case 1;
    slopedat=zeros(floor((years-invdelay)/invp),sim);
    slope=zeros(floor((years-invdelay)/invp),1);
case 0;
    slopedat=0;
case 2
    extprob=zeros(pert,sim);
    slopedat=0;
end

%baseline demographic rates
%f/m - female/male; s/br - survival/fecundity; age classes 1-3
%means      %stds
fsm1=0.43;  fssd1=0.11;
fsm2=0.52;  fssd2=0.247;
fsm3=0.46;  fssd3=0.21;

msm1=0.43;  mssd1=0.11;
msm2=0.52;  mssd2=0.247;
msm3=0.46;  mssd3=0.21;

fbrm1=1.78; fbrsd1=0.34;
fbrm2=1.4;  fbrsd2=0.79;
fbrm3=1.4;  fbrsd3=0.79;

mbrm1=1.61; mbrsd1=0.27;
mbrm2=1.25; mbrsd2=0.48;
mbrm3=1.25; mbrsd3=0.48;

%mean and std breeding attempt numbers
fembrmean=[1.32;1.21;1.21];
fembrstd=[0.05;0.21;0.21];
malebrmean=[1.19;1.7;1.7];
malebrstd=[0.14;0.11;0.11];

%rates expressed in matrix form
mean2mat= [fbrm1*fsm1*fembrmean(1)  fbrm2*fsm2*fembrmean(2)  fbrm3*fsm3*fembrmean(3)  0  0  0;
           fsm1      0      0      0      0      0;
           0      fsm2      fsm3      0      0      0;
           0  0  0  mbrm1*msm1*malebrmean(1)  mbrm2*msm2*malebrmean(2)  mbrm3*msm3*malebrmean(3);
           0      0      0      msm1      0      0;
           0      0      0      0      msm2      msm3];

%adjustments to rates
means1 = [fbrm1 fbrm2 fbrm3 (fsm1*(raise)) (fsm2*(raise)) (fsm3*(raise)) (msm1*(raise))
(msm2*(raise)) (msm3*(raise)) mbrm1 mbrm2 mbrm3];
means1mat=[fbrm1*fsm1 fbrm2*fsm2 fbrm3*fsm3; (fsm1) 0 0;0 (fsm2) (fsm3)];

means=means1;
%switches between stochastic and deterministic runs
switch env;
case 1;
    sds=[fbrsd1 fbrsd2 fbrsd3 fssd1 fssd2 fssd3 mssd1 mssd2 mssd3 mbrsd1 mbrsd2 mbrsd3];
case 0;
    sds=zeros(1,12);
end
sds=sds*redvar; %redvar adjusts rate variances
vars = (sds).^2;

%rate covariance routine
%corr defines the correlation structure between the rates
switch covar;
case 1;
    corr= [1 cov cov -cov -cov -cov -cov -cov -cov cov cov cov;
           0 1.0 cov -cov -cov -cov -cov -cov -cov cov cov cov;
           0 0 1.0 -cov -cov -cov -cov -cov -cov cov cov cov;
           0 0 0 1.0 cov cov cov cov cov cov -cov -cov -cov;
           0 0 0 0 1.0 cov cov cov cov -cov -cov -cov;

```

```

0 0 0 0 0 1.0 cov cov cov -cov -cov -cov;
0 0 0 0 0 0 1.0 cov cov -cov -cov -cov;
0 0 0 0 0 0 0 1.0 cov -cov -cov -cov;
0 0 0 0 0 0 0 0 1.0 -cov -cov -cov;
0 0 0 0 0 0 0 0 0 1.0 cov cov;
0 0 0 0 0 0 0 0 0 0 1.0 cov;
0 0 0 0 0 0 0 0 0 0 0 1.0];
case 0; %deter covar mx
    corr=eye(12);
end

elems = means;

%this turns the corr's into a symmetrical matrix and z12 is cov matrix
np=12; %number of non-zero entries in population matrix
corrs = corr + (corr' - (eye(np)));
[uuu,eee] = eig(corrs);
z12 = uuu*(sqrt(abs(eee))*uuu');

%calculates beta cdf's for survival rates
for iii = 4:(np-3)
    for fx100 = 1:101
        ffx = (fx100-1)/100;
        parabetas(fx100,(iii-3)) = betaval(means(iii),sqrt(vars(iii)),ffx);
    end; %fx100
    parabetas; %contains beta cdf's
end; %iii

[pb1,pb2]=find(parabetas>1);
parabetas(pb1,pb2)=1;

%-----
%file storage index variable - determines the max size for matrices
%held in memory before being saved
if rem (years,10000)==0;
    filesize=min(10000,years);
else filesize=min(5000,years);
end

switch invpopext
case 2
    if pert==0; endperts=1; else endperts=pert; end;
    %if pert==10; endperts=10; else endperts=13; end;
case 1
    endperts=1;
case 0
    endperts=1;
end

%-----population projection start-----
%t is no. of program runs
for t=1:sim; t %simulation loop, prints to screen

    switch invpopext
    case 2 %extra file stores for extinction elasticity runs
        [fid,msg]=fopen('pop1','w');
        fclose(fid);
        [fid,msg]=fopen('pop13','w');
        fclose(fid);
        [fid,msg]=fopen('pop14','w');
        fclose(fid);
        [fid,msg]=fopen('ssbdm','w');
        fclose(fid);
    end

    %-----perturbation loop start-----
    %rate perturbations for elasticity analysis
    for pertloop=1:endperts; %perturbation loop for extinction runs
        if pertloop==1 | pertloop==pert; pertloop

```



```

elseif rem (pertloop, (pert*0.5))==0, pertloop
end;

switch invpopext
case 1
    pop=0;
otherwise
    switch bigrun
    case 1
        pop=zeros(filesize,2);
    otherwise
        pop=zeros(filesize,9);
    end
    sbdm=zeros(filesize,12);
end

%adjust1/2 are used to change strength of d.d. for different
%simulation runs
popsizer=popsizer1;
adjust1=[1:0.5:15];
adjust2=[1:1:20];

%makes changes depending on which elasticities are being calculated
switch invpopext
%invasion
case 1
    y=[40;12;8;40;12;8];
    adjust=[1:1:25];
    %d1=((dlmain/popsizer)/(sum(y)/360))*adjust2(runloop);
    d1=(dlmain/popsizer)/(sum(y)/360);
    %d2=d2main;
    d2=d2main*adjust2(runloop);
    invprop=invprop1;
    init=sum(y);
    terrno=terrnomain*popsizer;
%population size
case 0
    y=[40;12;8;40;12;8];
    adjust=[1:1:25];
    %d1=((dlmain/popsizer)/(sum(y)/360))*adjust2(runloop);
    d1=(dlmain/popsizer)/(sum(y)/360);
    %d2=d2main;
    d2=d2main*adjust2(runloop);
    invprop=invprop1;
    init=sum(y);
    terrno=terrnomain*popsizer;
%extinction probability
case 2
    y=[40;12;8;40;12;8];
    init=y;
    invprop=invprop1;
    popsizer=popsizer1;
    %popsizer=popsizer1*adjust2(pertloop);
    d1=((dlmain/popsizer)/(sum(init)/360));
    %d1=((dlmain/popsizer)/(sum(y)/360))*adjust1(pertloop);
    d2=d2main;
    %d2=d2main*adjust1(pertloop);
    terrno=(terrnomain*popsizer)-adjust2(runloop);
    %terrno=terrnomain*popsizer;
    quasiext=quasiextmain*popsizer;
    %quasiext=quasiextmain*adjust2(pertloop);
    %quasiext=quasiextmain+adjust2(pertloop);
end

%resets randon number generators from the clock
rand('seed',sum(57*(clock)));
randn('seed',sum(100*(clock)));

y=y*popsizer;
invgen=1;

```

```

yiallstart=zeros(6,1);

%builds covar random pop matrix
gr=y;
v=years;
A=zeros(years,np);
for mat=1:v;
    uncov=randn(1,np);
    rawelems=(z12*(uncov'))';
    elems(4)=parabetas(round(100*stnormfx(rawelems(4)))+1,1);
    elems(5)=parabetas(round(100*stnormfx(rawelems(5)))+1,2);
    elems(6)=parabetas(round(100*stnormfx(rawelems(6)))+1,3);
    elems(7)=parabetas(round(100*stnormfx(rawelems(7)))+1,4);
    elems(8)=parabetas(round(100*stnormfx(rawelems(8)))+1,5);
    elems(9)=parabetas(round(100*stnormfx(rawelems(9)))+1,6);

    for zz=1:(np-9);
        elems(zz)=lnorms(means(zz),vars(zz),rawelems(zz));
    end;
    for zz1=10:np;
        elems(zz1)=lnorms(means(zz1),vars(zz1),rawelems(zz1));
    end;
    elems1=elems; %elems1 contains a set of rates for one year

    switch invpopext
    case 2
        switch stocha
        case 0 %normal extinction runs
            ratepert=ratepert1; %2:13 (add 1 to rate to be perturbed)
        case 1 %density independent stochastic sims
            ratepert=t;
        end
    otherwise
        ratepert=t;
    end

    switch invpopext;
    case 0; %population size
        ratepert=t;
        if ratepert<=1; elems1=elems1;
        elseif ratepert>=14; elems1=elems1;
        else elems1(1,ratepert-1)=elems(1,ratepert-1)+(inc*elems(1,ratepert-1));
        end;
    case 2; %extinction risk
        if ratepert<=1; elems1=elems1;
        elseif ratepert>=14; elems1=elems1;
        else elems1(1,ratepert-1)=elems(1,ratepert-1)+(inc*elems(1,ratepert-1));
        end;
    end

    elems1(find(elems1(4:9)>1)+3)=1;
    elems1(find(elems1(4:9)<0)+3)=0;
    %A stores all rates for the whole simulation, one row per year
    A(mat,:)=elems1;
    A1=[fbrm1 fbrm2 fbrm3 fsm1 fsm2 fsm3 msm1 msm2 msm3 mbrm1 mbrm2 mbrm3];

end
Am=mean(A);

%sets territory number to mean starting point
ball0=terrno;
terrds=1*popsizer;

%switches envirnomental stochasticity on/off
switch env;
case 0; %off
    A=repmat(A(1,:),years,1);
    %A=repmat(A1,years,1);
case 1; %on

```

```

    A=A;
end

%-----population simulation start-----
%gen is year
for gen=1:v;

    if t>=2, ref=gen+((t-1)*v);
    else ref=gen;end;
    mp=init;

    %demographic rates for year: (gen)
    fbr1=A(gen,1);
    fbr2=A(gen,2);
    fbr3=A(gen,3);
    fs0=A(gen,4);
    fs1=A(gen,5);
    fs2=A(gen,6);
    ms0=A(gen,7);
    ms1=A(gen,8);
    ms2=A(gen,9);
    mbr1=A(gen,10);
    mbr2=A(gen,11);
    mbr3=A(gen,12);

    %-----invaders-----
    %standard invasion
    yistart=yiallstart;

    switch invpopext;
    case 1;
        invdelay=invdelay;
    case 0;
        invdelay=years+1;
    case 2
        invdelay=years+1;
    end

    %invdelay lets res pop to get going before invs start
    if invdelay==0; delay=0; invstart=1;
    else invstart=invdelay+1; %delay=[1:1:invdelay];
    end

    %inv pop is set to be a propn of total pop at start of invasion
    warning off;
    yistart=round(y*invprop); %invprop sets the propn
    warning on;

    if gen<=invdelay;
        yi=zeros(6,1);
    else
        switch invstart;
        case gen;
            yi=yistart; %y
            switch terrlimit %switches between ghost and real inv
            case 1
                y=yistart*((1/invprop)-1);
            case 0
                y=y; %if ghost invasion
            end
            invgen=1;
        case (rem(gen-invstart,invp))+invstart;
            yi=yistart; %y
            switch terrlimit
            case 1
                y=yistart*((1/invprop)-1);
            case 0
                y=y;
            end
            invgen=1;
        otherwise

```

```

        yi=yi;
        y=y;
    end
end

%-----survival density dependent function-----
switch density;
case 1;
    %dd by sex, just residents
    totdd(1)=(1/(1+((d1*fred)*sum(y(1:6))^d2)));
    totdd(2)=(1/(1+((d1*sum(y(1:6)))^d2)));

    %dd by sex, residents and invaders
    invdd(1)=(1/(1+((d1*fred)*(sum(y(1:6))+sum(yi(1:6))))^d2)));
    invdd(2)=(1/(1+((d1*(sum(y(1:6))+sum(yi(1:6))))^d2)));

case 0;
    totdd=ones(1,2);
    invdd=ones(1,2);
end

switch savef==1;
case 1;
    dden(gen,1:2)=totdd; dden(gen,3:4)=invdd;
end;
dden(gen,1:2)=totdd;
%if unlimited territories then dd affects res only
%if terr limit is operating then invaders contribute to dd
switch terrlimit
case 1
    dd=invdd;
case 0
    dd=totdd;
end

%-----survival routine-----

%-----residents-----
sv=[fs0;fs1;fs2;ms0;ms1;ms2];
%switches density dependent survival between all ages (0) and
%just juveniles (1)
switch juvdd
case 1;
    ressurvs(1)=sv(1)*dd(1);
    ressurvs(2:3)=sv(2:3);
    ressurvs(4)=sv(4)*dd(2);
    ressurvs(5:6)=sv(5:6);
case 0;
    ressurvs(1:3,1)=sv(1:3).*dd(1);
    ressurvs(4:6,1)=sv(4:6).*dd(2);
end

switch demogl
%demographic stochasticity off (rounding)
case 0;
    if y(1,1)<=0, ydd(1,1)=0; else ydd(1,1)=round(y(1)*ressurvs(1)); end;
    if y(2,1)<=0, ydd(2,1)=0; else ydd(2,1)=round(y(2)*ressurvs(2)); end;
    if y(3,1)<=0, ydd(3,1)=0; else ydd(3,1)=round(y(3)*ressurvs(3)); end;
    if y(4,1)<=0, ydd(4,1)=0; else ydd(4,1)=round(y(4)*ressurvs(4)); end;
    if y(5,1)<=0, ydd(5,1)=0; else ydd(5,1)=round(y(5)*ressurvs(5)); end;
    if y(6,1)<=0, ydd(6,1)=0; else ydd(6,1)=round(y(6)*ressurvs(6)); end;

%demographic stochasticity on (binomial)
case 1;
    warning off;
    if y(1,1)<=0, ydd(1,1)=0; else ydd(1,1)=bino_rndc(1,y(1),(ressurvs(1))); end;
    if y(2,1)<=0, ydd(2,1)=0; else ydd(2,1)=bino_rndc(1,y(2),(ressurvs(2))); end;
    if y(3,1)<=0, ydd(3,1)=0; else ydd(3,1)=bino_rndc(1,y(3),(ressurvs(3))); end;
    if y(4,1)<=0, ydd(4,1)=0; else ydd(4,1)=bino_rndc(1,y(4),(ressurvs(4))); end;
    if y(5,1)<=0, ydd(5,1)=0; else ydd(5,1)=bino_rndc(1,y(5),(ressurvs(5))); end;
    if y(6,1)<=0, ydd(6,1)=0; else ydd(6,1)=bino_rndc(1,y(6),(ressurvs(6))); end;
end

```

```

warning on;
end
%ydd contains the density dependent survivors
ydd=max(ydd,0);

%-----
warning off;
dds1=ydd./y;
dds=max(dds1,0);
dis(1:3,1)=min(dds(1:3) ./dd(1),sv(1:3));
dis(4:6,1)=min(dds(4:6) ./dd(2),sv(4:6));
warning on;
%dds - density dependent survival rate
%dis - density independent survival rates

%-----survival perturbation for invaders-----
%same survival rate as res, but turned back into d.i. rate
invsurvs(1:3,1)=dds(1:3,1) ./dd(1);
invsurvs(4:6,1)=dds(4:6,1) ./dd(2);
idds=zeros(6,1);
%now perturbation is applied, to d.i. rate
if t>=5 & t<=7;
    invsurvs(t-4)=(invsurvs(t-4)*(1+inc));
elseif t>=8 & t<=10;
    invsurvs(t-4)=(invsurvs(t-4)*(1+inc));
else invsurvs=invsurvs;
end
%d.d. is reapplied - invsurvs now identical to ressurvs plus
%perturbation of rate
invsurvs(1:3)=invsurvs(1:3)*dd(1);
invsurvs(4:6)=invsurvs(4:6)*dd(2);
invsurvs(find(invsurvs(1:6)>1))=1;
invsurvs(find(invsurvs(1:6)<0))=0;

%-----invader survival-----
switch demog2;
case 1; %invaders binomial survival seperately from residents
    if yi(1,1)<=0, yddi(1,1)=0; else yddi(1,1)=bino_rndc(1,yi(1),(invsurvs(1))); end;
    if yi(2,1)<=0, yddi(2,1)=0; else yddi(2,1)=bino_rndc(1,yi(2),(invsurvs(2))); end;
    if yi(3,1)<=0, yddi(3,1)=0; else yddi(3,1)=bino_rndc(1,yi(3),(invsurvs(3))); end;
    if yi(4,1)<=0, yddi(4,1)=0; else yddi(4,1)=bino_rndc(1,yi(4),(invsurvs(4))); end;
    if yi(5,1)<=0, yddi(5,1)=0; else yddi(5,1)=bino_rndc(1,yi(5),(invsurvs(5))); end;
    if yi(6,1)<=0, yddi(6,1)=0; else yddi(6,1)=bino_rndc(1,yi(6),(invsurvs(6))); end;
case 0; %invader survival rates identical to resident
    if yi(1,1)<=0, yddi(1,1)=0; else yddi(1,1)=round(yi(1)*invsurvs(1)); end;
    if yi(2,1)<=0, yddi(2,1)=0; else yddi(2,1)=round(yi(2)*invsurvs(2)); end;
    if yi(3,1)<=0, yddi(3,1)=0; else yddi(3,1)=round(yi(3)*invsurvs(3)); end;
    if yi(4,1)<=0, yddi(4,1)=0; else yddi(4,1)=round(yi(4)*invsurvs(4)); end;
    if yi(5,1)<=0, yddi(5,1)=0; else yddi(5,1)=round(yi(5)*invsurvs(5)); end;
    if yi(6,1)<=0, yddi(6,1)=0; else yddi(6,1)=round(yi(6)*invsurvs(6)); end;
end

yddi=max(0,yddi);

warning off;
idds1=yddi./yi;
warning on;

idds=max(idds1,0);

%-----reproduction-----
%territory number changes randomly each year, mid keeps the
%change small and prevents big jumps up and down. if
%territory no. falls in one year it is likely to go up again next.
mid=(1-(ball0/terrno))*10*popsizer;

```

```

switch randterr;
case 1;
    ball=round(rnorm(1,mid,terrsd))+ball0;
case 0;
    ball=terrno;
end

%territory no. even so no territory advantage for inv or res
if rem(ball,2)==1; ball=ball+1;
else ball=ball;
end

%use to turn off territory density dependence
if terrlimit==0; ball=Inf; else ball=ball; end

% lastyr is used to set immi rate, using
% if gen<=1, lastyr1=ball; else lastyr1=sum(Mres)-Kplus; end;
% if lastyr1<=0, lastyr=0; else lastyr=lastyr1; end;

%resident older males (Mres(2:3))
Mres(3,1)=ydd(6);
Mres(2,1)=ydd(5);
Mres(1,1)=0;

%invader older males (Minv(2:3))
Minv(3,1)=yddi(6);
Minv(2,1)=yddi(5);
Minv(1,1)=0;

Mres=max(Mres,0);

%-----male territory allocation-----
switch terrlimit
case 0
    Mres(1)=ydd(4);
    Minv(1)=yddi(4);
case 1

    if ydd(4)+yddi(4)<=(ball-(sum(Mres(2:3))+sum(Minv(2:3))));
        Mres(1)=ydd(4); Minv(1)=yddi(4);
    elseif yddi(4)==0; Minv(1)=0;
        Mres(1)=min((ball-(sum(Mres(2:3))+sum(Minv(2:3)))),ydd(4));
    else
        switch binoterrm; %invader first
        case 1; %binomial sharing of territories based on proportions of inv and res
            if (ball-(sum(Minv(2:3))+sum(Mres(2:3))))<=0; Mres(1)=0;
            else
                Minv(1)=bino_rndc(1,(ball-
                    (sum(Mres(2:3))+sum(Minv(2:3))),(yddi(4)/(yddi(4)+ydd(4))));
            end
        case 0; %territories shared in proportion to nos of inv and res
            if (ball-(sum(Mres(2:3))+sum(Minv(2:3))))<=0; Minv(1)=0;
            else
                Mres(1)=round((ydd(4)/(ydd(4)+yddi(4)))*(ball-(sum(Minv(2:3))+sum(Mres(2:3))));
            end
        end
    end;

%alternative territory allocation by rounding, inv or res first:
if Mres(1)==0;
    %%if invs went first
    if Minv(1)>=(ball-(sum(Mres(2:3))+sum(Minv(2:3))));
        Minv(1)=(ball-(sum(Mres(2:3))+sum(Minv(2:3))));
    elseif Minv(1)>yddi(4); Minv(1)=yddi(4);
    else Minv(1)=Minv(1);
    end;
    Mres(1)=max(ball-(sum(Mres(2:3))+sum(Minv)),0);
    if Mres(1)>ydd(4); Mres(1)=ydd(4);

```

```

        else Mres(1)=Mres(1);
    end
else
    %if res went first
    if Mres(1)>=(ball-(sum(Mres(2:3))+sum(Minv(2:3))));
        Mres(1)=(ball-(sum(Mres(2:3))+sum(Minv(2:3))));
    elseif Mres(1)>ydd(4); Mres(1)=ydd(4);
    else Mres(1)=Mres(1);
    end;
    Minv(1)=max(ball-(sum(Minv(2:3))+sum(Mres)),0);
    if Minv(1)>yddi(4); Minv(1)=yddi(4);
    else Minv(1)=Minv(1);
    end
end
end

%-----
%population vectors updated
y1(5,1)=Mres(1);
y1(6,1)=sum(Mres(2:3));
yil(5,1)=Minv(1);
yil(6,1)=sum(Minv(2:3));

%randomly changes sex ratio for breeding territories
switch breedratio;
case 0;
    sr=1;
case 1;
    sr=rnorm(1,1,0.16);
end

switch randterr2;
case 1;
    femterr=round(sr*(ball));
case 0;
    femterr=ball;
end

if rem(femterr,2)==1; femterr=femterr+1;
else femterr=femterr;
end

%resident older females (Fres(2:3))
Fres(3,1)=ydd(3);
Fres(2,1)=ydd(2);
Fres(1,1)=0;

%invader older females (Finv(2:3))
Finv(3,1)=yddi(3);
Finv(2,1)=yddi(2);
Finv(1,1)=0;

%-----female territory allocation-----
switch terrlimit
case 0
    Fres(1)=ydd(1);
    Finv(1)=yddi(1);
case 1

    if ydd(1)+yddi(1)<=(femterr-(sum(Fres(2:3))+sum(Finv(2:3))));
        Fres(1)=ydd(1); Finv(1)=yddi(1);
    elseif yddi(1)==0; Finv(1)=0;
        Fres(1)=min((femterr-(sum(Fres(2:3))+sum(Finv(2:3)))),ydd(1));
    else
        switch binoterrf;
        case 1;
            if (femterr-(sum(Finv(2:3))+sum(Fres(2:3))))<=0; Fres(1)=0;
            else
                Fres(1)=bino_rndc(1,(femterr-
                    (sum(Fres(2:3))+sum(Finv(2:3))),((ydd(1))/(ydd(1)+yddi(1))));
            end
        end
    end
end
end

```

```

        end
    case 0;
        if (femterr-(sum(Fres(2:3))+sum(Finv(2:3))))<=0; Finv(1)=0;
        else
            Fres(1)=round((femterr-
                (sum(Finv(2:3))+sum(Fres(2:3))))*((ydd(1)/((yddi(1))+ydd(1)))));
        end
    end
end

%alternative territory allocation using rounding:

if Fres(1)==0;
    %%if inv went first
    if Finv(1)>=(femterr-(sum(Fres(2:3))+sum(Finv(2:3))));
        Finv(1)=(femterr-(sum(Fres(2:3))+sum(Finv(2:3))));
    elseif Finv(1)>yddi(1); Finv(1)=yddi(1);
    else Finv(1)=Finv(1);
    end;
    Fres(1)=max(femterr-(sum(Fres(2:3))+sum(Finv)),0);
    if Fres(1)>ydd(1); Mres(1)=ydd(1);
    else Fres(1)=Fres(1);
    end
else
    %%if res went first
    if Fres(1)>=(femterr-(sum(Fres(2:3))+sum(Finv(2:3))));
        Fres(1)=(femterr-(sum(Fres(2:3))+sum(Finv(2:3))));
    elseif Fres(1)>ydd(1); Fres(1)=ydd(1);
    else Fres(1)=Fres(1);
    end;
    Finv(1)=max(femterr-(sum(Finv(2:3))+sum(Fres)),0);
    if Finv(1)>yddi(1); Finv(1)=yddi(1);
    else Finv(1)=Finv(1);
    end
end
end
%-----

%breeding slots split between residents and invaders, invaders mating with surplus residents
aFres(3,1)=(min(Fres(3),round(sum(Mres)*sr)));
aFres(2,1)=(min(Fres(2),round(sum((Mres)*sr)-(aFres(3)))));
aFres(1,1)=(min(Fres(1),round(sum((Mres)*sr)-(aFres(3)+aFres(2)))));
Frsp=(Fres)-(aFres);
if sum(Frsp)>0, Frsp=Frsp; else Frsp=0; end

aMres(3,1)=(min(Mres(3),round(sum(aFres)/sr)));
aMres(2,1)=(min(Mres(2),round(sum((aFres)/sr)-(aMres(3)))));
aMres(1,1)=(min(Mres(1),round(sum((aFres)/sr)-(aMres(3)+aMres(2)))));
Mrsp=(Mres)-(aMres);
if sum(Mrsp)>0, Mrsp=Mrsp; else Mrsp=0; end

switch terrlimit %if ghost invasions no limit to invader breeding
case 0
    aFinv=Finv;
    aMinv=Minv;
case 1

    switch dominant;
    case 1; %all mixed pairs produce invaders - invader dominant
        %---spare residents breed with invaders
        aFinv(3,1)=(min(Finv(3),round((sum(Mrsp)+sum(Minv))*sr)));
        aFinv(2,1)=(min(Finv(2),round(((sum(Mrsp)+sum(Minv))*sr)-(aFinv(3)))));
        aFinv(1,1)=(min(Finv(1),round(((sum(Mrsp)+sum(Minv))*sr)-(aFinv(3)+aFinv(2)))));
        Fisp=sum(Finv)-sum(aFinv);
        if sum(Fisp)>0, Fisp=Fisp; else Fisp=0; end

        aMinv(3,1)=(min(Minv(3),round((sum(aFrsp)+sum(Finv))/sr)));
        aMinv(2,1)=(min(Minv(2),round(((sum(aFrsp)+sum(Finv))/sr)-(aMinv(3)))));
        aMinv(1,1)=(min(Minv(1),round(((sum(aFrsp)+sum(Finv))/sr)-(aMinv(3)+aMinv(2)))));

```



```

Misp=sum(Minv)-sum(aMinv);
if sum(Misp)>0, Misp=Misp; else Misp=0; end

%----spare residents DONT breed with invaders, yet....
case 0; %no dominance
aFinv(3,1)=(min(Finv(3),round(sum(Minv)*sr)));
aFinv(2,1)=(min(Finv(2),round(sum((Minv)*sr)-(aFinv(3)))));
aFinv(1,1)=(min(Finv(1),round(sum((Minv)*sr)-(aFinv(3)+aFinv(2)))));
Fisp=(Finv)-(aFinv);
if sum(Fisp)>0, Fisp=Fisp; else Fisp=0; end

aMinv(3,1)=(min(Minv(3),round(sum(aFinv)/sr)));
aMinv(2,1)=(min(Minv(2),round(sum((aFinv)/sr)-(aMinv(3)))));
aMinv(1,1)=(min(Minv(1),round(sum((aFinv)/sr)-(aMinv(3)+aMinv(2)))));
Misp=(Minv)-(aMinv);
if sum(Misp)>0, Misp=Misp; else Misp=0; end

%mixed pairings - half invader offspring and half resident
switch mixedpairs
case 1; %even split of offspring from mixed pairs
mixed(1,1)=min(round(sum(Mrsp)*sr),sum(Fisp));
mixed(2,1)=min(round(sum(Misp)*sr),sum(Frsp));
extra=zeros(2,1);
%mixed=zeros(2,1); %turned off mixed pairs
if mixed(1)<=0; aFinv=aFinv; aMres=aMres;
else
switch binomix;
case 1;
extra(1)=(bino_rndc(1,mixed(1),0.5)); %mixed(1);
case 0;
extra(1)=round(mixed(1)*0.5);
end
%instead - add all overlap to both male and female
extra=mixed;
aFinv(1)=aFinv(1)+extra(1);
%aMinv(1)=aMinv(1)+extra(1);
aMres(1)=aMres(1)+(extra(1));
%aFres(1)=aFres(1)+(mixed(1)-extra(1));
end

if mixed(2)<=0; aFres=aFres; aMinv=aMinv;
else
switch binomix;
case 1;
extra(2)=(bino_rndc(1,mixed(2),0.5)); %mixed(2);
case 0;
extra(2)=round(mixed(2)*0.5);
end
%instead add all to both
extra=mixed;
aMinv(1)=aMinv(1)+extra(2);
aFres(1)=aFres(1)+(extra(2));
end
end
end
end

%-----
%fembrmean/std = mean/std female breeding attempts by age class
%br=fem breeding attempts:either mean or random
switch breedattempts;
case 0;
br=fembrmean;
case 1;
br(1,1)=rnorm(1,fembrmean(1),fembrstd(1));
br(2,1)=rnorm(1,fembrmean(2),fembrstd(2));
br(3,1)=br(2,1);
end

```

```

%bratts=total no. feeding attempts for both res and inv females
%bratts=round(br.*(aFres+aFInv));

%breeding attempts split into res and inv
%totfbr=total no. breeding attempts for both res and inv females
resfbr=round(aFres.*br);
invfbr=round(aFInv.*br);
totfbr=resfbr+invfbr;
bratts=sum(totfbr);

%male breeding attempts
%apportioning breeding attempts by male age
switch breedattempts;
case 0;
    br2=malebrmean;
case 1;
    br2(1,1)=lnorms(1,malebrmean(1),malebrstd(1));
    br2(2,1)=rnorm(1,malebrmean(2),malebrstd(2));
    br2(3,1)=br2(2,1);
end

%maleadjust keeps br atts in the age specific proportions,
%but modifies to match the number of female br atts
warning off;
maleadjust=max(sum(totfbr)/sum(br2.*(aMres+aMInv)),0);
%malebr=modified rates
br3=br2.*maleadjust;
warning on;

resmbr=round(br3.*aMres);
invmbr=round(br3.*aMInv);
totmbr=resmbr+invmbr;

%ensures that total breeding is equal for both sexes, by
%randomly reducing any extras caused by rounding
%p and q used to randomly select which age to reduce
p=ceil(2*(rand(1))); %rand no between 1 and 2
q=ceil(3*(rand(1))); %rand no between 1 and 3
if sum(totmbr)==sum(totfbr); totmbr=totmbr; totfbr=totfbr;
elseif sum(totmbr)>sum(totfbr) & sum(invmbr)<=0;
    resmbr(q)=resmbr(q)-(sum(totmbr)-sum(totfbr));
elseif sum(totmbr)>sum(totfbr) & sum(invmbr)>0;
    if p==1; resmbr(q)=resmbr(q)-(sum(totmbr)-sum(totfbr));
    else p==2; invmbr(q)=invmbr(q)-(sum(totmbr)-sum(totfbr));
    end;
elseif sum(totmbr)<sum(totfbr) & sum(invmbr)<=0;
    resfbr(q)=resfbr(q)-(sum(totfbr)-sum(totmbr));
elseif sum(totmbr)<sum(totfbr) & sum(invmbr)>0;
    if p==1; resfbr(q)=resfbr(q)-(sum(totfbr)-sum(totmbr));
    else p==2; invfbr(q)=invfbr(q)-(sum(totfbr)-sum(totmbr));
    end;
end;

totmbr=resmbr+invmbr;
totfbr=resfbr+invfbr;
%sum(totmbr) should equal sum(totfbr).
%if not then 'gen' is printed to screen as a warning!
if (sum(totmbr)-sum(totfbr))>=1; gen
elseif (sum(totmbr)-sum(totfbr))<=-1; gen
end

%-----breeding data store-----
if gen==1; rateind2=rateindexstart;
elseif gen>1 & rem((gen-1),filesize)==0; rateind2=rateindexstart;
else rateind2=rateind2;
end

switch savef;
case 1;

    switch invpopext;

```

```

case 1;
    finvad1(rateind2,1:3)=aFinv';
    finvad1(rateind2,4:6)=invfbr';
    finvad1(rateind2,7)=sum(Fisp);

    minvad1(rateind2,1:3)=aMinv';
    minvad1(rateind2,4:6)=invmbr';
    minvad1(rateind2,7)=sum(Misp);

    spare1(rateind2,1)=sum(Frsp);
    spare1(rateind2,2)=sum(Mrsp);
    spare1(rateind2,3)=sum(Fisp);
    spare1(rateind2,4)=sum(Misp);

    switch rateind2;
    case filesize;
        fid=fopen('finvad', 'a');
        fprintf(fid,'%10g %10g %10g %10g %10g %10g %10g\r',finvad1');
        fclose(fid);
        fid=fopen('minvad', 'a');
        fprintf(fid,'%10g %10g %10g %10g %10g %10g %10g\r',minvad1');
        fclose(fid);
        fid=fopen('spare', 'a');
        fprintf(fid,'%10g %10g %10g %10g\r',spare1');
        fclose(fid);
    end

case 0;
    finvad1=0;
    minvad1=0;
    spare1=0;

case 2;
    finvad1=0;
    minvad1=0;
    spare1=0;

end

fresid1(rateind2,1:3)=aFres';
fresid1(rateind2,4:6)=resfbr';
fresid1(rateind2,7)=sum(Frsp);

mresid1(rateind2,1:3)=aMres';
mresid1(rateind2,4:6)=resmbr';
mresid1(rateind2,7)=sum(Mrsp);

gendat1(rateind2,1)=ball;
gendat1(rateind2,2)=femterr;
gendat1(rateind2,3:5)=br';
gendat1(rateind2,6:8)=br3';
gendat1(rateind2,9)=bratts;

switch rateind2;
case filesize;
    fid=fopen('fresid', 'a');
    fprintf(fid,'%10g %10g %10g %10g %10g %10g %10g\r',fresid1');
    fclose(fid);
    fid=fopen('mresid', 'a');
    fprintf(fid,'%10g %10g %10g %10g %10g %10g %10g\r',mresid1');
    fclose(fid);
    fid=fopen('gendat', 'a');
    fprintf(fid,'%10g %10g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %10g\r',gendat1');
    fclose(fid);
end

case 0;
    finvad1=0;
    minvad1=0;
    fresid1=0;
    mresid1=0;

```

```

    gendat1=0;
    spare1=0;
end

reps1=[fbr1;fbr2;fbr3;mbr1;mbr2;mbr3];

%-----breeding attempt reproduction-----
ylrf(1,1)=round(resfbr(1)*reps1(1));
ylrf(2,1)=round(resfbr(2)*reps1(2));
ylrf(3,1)=round(resfbr(3)*reps1(3));
ylrm(1,1)=round(resmbr(1)*reps1(4));
ylrm(2,1)=round(resmbr(2)*reps1(5));
ylrm(3,1)=round(resmbr(3)*reps1(6));

warning off;
reps2(1:3)=max(0,ylrf./resfbr);
reps2(4:6)=max(0,ylrm./resmbr);
warning on;

%-----

invreps=reps2;
if t>=2 & t<=4;
    invreps(t-1)=invreps(t-1)*(inc+1);
elseif t>=11 & t<=13;
    invreps(t-7)=invreps(t-7)*(inc+1);
else invreps=invreps;
end

ylif(1,1)=round(invfbr(1)*invreps(1));
ylif(2,1)=round(invfbr(2)*invreps(2));
ylif(3,1)=round(invfbr(3)*invreps(3));
ylim(1,1)=round(invmbr(1)*invreps(4));
ylim(2,1)=round(invmbr(2)*invreps(5));
ylim(3,1)=round(invmbr(3)*invreps(6));

%offspring combined
ylrt=ylrf+ylrm;
ylit=ylif+ylim;

%and split into males and females
switch demog3
case 0; %deterministic
    %resident
    if ylrt(1,1)<=0, ylm(1,1)=0;
    else ylm(1,1)=ylrt(1,1)*0.5;
    end;
    if ylrt(2,1)<=0, ylm(2,1)=0;
    else ylm(2,1)=ylrt(2,1)*0.5;
    end;
    if ylrt(3,1)<=0, ylm(3,1)=0;
    else ylm(3,1)=ylrt(3,1)*0.5;
    end;
    %invader
    if ylit(1,1)<=0, yilm(1,1)=0;
    else yilm(1,1)=ylit(1,1)*0.5;
    end;
    if ylit(2,1)<=0, yilm(2,1)=0;
    else yilm(2,1)=ylit(2,1)*0.5;
    end;
    if ylit(3,1)<=0, yilm(3,1)=0;
    else yilm(3,1)=ylit(3,1)*0.5;
    end;
case 1; %binomial
    %resident
    if ylrt(1,1)<=0, ylm(1,1)=0;
    else ylm(1,1)=bino_rndc(1,ylrt(1,1),0.5);

```

```

end;
if ylrt(2,1)<=0, ylm(2,1)=0;
else ylm(2,1)=bino_rndc(1,ylrt(2,1),0.5);
end;
if ylrt(3,1)<=0, ylm(3,1)=0;
else ylm(3,1)=bino_rndc(1,ylrt(3,1),0.5);
end;

warning off;
maleprop=ylm./ylrt;
maleprop=max(maleprop,0);
warning on;

%invader split done using resident data
if ylit==0; yilm=0;
else yilm=ylit.*maleprop;
end
end

yilm=round(yilm);
yilf=yilit-yilm;
ylm=round(ylm);
ylf=ylrt-ylm;

y1(1,1)=sum(ylf);
y1(4,1)=sum(ylm);

unpert=ones(6,1);
warning off;
iBdm(1,1)=max(((ylif(1,1)/(aFinv(1))))*invsurvs(1),0);
iBdm(2,1)=max(((ylif(2,1)/(aFinv(2))))*invsurvs(2),0);
iBdm(3,1)=max(((ylif(3,1)/(aFinv(3))))*invsurvs(3),0);
iBdm(4:9,1)=min(yddi,idds);
iBdm(10,1)=max(((ylim(1,1)/(aMinv(1))))*invsurvs(4),0);
iBdm(11,1)=max(((ylim(2,1)/(aMinv(2))))*invsurvs(5),0);
iBdm(12,1)=max(((ylim(3,1)/(aMinv(3))))*invsurvs(6),0);
warning on;

%file store: reproduction parameters,
warning off;
%Bim1-6 are d.i. rates (rand rep rates*den ind survival)
Bim(1,1)=max(((fbr1*(ylf(1))/(ylrt(1)))*dis(1),0);
Bim(2,1)=max(((fbr2*(ylf(2))/(ylrt(2)))*dis(2),0);
Bim(3,1)=max(((fbr3*(ylf(3))/(ylrt(3)))*dis(3),0);
Bim(4:6)=dis(1:3);
Bim(7:9)=dis(4:6);
Bim(10,1)=max(((mbr1*(ylm(1))/(ylrt(1)))*dis(4),0);
Bim(11,1)=max(((mbr2*(ylm(2))/(ylrt(2)))*dis(5),0);
Bim(12,1)=max(((mbr3*(ylm(3))/(ylrt(3)))*dis(6),0);
warning on;

%prevents minus values
y1=max(y1,0);

%Bdm4-6 are density dependent survival rates
Bdm(4:9,1)=min(y,dds);
%Bdm1-3 are density dependent fecudity rates
warning off;
Bdm(1:3,1)=max(y1rf(1:3,1)./aFres(1:3,1),0);
Bdm(10:12,1)=max(y1rm(1:3,1)./aMres(1:3,1),0);
iBdm(1:3,1)=max(ylif(1:3,1)./aFinv(1:3,1),0);
iBdm(10:12,1)=max(ylim(1:3,1)./aMinv(1:3,1),0);
warning on;

Bdm(find(isinf(Bdm)))=0;
Bdm(find(isnan(Bdm)))=0;
iBdm(find(isinf(iBdm)))=0;
iBdm(find(isnan(iBdm)))=0;

switch saverates; %saves demographic rates

```

```

case 1;
    if gen==1; rateind=rateindexstart;
    elseif rem((gen-1),filesize)==0; rateind=rateindexstart;
    else rateind=rateind;
    end

    %filesize=min(10000,years);
    switch bigrun
    case 1
        switch invpopext
        case 0
            switch t
            case 1
                sbdm(rateind,:)=Bdm';
                switch rateind;
                case filesize;
                    fid=fopen('ssbdm', 'a');
                    fprintf(fid,'%0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g
%0.4g %0.4g\r',sbdm');
                    fclose(fid);
                end
            end
        otherwise
            sbdm(rateind,:)=Bdm';
            switch rateind;
            case filesize;
                fid=fopen('ssbdm', 'a');
                fprintf(fid,'%0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g
%0.4g\r',sbdm');
                fclose(fid);
            end
        end
    otherwise
        sbdm(rateind,:)=Bdm';
        switch rateind;
        case filesize;
            fid=fopen('ssbdm', 'a');
            fprintf(fid,'%0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g
%0.4g\r',sbdm');
            fclose(fid);
        end
    end

    switch invpopext;
    case 1;
        sibdm(rateind,:)=iBdm';
        switch rateind;
        case filesize;
            fid=fopen('ssibdm', 'a');
            fprintf(fid,'%0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g %0.4g
%0.4g\r',sibdm');
            fclose(fid);
        end
    case 0;
        sibdm=0;
    case 2;
        sibdm=0;
    end
    rateind=rateind+1;

case 0;
    sbdm=0;
    sibdm=0;
end

%baserates saves rates from baseline invasion (when inc=0)
switch t;
case 1;
    baserates(gen,:)=iBdm';

```

```

end

transition=zeros(6,6);
transition(2,1)=1;
transition(3,2)=1;
transition(3,3)=1;
transition(5,4)=1;
transition(6,5)=1;
transition(6,6)=1;

yi(1:3,1)=aFinv;
yi(4:6,1)=aMinv;
y(1:3,1)=aFres;
y(4:6,1)=aMres;

if rem (invgen,invp+1)==0; invgen=1; invpop=zeros(invvp,1);
else invgen=invgen; end

if gen<=invdelay; invgen=1; else invgen=invgen; end;
%invend set as smaller:50 or invp/2
invend=invp-max(50,round(invvp/2));
if invgen>=invend; yi=zeros(6,1); yilf=0; yilm=0; else yi=yi;end

yil=(transition*yi);
yl=(transition*y);

yil(1,1)=sum(yilf);
yil(4,1)=sum(yilm);
yl(1,1)=sum(ylf);
yl(4,1)=sum(ylm);

%-----invasion tracking and slope calculation-----
linvpop(1:(invend-1-cut),1)=ones;
linvpop(1:(invend-1-cut),2)=(1:1:(invend-cut-1));
linvpop(1:(invend-1-cut),3)=zeros;

%resident check - to compare to invaders
linvpop2(1:(invend-1-cut),1)=ones;
linvpop2(1:(invend-1-cut),2)=(1:1:(invend-cut-1));
linvpop2(1:(invend-1-cut),3)=zeros;

if sum(yi)==0; invpop(invgen,1)=1;
else invpop(invgen,1)=sum(yil);
end

%resident check
if sum(y)==0; invpop2(invgen,1)=1;
else invpop2(invgen,1)=sum(yl);
end

yi=yil;
if invgen<=invp-1; linvpop=linvpop;
else invgen>=invp; invgen=invp; linvpop(:,3)=log(invpop(cut+1:invend-1,1));
if sum(linvpop(:,3))<=0; ireg=zeros(2,1);
else ireg=regress(linvpop(:,3),linvpop(:,1:2));
end;
slope((gen-invdelay)/invp,1)=ireg(2);
end

%resident check
if invgen<=invp-1; linvpop2=linvpop2;
else invgen>=invp; invgen=invp; linvpop2(:,3)=log(invpop2(cut+1:invend-1,1));
if sum(linvpop2(:,3))<=0; ireg2=zeros(2,1);
else ireg2=regress(linvpop2(:,3),linvpop2(:,1:2));
end;
slope2((gen-invdelay)/invp,1)=ireg2(2);
end

invgen=invgen+1;

```

```

%age class pop size stored for each year, females then males
switch invpopext
case 0
    switch bigrun
    case 1;
        pop(rateind2,1)=sum(y1(1:3,1));
        pop(rateind2,2)=sum(y1(4:6,1));
    otherwise
        pop(rateind2,1:3)=y1(1:3,1)';
        pop(rateind2,4)=sum(y1(1:3,1));
        pop(rateind2,5:7)=y1(4:6,1)';
        pop(rateind2,8)=sum(y1(4:6,1));
        pop(rateind2,9)=sum(y1);
    end
case 1
    pop(rateind2,1:3)=y1(1:3,1)';
    pop(rateind2,4)=sum(y1(1:3,1));
    pop(rateind2,5:7)=y1(4:6,1)';
    pop(rateind2,8)=sum(y1(4:6,1));
    pop(rateind2,9)=sum(y1);
case 2
    pop(rateind2,1:3)=y1(1:3,1)';
    pop(rateind2,4)=sum(y1(1:3,1));
    pop(rateind2,5:7)=y1(4:6,1)';
    pop(rateind2,8)=sum(y1(4:6,1));
    pop(rateind2,9)=sum(y1);
end

switch invpopext
case 2
    switch mfext
    case 0
        %total pop
        if sum(y1)<=(quasiext); rateind2=filesize;
        else rateind2=rateind2;
        end
    case 1
        %male/female version
        if min((sum(y1(1:3))), (sum(y1(4:6))))<=(quasiext); rateind2=filesize;
        else rateind2=rateind2;
        end
    end
end

gr=y;
yext(1)=max(sum(y1(1:3,1)),0);
yext(2)=max(sum(y1(4:6,1)),0);
yex=sum(yext);

%extstore=1:not extinct, extstore=0:extinct
switch mfext
case 0
    %total pop
    if yex<=quasiext & gen<years; extstore=0; else extstore=1; end;
case 1
    %male/female
    if min(yext)<=quasiext & gen<years; extstore=0; else extstore=1; end;
end

end

%popl file store: population size
%popl - stores everything, all years from all runs
%popl2 - is just the nonzero entries of popl
%popl3 - is all years but only runs which don't go extinct
%popl4 - is same as popl2, but with a row of zeros between runs

```



```

switch savepop;
case 1;
  switch invpopext;
  case 0;
    switch bigrun
    case 1
      switch rateind2;
      case filesize;
        fid=fopen('pop1', 'a');
        fprintf(fid,'%10g %10g\r',pop');
        fclose(fid);
      end
    otherwise
      switch rateind2;
      case filesize;
        fid=fopen('pop1', 'a');
        fprintf(fid,'%10g %10g %10g %10g %10g %10g %10g %10g\r',pop');
        fclose(fid);
      end
    end
  case 2
    switch bigrun
    case 1
      pop3(:,1)=pop(:,4); %total females
      pop3(:,2)=pop(:,8); %total males
      switch rateind2;
      case filesize;
        fid=fopen('pop1', 'a');
        fprintf(fid,'%10g %10g\r',pop3');
        fclose(fid);
      end
    otherwise
      switch rateind2;
      case filesize;
        fid=fopen('pop1', 'a');
        fprintf(fid,'%10g %10g %10g %10g %10g %10g %10g %10g\r',pop');
        fclose(fid);
      end
    end
  end

  switch rateind2
  case filesize
    pop2=pop(:,9);
    pop2=pop2(1:(min(gen+1,years)),:);
    fid=fopen('pop14', 'a');
    fprintf(fid,'%10g\r',pop2');
    fclose(fid);

    switch extstore
    case 1 %not extinct
      fid=fopen('pop13', 'a');
      fprintf(fid,'%10g %10g %10g %10g %10g %10g %10g %10g\r',pop');
      fclose(fid);
    end
  end
end
end

rateind2=rateind2+1;

switch invpopext
case 2
  switch mfext
  case 0
    %total pop
    if yex<=(quasiext), break; end;
  case 1
    %male/female
    if min(yext)<=(quasiext), break; end;
  end
end
end

```

```

ball0=ball;

%resident population vector updated at end of annual cycle
y=y1;
gen=gen+1;

end; %population loop
%-----end of population loop-----

%calcs mean and std of unperturbed (t=1) vital rates
switch invpopext;
case 1;
    switch t; %first year - base rates for unperturbed inv rate
    case 1;
        [g,h,j]=find(baserates(:,1));
        ms=mean(baserates(g,:));
        basestd=std(baserates(g,:));
        basestd=std(baserates);
        clear j h g;
    end
    slopeind=ceil(min(((years/invp)*0.1),500));

    if max(slope)==0; z1=0; z2=0; z3=0;
    else [z1,z2,z3]=find(slope);
    end
    invmn=mean(z3);
    invsd=std(z3);
    invse=invsd/(length(z1))^0.5;

    slopedat(1:(length(slope)),t)=slope;

    invdat(1,t)=invmn;
    invdat(2,t)=invsd;
    invdat(3,t)=invse;
    invdat(4,t)=length(z3);
    invdat(5,t)=invprop;
    base=invdat(1,1);

    if max(slope2)==0; z1a=0; z2a=0; z3a=0;
    else [z1a,z2a,z3a]=find(slope2);
    end
    invmn2=mean(z3a);
    invsd2=std(z3a);
    invse2=invsd2/(length(z1a))^0.5;

    slopedat2(1:(length(slope2)),t)=slope2;

    invdat2(1,t)=invmn2;
    invdat2(2,t)=invsd2;
    invdat2(3,t)=invse2;
    invdat2(4,t)=length(z3a);
    base2=invdat2(1,1);

    switch t==13; %sim;
    case 1;
        els=(invdat(1,2:end)-base)/log(1+inc);
        iels=[els(1) els(2) els(3) 0 0 0;
            els(4) 0 0 0 0 0;
            0 els(5) els(6) 0 0 0;
            0 0 0 els(10) els(11) els(12);
            0 0 0 els(7) 0 0;
            0 0 0 0 els(8) els(9)];
        elsum=sum(els);
        elsum2=sum(invdat(1,2:end)-0)/log(1+inc);

        zbase=0;

```

```

        zels=(invdat(1,2:end)-0)/log(1+inc);
        ziels=[zels(1) zels(2) zels(3) 0 0 0;
              zels(4) 0 0 0 0 0;
              0 zels(5) zels(6) 0 0 0;
              0 0 0 zels(10) zels(11) zels(12);
              0 0 0 zels(7) 0 0;
              0 0 0 0 zels(8) zels(9)];
    end;

case 0
    iels=0;

case 2
    %which sex goes extinct?
    if yext(1)<=quasiext; sex(t,pertloop)=1; %1=females
    elseif yext(2)<=quasiext; sex(t,pertloop)=2; %2=males
    else sex(t,pertloop)=0; %0=neither
    end;

    iels=0;
end

switch invpopext
case 1
    tally=[years:years:(years*sim)'];
case 0
    tally=[years:years:(years*sim)'];
case 2;
    tally=[years:years:(years*pert)'];
end

end %perturbation loop for elasticity analysis
%-----

%extinction rates from the repeat runs
index=round(min(500,years*0.1));
switch invpopext
case 2 %extinction run
    load popl;
    load ssbdm;
    zallt=zeros(years,pert);
    for count1=1:pert;
        switch bigrun
        case 1
            if count1<=1, zallm(1:tally(count1),1)=popl(1:tally(count1),2);
            else zallm(1:tally(count1)-tally(count1-1),count1)=
                popl(tally(count1-1)+1:tally(count1),2);
            end;
            if count1<=1, zallf(1:tally(count1),1)=popl(1:tally(count1),1);
            else zallf(1:tally(count1)-tally(count1-1),count1)=
                popl(tally(count1-1)+1:tally(count1),1);
            end;
            if count1<=1, zallt(1:tally(count1),1)=sum(popl(1:tally(count1),:),2);
            else zallt(1:tally(count1)-tally(count1-1),count1)=
                sum(popl(tally(count1-1)+1:tally(count1),:),2);
            end;
        otherwise
            if count1<=1, zallm(1:tally(count1),1)=popl(1:tally(count1),8);
            else zallm(1:tally(count1)-tally(count1-1),count1)=
                popl(tally(count1-1)+1:tally(count1),8);
            end;
            if count1<=1, zallf(1:tally(count1),1)=popl(1:tally(count1),4);
            else zallf(1:tally(count1)-tally(count1-1),count1)=
                popl(tally(count1-1)+1:tally(count1),4);
            end;
            if count1<=1, zallt(1:tally(count1),1)=popl(1:tally(count1),9);
            else zallt(1:tally(count1)-tally(count1-1),count1)=
                popl(tally(count1-1)+1:tally(count1),9);
        end;
    end;
end;

```

```

        end;
    end
    count1=count1+1;
end

switch saverates;
case 1
    if length(ssbdm)==0; rates=zeros(1,12); mrates=zeros(1,12); sdrates=zeros(1,12);
    else
        rates=ssbdm;
        rates(:,1)=rates(:,1).*rates(:,4);
        rates(:,2)=rates(:,2).*rates(:,5);
        rates(:,3)=rates(:,3).*rates(:,6);
        rates(:,10)=rates(:,10).*rates(:,7);
        rates(:,11)=rates(:,11).*rates(:,8);
        rates(:,12)=rates(:,12).*rates(:,9);
        mrates(t,:)=mean(rates((min(15,round(years/10)):end,:)));
        sdrates(t,:)=std(rates((min(15,round(years/10)):end,:)));
    end
case 0;
    rates=zeros(1,12);
    mrates=zeros(1,12);
    sdrates=zeros(1,12);
end

for count2=1:per;
    if min(zallt(index:end,count2))==0;
        extprob(count2,t)=1; %1 means pop went below threshold
    else extprob(count2,t)=0;
    end
    finalpop(count2,t)=zallt(end,count2);
    count2=count2+1;
end

%calculates mean and 95% intervals, for runs which don't go extinct
w=find(zallt(end,:)>0);
zallt2=max(zallt(:,w),0);
meantot=mean(zallt2,2);
meanstd=std(zallt2,0,2);
q=size(zallt2);
e=q(2);
meantot(:,2)=meantot(:,1)-2*(meanstd/sqrt(e));
meantot(:,3)=meantot(:,1)+2*(meanstd/sqrt(e));
meantot(:,4)=meantot(:,1)-meanstd;
meantot(:,5)=meantot(:,1)+meanstd;

%popl3 is a saved matrix with only extant runs saved
load popl3;
[q,e]=find(popl(:,end));

%popl2=popl(q,:);
warning off;
r1=max(mean(popl3),0);
w1=max(std(popl3,0,1),0);
q1=max(w1/sqrt(length(popl3)),0);

switch bigrun
case 0;
    r2=max(mean(popl(q,:)),0);
    w2=max(std(popl(q,:),0,1),0);
    q2=max(w2/sqrt(length(q)),0);
case 1;
    r2(1,1:2)=max(mean(popl(q,:)),0);
    r2(1,3)=max(mean(sum(popl(q,:),2)),0);
    w2(1,1:2)=max(std(popl(q,:),0,1),0);
    w2(1,3)=max(std(sum(popl(q,:),2),0,1),0);
    q2=max(w2/sqrt(length(q)),0);
end

```

```

warning on;
if sum(r1)<=0; r1=zeros(1,9); else r1=r1; end;
if sum(q1)<=0; q1=zeros(1,9); else q1=q1; end;
if sum(w1)<=0; w1=zeros(1,9); else w1=w1; end;

%non-extinct run stats
stableage(1:6,1)=init;
stableage(7,1)=sum(init);
stableage(1:3,t+1)=r1(1:3)'; stableage(4:6,t+1)=r1(5:7)';
stableage(7,t+1)=sum(stableage(1:6,t+1));

stablesd(1:7,1)=0;
stablesd(1:3,t+1)=w1(1:3)'; stablesd(4:6,t+1)=w1(5:7)';
stablesd(7,t+1)=w1(9);

stablese(1:7,1)=0;
stablese(1:3,t+1)=q1(1:3)'; stablese(4:6,t+1)=q1(5:7)';
stablese(7,t+1)=q1(9);

switch bigrun
case 0;
    if sum(r2)<=0; r2=zeros(1,9); else r2=r2; end;
    if sum(q2)<=0; q2=zeros(1,9); else q2=q2; end;
    if sum(w2)<=0; w2=zeros(1,9); else w2=w2; end;

    aexprob(t,1)=r2(9); %mean analytical tot pop size
    aexprob(t,2)=w2(9); %std analytical tot pop size
    aexprob(t,3)=r2(4); %mean anal female pop size
    aexprob(t,4)=w2(4); %std anal fem
    aexprob(t,5)=r2(8); %mean male
    aexprob(t,6)=w2(8); %std male
case 1
    if sum(r2)<=0; r2=zeros(1,3); else r2=r2; end;
    if sum(q2)<=0; q2=zeros(1,3); else q2=q2; end;
    if sum(w2)<=0; w2=zeros(1,3); else w2=w2; end;

    aexprob(t,1)=r2(3); %mean analytical tot pop size
    aexprob(t,2)=w2(3); %std analytical tot pop size
    aexprob(t,3)=r2(1); %mean anal female pop size
    aexprob(t,4)=w2(1); %std anal fem
    aexprob(t,5)=r2(2); %mean male
    aexprob(t,6)=w2(2); %std male
end

anext(t,1)=quasiext;

clear popl A sbdm;

%save data
runstoretxt=['d1 d2 juvdd env demog surv demog fec redvar raised rates randterr'];
runstore1=[d1 d2 juvdd env demog1 demog3 redvar raise randterr];
runstore(:,t)=runstore1';
allpops(1:7,1)=stableage(1:7,1);
allpops(1:7,t+1)=stableage(1:7,2);
allpops(8,t+1)=mean(extprob(:,t));

%probability of small populations declining further
load popl4;
if length(popl4)<=0; decliner=0; else decliner=1; end
switch decliner
case 1
    warning off;
    half=find(popl4(:,1)<(0.5*aexprob(t,1)));
    half1=half+1;
    half1=half1(1:end-1);
    halfprob(t,1)=max((length(find(popl4(half1,1)<(aexprob(t,1)*0.5)))/length(half1),0);

    quart=find(popl4(:,1)<(0.25*aexprob(t,1)));
    quart1=quart+1;

```

```

        quart1=quart1(1:end-1);
        quartprob(t,1)=max((length(find(popl4(quart1,1)<(aexp(t,1)*0.25))))/length(quart1),0);
        warning on;
    case 0
        halfprob(t,1)=0;
        quartprob(t,1)=0;
    end
end
clear popl4;

switch invpopext
case 2
    if t==13; extinction=1; else extinction=0; end
    extrisk(t,1)=mean(extprob(:,t));
end

%-----

t=t+1;

end;

load ssbdm;
load ssibdm;
load finvad;
load fresid;
load minvad;
load mresid;
load spare;
load gendat;

switch invpopext;
case 0;
    load popl;
    load ssbdm;
    zallm=zeros(years,sim);
    zallf=zeros(years,sim);
    zallt=zeros(years,sim);

    for count1=1:sim;
        switch bigrun
        case 1
            if count1<=1, zallm(1:tally(count1),1)=popl(1:tally(count1),2);
            else zallm(1:tally(count1)-tally(count1-1),count1)=popl(tally(count1-1)+1:tally(count1),2);
            end;
            if count1<=1, zallf(1:tally(count1),1)=popl(1:tally(count1),1);
            else zallf(1:tally(count1)-tally(count1-1),count1)=popl(tally(count1-1)+1:tally(count1),1);
            end;
            if count1<=1, zallt(1:tally(count1),1)=sum(popl(1:tally(count1),:),2);
            else zallt(1:tally(count1)-tally(count1-1),count1)=sum(popl(tally(count1-
1)+1:tally(count1),:),2);
            end;
        otherwise
            if count1<=1, zallm(1:tally(count1),1)=popl(1:tally(count1),8);
            else zallm(1:tally(count1)-tally(count1-1),count1)=popl(tally(count1-1)+1:tally(count1),8);
            end;
            if count1<=1, zallf(1:tally(count1),1)=popl(1:tally(count1),4);
            else zallf(1:tally(count1)-tally(count1-1),count1)=popl(tally(count1-1)+1:tally(count1),4);
            end;
            if count1<=1, zallt(1:tally(count1),1)=popl(1:tally(count1),9);
            else zallt(1:tally(count1)-tally(count1-1),count1)=popl(tally(count1-1)+1:tally(count1),9);
            end;
        end
    end

    switch saverates;
    case 1
        switch bigrun
        case 1

```

```

rates=ssbdm;
rates(:,1)=rates(:,1).*rates(:,4);
rates(:,2)=rates(:,2).*rates(:,5);
rates(:,3)=rates(:,3).*rates(:,6);
rates(:,10)=rates(:,10).*rates(:,7);
rates(:,11)=rates(:,11).*rates(:,8);
rates(:,12)=rates(:,12).*rates(:,9);

mrates(1,:)=mean(rates((min(15,round(years/10)):end,:));
sdrates(1,:)=std(rates((min(15,round(years/10)):end,:));
otherwise
if count1<=1, rates(1:tally(count1),:)=ssbdm(1:tally(count1),:);
else rates(1:tally(count1)-tally(count1-1),:)=ssbdm(tally(count1-1)+1:tally(count1),:);
end;
rates(:,1)=rates(:,1).*rates(:,4);
rates(:,2)=rates(:,2).*rates(:,5);
rates(:,3)=rates(:,3).*rates(:,6);
rates(:,10)=rates(:,10).*rates(:,7);
rates(:,11)=rates(:,11).*rates(:,8);
rates(:,12)=rates(:,12).*rates(:,9);

mrates(count1,:)=mean(rates((min(15,round(years/10)):end,:));
sdrates(count1,:)=std(rates((min(15,round(years/10)):end,:));
end
case 0;
rates=zeros(1,12);
mrates=zeros(1,12);
sdrates=zeros(1,12);
end

count1=count1+1;
end

%-----calculates means and elasticities-----
%index chops off early years of wobble
index=round(min(500,years*0.1));

%base geometric means for males, females and total
bgeozm=mean(log(zallm(index:end,1)));
bgeozf=mean(log(zallf(index:end,1)));
bgeozt=mean(log(zallt(index:end,1)));

%base geometric standard errors
bgeozmerrs=std(log(zallm(index:end,1)))/sqrt(length(zallm)-index)';
bgeozferrs=std(log(zallf(index:end,1)))/sqrt(length(zallf)-index)';
bgeozterr=std(log(zallt(index:end,1)))/sqrt(length(zallt)-index)';

%geometric means for perturbed runs
geozms=mean(log(zallm(index:end,2:end)))';
geozfs=mean(log(zallf(index:end,2:end)))';
geozts=mean(log(zallt(index:end,2:end)))';

%geometric standard errors for perturbed runs
geozmerrs=(std(log(zallm(index:end,2:end)))/sqrt(length(zallm)-index))';
geozferrs=(std(log(zallf(index:end,2:end)))/sqrt(length(zallf)-index))';
geozterr=(std(log(zallt(index:end,2:end)))/sqrt(length(zallt)-index))';

%standard error of the difference between the log mean
sediffm=sqrt(((bgeozmerrs).^2)+((geozmerrs).^2));
sedifff=sqrt(((bgeozferrs).^2)+((geozferrs).^2));
sediftt=sqrt(((bgeozterr).^2)+((geozterr).^2));

%elasticities - mean
popelm(:,2)=(geozms-bgeozm)/log(1+inc);
popelf(:,2)=(geozfs-bgeozf)/log(1+inc);
popelt(:,2)=(geozts-bgeozt)/log(1+inc);

%elasticities - lower
popelm(:,1)=popelm(:,2)-(2*sediffm);

```

```

popelf(:,1)=popelf(:,2)-(2*sediff);
popelt(:,1)=popelt(:,2)-(2*sedifft);

%elasticities - upper
popelm(:,3)=popelm(:,2)+(2*sediffm);
popelf(:,3)=popelf(:,2)+(2*sediff);
popelt(:,3)=popelt(:,2)+(2*sedifft);

for me=2:sim;
    clear h1 sig1;
    [h1,sig1]=ttest2((zallt(:,1)),(zallt(:,me)));
    popelt(me-1,5)=h1;
    popelt(me-1,6)=sig1;
end

popeltnx=[popelt(1,2) popelt(2,2) popelt(3,2) 0 0 0;
          popelt(4,2) 0 0 0 0 0;
          0 popelt(5,2) popelt(6,2) 0 0 0;
          0 0 0 popelt(10,2) popelt(11,2) popelt(12,2);
          0 0 0 popelt(7,2) 0 0;
          0 0 0 0 popelt(8,2) popelt(9,2)];

case 1;
    popeltnx=0;
end

if invpopext==0 | invpopext==2;
    timeavmat=[mrates(1,1) mrates(1,2) mrates(1,3) 0 0 0;
              mrates(1,4) 0 0 0 0 0;
              0 mrates(1,5) mrates(1,6) 0 0 0;
              0 0 0 mrates(1,10) mrates(1,11) mrates(1,12);
              0 0 0 mrates(1,7) 0 0;
              0 0 0 0 mrates(1,8) mrates(1,9)];
else
    msb=ms;
    timeavmat=[msb(1,1) msb(1,2) msb(1,3) 0 0 0;
              msb(1,4) 0 0 0 0 0;
              0 msb(1,5) msb(1,6) 0 0 0;
              0 0 0 msb(1,10) msb(1,11) msb(1,12);
              0 0 0 msb(1,7) 0 0;
              0 0 0 0 msb(1,8) msb(1,9)];
end

switch invpopext
case 2
    %analytical extinction rate
    for sexer=1:part;
        whichsex(sexer,1)=length(find(sex(:,sexer)==1))/length(sex);
        whichsex(sexer,2)=length(find(sex(:,sexer)==2))/length(sex);
        whichsex(sexer,3)=length(sex);
    end

    ext2(:,1)=normcdf(0,aexprob(:,1),aexprob(:,2)); %total
    ext2(:,2)=normcdf((2*anext(:,1)),aexprob(:,1),aexprob(:,2));
    ext2(:,3)=normcdf(0,aexprob(:,3),aexprob(:,4)); %female
    ext2(:,4)=normcdf(anext(:,1),aexprob(:,3),aexprob(:,4));
    ext2(:,5)=normcdf(0,aexprob(:,5),aexprob(:,6)); %male
    ext2(:,6)=normcdf(anext(:,1),aexprob(:,5),aexprob(:,6));

    ext3(:,1)=1-((1-ext2(:,1)).^years); %total
    ext3(:,2)=1-((1-ext2(:,2)).^years);
    ext3(:,3)=1-((1-ext2(:,3)).^years); %female
    ext3(:,4)=1-((1-ext2(:,4)).^years);
    ext3(:,5)=1-((1-ext2(:,5)).^years); %male
    ext3(:,6)=1-((1-ext2(:,6)).^years);

    ext4(:,1:2)=aexprob(:,1:2);
    ext4(:,3:5)=ext3(:,2:2:6);
    ext4(:,6)=extrisk;

```



```

ext4(:,7)=halfprob;
ext4(:,8)=quartprob;
%ext4(:,6:7)=runstore(1:2,:);

switch sim
case 13
    for x=1:4;
        extels(:,x)=(ext4(1,x+2)-ext4(2:end,x+2))./log(1+inc)';
    end
    allextmx=[extels(1,1) extels(2,1) extels(3,1) 0 0 0;
              extels(4,1) 0 0 0 0 0;
              0 extels(5,1) extels(6,1) 0 0 0;
              0 0 0 extels(10,1) extels(11,1) extels(12,1);
              0 0 0 extels(7,1) 0 0;
              0 0 0 0 extels(8,1) extels(9,1)];
    femextmx=[extels(1,2) extels(2,2) extels(3,2) 0 0 0;
              extels(4,2) 0 0 0 0 0;
              0 extels(5,2) extels(6,2) 0 0 0;
              0 0 0 extels(10,2) extels(11,2) extels(12,2);
              0 0 0 extels(7,2) 0 0;
              0 0 0 0 extels(8,2) extels(9,2)];
    malextmx=[extels(1,3) extels(2,3) extels(3,3) 0 0 0;
              extels(4,3) 0 0 0 0 0;
              0 extels(5,3) extels(6,3) 0 0 0;
              0 0 0 extels(10,3) extels(11,3) extels(12,3);
              0 0 0 extels(7,3) 0 0;
              0 0 0 0 extels(8,3) extels(9,3)];
    simextmx=[extels(1,4) extels(2,4) extels(3,4) 0 0 0;
              extels(4,4) 0 0 0 0 0;
              0 extels(5,4) extels(6,4) 0 0 0;
              0 0 0 extels(10,4) extels(11,4) extels(12,4);
              0 0 0 extels(7,4) 0 0;
              0 0 0 0 extels(8,4) extels(9,4)];
otherwise
    allextmx=0;
    femextmx=0;
    malextmx=0;
    simextmx=0;
end

end

%--calculates elasticities for underlying vital rates-----
%for mean matrix
if runloop>1;
    clear mels3 msens mlam mean4mat mean3mat mels2 msens2 mlam2 mels5 mels4 msens4 mlam4 q w e;
end

[q,w,e]=find(mean2mat');
[mels,msens,mlam]=elinv(mean2mat);
for r=1:12;
    mean4mat=mean2mat';
    mean3mat=mean4mat;
    mean3mat(q(r),w(r))=mean4mat(q(r),w(r))*(1+inc);
    if r>=4 & r<=6; mean3mat(q(r-3),w(r-3))=mean4mat(q(r-3),w(r-3))*(1+inc);
    elseif r>=10 & r<=12; mean3mat(q(r-3),w(r-3))=mean4mat(q(r-3),w(r-3))*(1+inc);
    else mean3mat=mean3mat;
    end
    [mels2,msens2,mlam2]=elinv(mean3mat');
    mels3(q(r),w(r))=(mlam2-mlam)/(mlam*inc); %mels3=lower rate elasticity matrix
end
mels3=mels3';
clear q w e r mean4mat mean3mat

%for time averaged rates
[tavels,tavsens,tavlamlam]=elinv(timeavmat);
[q,w,e]=find(timeavmat');
if length(q)==0; gh=0; mels5=zeros(6,6); else gh=12; end
for r=1:gh;

```

```

mean4mat=timeavmat';
mean3mat=mean4mat;
mean3mat(q(r),w(r))=mean4mat(q(r),w(r))*(1+inc);
if r>=4 & r<=6; mean3mat(q(r-3),w(r-3))=mean4mat(q(r-3),w(r-3))*(1+inc);
elseif r>=10 & r<=12; mean3mat(q(r-3),w(r-3))=mean4mat(q(r-3),w(r-3))*(1+inc);
else mean3mat=mean3mat;
end
[mels4,msens4,mlam4]=elinv(mean3mat');
warning off;
mels5(q(r),w(r))=(mlam4-tavlam)/(tavlam*inc); %mels3=lower rate elasticity matrix
warning on;
end
mels5=mels5';

%-----

[mels,msens,mlam]=elinv(mean2mat);
[tavels,tavsens,tavlam]=elinv(timeavmat);
switch invpopext;
case 0;
    mels2=mels';
    [q,w,e]=find(mels2);
    popelt(1:12,4)=e;
end

switch invpopext;
case 1;
    sigg;
end

%saves data for each runloop simulation into a different file
if runloop==1;
    save g:\afhpc\mnt1a;
elseif runloop==2;
    save g:\afhpc\mnt2a;
elseif runloop==3;
    save g:\afhpc\mnt3a;
elseif runloop==4;
    save g:\afhpc\mnt4a;
elseif runloop==5;
    save g:\afhpc\mnt5a;
elseif runloop==6;
    save g:\afhpc\mnt6a;
elseif runloop==7;
    save g:\afhpc\mnt7a;
elseif runloop==8;
    save g:\afhpc\mnt8a;
elseif runloop==9;
    save g:\afhpc\mnt9a;
elseif runloop==10;
    save g:\afhpc\mnt10a;
elseif runloop==11;
    save g:\afhpc\mnt11b;
elseif runloop==12;
    save g:\afhpc\mnt12b;
elseif runloop==13;
    save g:\afhpc\mnt13b;
elseif runloop==14;
    save g:\afhpc\mnt14b;
elseif runloop==15;
    save g:\afhpc\mnt15b;
end

%displays summary run info and elasticity values
disp(date);clock; disp(ans(4:5))

if invpopext==1; out='invasion run';
elseif invpopext==0; out='population size run';

```

```

else out='extinction risk run';
end
disp(out)

disp('no. years:'); disp(years)
disp('no. sims:'); disp(sim)
disp('perturbation size:'); disp(inc)

if invpopext==1; out='invasion elasticities:';
elseif invpopext==0; out='population size elasticities:';
else out='extinction risk elasticities:';
end
disp(out)
if invpopext==1; disp(iels);
elseif invpopext==0; disp(popeltnmx);
else %disp(extmx);
end

if invpopext==0 & length(popelt)==13; out='territory elasticity:'; disp(out); disp(popelt(end,2));
end
disp('time averaged matrix elasticities:'); disp(tavels)
disp('time averaged lower rate elasticities:'); disp(mels5)
disp('mean matrix elasticities:'); disp(mels)
disp('mean lower rate elasticities:'); disp(mels3)
if invpopext==1; disp('sig. results:'); disp(sigs);
elseif invpopext==0; disp('sum pop els:'); disp(sum(popelt(1:12,2)));
else disp('population size and extinction probabilities:'); disp(ext4(:,1:6));
    disp('simulation ext elasticities:'); disp(simextmx);
    disp('analytical all ext elasticities:'); disp(allextmx);
    disp('analytical female ext elasticities:'); disp(femextmx);
    disp('analytical male ext elasticities:'); disp(malextmx);
end

if invpopext==2;
    totmean(runloop,:)=mean(ext4(:,1:6));
    totstd(runloop,:)=std(ext4(:,1:6));
    totse(runloop,:)=(std(ext4(:,1:6)))/sqrt(length(ext4(:,1)));
end

runloop=runloop+1;
end

%program ends

```