INTERACTIONS BETWEEN STRUCTURE AND STOCHASTICITY IN DEMOGRAPHIC MODELS

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DECLARATION

This thesis is my own work.

Co-authors (and citations where appropriate) on published and submitted chapters are listed as footnotes at the start of each chapter. Folk, who provided less formal advice, are listed in the acknowledgements.

ABSTRACT

Demography is the study of population dynamics. Populations can be considered as groups of individuals living within a given region. These simple statements encompass highly disparate systems, which respond to demographic and environmental stochasticity in predictable and unpredictable ways. The responses depend on the structure of the population, since individuals can have vastly different survival and recruitment, which, with dispersal, determine population abundance. Whilst some variation is inter-st(age) – increases in reproductive performance with age, for example – substantial intra-st(age) variation is not uncommon. Using long-term individual-based data on two disparate vertebrate populations, the focus of this thesis is the interaction between structure and stochasticity in demographic models, and consequences on resultant aspects of population growth.

Structured models that incorporated variation in demographic rates detected marked differences within, between and across diverse habitats for different age-classes in both populations. These results were consistent for a wide range of scaling and definition to account for mathematical dependence. Spatial structure was more influential than age-structure in responses to stochastic predation. Despite significant changes in performance and phenotype with age, individual heterogeneity within age-classes was vast.

These results are of importance for conservation and management action, as well as predictors of evolutionary change. The population is a fundamental force in ecology and evolution. This work adds weight to the argument that characteristics of individual performance in response to variability in their environments are pivotal to increased understanding of changes in population abundance. These individual responses are dependent upon the opportunity generated by population structure. A failure to incorporate either structure or stochasticity neglects crucial aspects in population regulation, and therefore ecological and evolutionary change.

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CHAPTER 1

INTRODUCTION

1.1 THE IMPORTANCE OF THE POPULATION

Demography is the study of population dynamics. Populations can be considered as groups of individuals living within some region. Population abundance may vary from one to millions, relative abundance may vary temporally at different points of the life-cycle and individuals may vary in developmental or physiological condition. The dynamics of any population depend on survival, fecundity and dispersal: the demographic rates of individuals. Two populations very similar in appearance can potentially follow quite different trajectories: the "devil is in the detail" (Benton et al. 2006). Prediction of demographic change – in either the long or short term – requires consideration of abundant aspects that determine the demographic rates of individuals (Ricklefs and Wikelski 2002, Coulson et al. 2006a). Evolutionary and ecological changes have the potential to affect population dynamics, and vice versa (Hairston et al. 2005, Saccheri and Hanski 2006). Fisher (1958) objected to the idea that natural selection could have an effect on the average fitness of a population as natural selection in reality acts upon individuals. Any advantage enjoyed by an individual must be considered relative to others in its population (Coulson et al. 2006b) . As Gore Vidal noted:

"It is not enough to succeed; others must fail"

Differences between individuals occur for many reasons. Latent fitness - *a priori* individual survival and fecundity probabilities (Link et al. 2002) – is inconstant between individuals. Stochasticity perturbs realised fitness away from this expectation and results in heterogeneous life histories, variable realised fitness and consequently variation in population growth (Stearns 1992, Link et al. 2002). The lives, and deaths, of individuals within populations reflect the inherent stochasticity of their environments, and hold the key for accurate population projection. Linking patterns of variability in population growth with patterns of variability in underlying demographic rates and phenotypic traits, this thesis will argue, asserts and accentuates the non-trivial manner in which interactions between structure and stochasticity influence population growth.

1.2 POPULATION STRUCTURE

Population dynamics result from the demographic rates of individuals both within the focal population (survival and recruitment) and outwith it (dispersal). Density-dependence is considered to feedback negatively on at least one demographic rate as population size approaches its equilibrium (reviewed in, amongst others, Sibly and Hone 2002). The response of any population may depend not on overall population abundance but rather its structure (Grenfell et al. 1998, Coulson et al. 2001, Benton and Beckerman 2005). Population structure is defined by classes, which link class-specific demographic rates to total population growth; this is often achieved using matrix population models (Caswell 2001). Class often serves as a proxy for ability; the assumption of uniform ability across the population becomes the assumption of uniform ability across the class. This assumption is frequently violated (Pfister and Stevens 2003, Coulson et al. 2006b). Analysis of the link between demographic rates and population growth therefore demands consideration of inter- and intra-class differences.

1.2.1 Inter-Class Differences

If a population projection matrix describes changes in population size from one time to the next and the population is divided into age-classes, then the model is referred to as a Leslie matrix (Leslie 1945, 1948). Matrix models are popular in population biology since demographic rates can change with age (e.g. Curio 1983, Forslund and Pärt 1995, Ricklefs and Scheuerlein 2001, Jones et al. in press) or be size-dependent (p. 39 of Caswell 2001 summarizes evidence supporting stage structured models across diverse taxa, Franco and Silvertown 2004). The structure of a population is implied by its life-cycle, and a major cause of heterogeneity between individuals is due to differences in developmental (st)age (Benton et al. 2006). This incorporation of structure in population models is necessary as different age classes have variable frailty: the oldest and youngest Soay sheep (*Ovis aries*) are more susceptible to severe environmental conditions (Coulson et al. 2001) and density-dependent and -independent factors combine to affect different demographic rates of multi-mammate rats (*Mastomys natalensis*) in different ways (Leirs et al. 1997). Adult soil mites (*Sancassania berlesei*) respond to food by investing in fecundity; juvenile soil mites respond to food by investing in growth (Benton and Beckerman 2005).

The response of a population to a variable environment is therefore, in part, conditional upon its structure. A failure to incorporate sufficient population structure can lead to a lack of reconciliation between observed dynamics and model predictions (Benton et al. 2004). Population dynamics result however from the demographic rates of individuals. Structured projection models frequently use mean rates within each (st)age and thus neglect heterogeneity within (st)ages. If diverse aspects of an environment are held constant, there is no guarantee that the same applies to individual development (Link et al. 2002): changes in individual development can generate markedly different dynamics (Benton and Beckerman 2005). All individuals of a specific (st)age are not equal.

1.2.2 Intra-Class Differences

Use of mean rates in structured analysis can be insufficient, since variation between individuals can have population dynamical consequences (Pfister and Stevens 2003). The predicted response of red deer birth weight – a trait considered to be under directional selection (Coulson et al. 2003) and a key determinant of lifetime reproductive success (Kruuk et al. 1999) – to changes in spring temperature was not constant when analysis was conducted at the population and individual levels because individuals differ in their ability to respond to changes in their environment (Nussey et al. 2005). This heterogeneity in individual quality (Vaupel et al. 1979) is a persistent theme in evolutionary demography, but a conclusive definition and assessment procedure remains elusive (Cam et al. 2004a). Demographic rates of individuals are determined by some combination of behavioural, physiological and phenotypic traits (Ricklefs and Wikelski 2002, Coulson et al. 2006a). Individual performance is dependent upon responses to their environment.

Environment is not simply that of the present, since in experimental soil mite (Lindström and Kokko 2002, Beckerman et al. 2003) and long-lived vertebrate (Cam et al. 2003, Reid et al. 2003b) populations, conditions early in life have lifelong fitness consequences and generate marked cohort effects. These lagged effects generate differences in phenotypes of individuals. In many cases, measures of quality are static (e.g. birth weight in red deer, Kruuk et al. 1999), which poses no problem when considering generation-based fitness measures such as lifetime reproductive success (Clutton-Brock 1988). Generation-based fitness measures however neglect temporal changes in individual development and population composition. Selection is a continuous process that operates on the distribution of phenotypic traits within a population at a point in time (Coulson et al. 2006b). How environmental variability affects population dynamics is dependent partially upon the life-history of the focal organism: lagged effects alter demographic rates of different age classes at different speeds (Clutton-Brock and Coulson 2002, Eberhardt 2002). The disparate responses of individuals of different (st)age to environmental variability can fundamentally alter model predictions (Benton and Grant 1996, Lande et al. 2003).

1.3 STOCHASTICITY

Stochasticity creates a risk of extinction that does not exist in deterministic environments because population growth in a stochastic environment (λ_S) will be lower than population growth in a deterministic environment (λ_0) (Lewontin and Cohen 1969). If $\lambda_0 = 1$ then the population would persist indefinitely, but then $\lambda_S < 1$, which implies that the population would eventually become extinct. Increasing environmental stochasticity can decrease time to extinction (Lande 1993, Drake and Lodge 2004). This scenario is common in ecological and evolutionary models of stochastic population dynamics (Boyce et al. 2006). Density-dependence acts in a deterministic fashion – even in open populations (Tavecchia et al. 2007) – to converge population size towards some carrying capacity or equilibrium, even if it probably will not reach it (Begon et al. 1996). Stochasticity is considered to operate around this deterministic functional form and has a greater influence on population dynamics than individual heterogeneity in sufficiently large populations (Lande et al. 2003). Fluctuations in the environment generate consequences that span the spectrum from small fluctuations in survival and fecundity to catastrophic events that cause extinctions (e.g.: asteroids, Sharpton et al. 1992) or alter population structure (e.g. hurricanes: Pascarella and Horvitz 1998, fire: Menges and Quintana-Ascencio 2004). Environmental stochasticity is a frequent cause of density-independent mortality that limits the maximum rate of population growth (Myers et al. 1999). Where variance in demographic rates – and as a consequence potential variance in population growth – is high, it is predicted that analysis of λ_S will produce dissimilar results compared with analysis of λ_0 (Lande et al. 2003).

1.4 SUMMARY

If variation in demographic rates of different age-classes is variable, as has long been postulated (Schaffer 1974) and recently demonstrated (e.g. Coulson et al. 2001, Tavecchia et al. 2001, Coulson et al. 2005, Ezard et al. 2006), then stochastic models need to incorporate population structure to capture accurately the consequences of environmental variation. The interaction between the deterministic functional form and environmental variation has population dynamic consequences (Coulson et al. 2004b, Stenseth et al. 2004). Variation in demographic rates, whether due to density- or environment-related effects, can have a significant impact on life histories (Benton and Grant 1999b). The interactions between structure and stochasticity are therefore pivotal if demographic models are to capture accurately patterns of observed variation in demographic rates and in population growth.

This thesis probes the relationship between environment, demographic rates of individuals and patterns of variability in population growth. It demonstrates and describes how stochasticity alters the predictions of deterministic models in such a way that informative detail is neglected when environmental variability is not incorporated. The analyses are based upon two long-term individually-based data sets that show significant temporal variation in environmental conditions and demographic rates: Soay sheep (*Ovis aries*) on the island of Hirta in the St Kilda archipelago and common terns (*Sterna hirundo*) in Wilhelmshaven, Northern Germany.

1.5 STUDY POPULATIONS

The level of individual-based data in both systems is such that uncertainty caused by measurement error is minimized and therefore considered to be of negligible consequence on the conclusions drawn.

Soay sheep have been individually marked on the island of Hirta in the St Kilda archipelago (57º49' 8º34') since 1985 and identification has followed an identical protocol throughout (Clutton-Brock and Pemberton 2004). Three visits are made annually: during lambing (late spring), in August to obtain genetic and morphometric data and during the rut (October – November). An individual is considered a resident of the study area based on approximately 30 censuses throughout a year, such that the probability of recapture is considered to be 1 (Clutton-Brock and Pemberton 2004).

The Banter See common tern colony in the harbour area of Wilhelmshaven has been studied on an individual basis since 1984. Since 1992 all fledglings have been ringed and marked with passive transponders (TROVAN 100, Cologne, Germany); since then each individual has been "re-captured" using a remote, automatic detection system (Becker and Wendeln 1997). The amount of data generated is vast. As estimates of survival of adults in both populations did not differ significantly from those calculated using capture-mark-recapture analysis (see Appendix A1), all other analyses in this thesis do not use this framework.

The study populations have much in common, yet important differences between them coupled to the high-quality data enables detailed investigation of various hypotheses. Both organisms experience age-specific changes in performance (Catchpole et al. 2000, Nisbet et al. 2002, Nisbet and Cam 2002) and have a noticeable birth pulse in spring. There are however differences. The dynamics of the Soay sheep population are highly unstable (Grenfell et al. 1992, Grenfell et al. 1998); the Banter See colony has increased in abundance over the course of the individual-based study (Becker et al. 2001). Soay sheep are the sole vertebrate herbivores on their island (Clutton-Brock and Pemberton 2004); common terns are migratory: individuals of this population overwinter in Western Africa (according to ringing recoveries, Becker unpubl. data) and return to the breeding site from late April or early May and remain there until August (Becker and Ludwigs 2004). Soay sheep are capital breeders; common terns are income breeders. Soay sheep can produce offspring in their first year of life; common terns show delayed reproduction, often recruiting (Ludwigs and Becker 2002) after at least one year of prospection (Dittmann and Becker 2003) when 3 or 4 years of age. Male Soay sheep rut during October and November to gain access to females, who conceive in late autumn and give birth from the following April; common terns lay clutches (typically) of up to three eggs shortly after arrival at the breeding site, which hatch around (a minimum of) three weeks later and fledge around twenty days after that. Common terns have wings; Soay sheep do not. Whilst both species are considered to be long-lived, these marked differences in individual characteristics contribute to form markedly different population dynamics.

1.6 AIMS AND HYPOTHESES

The project aimed to apply and extend recently developed individual- and demography-based methods of characterising population growth. In order to improve estimates and predictions of demographic models, the causes and consequences of interactions between structure and stochasticity in population projection modelling were assessed by analyzing:

- The correlation between deterministic and stochastic perturbation analysis: under what, if any, circumstances do less data-intensive deterministic methods provide an acceptable approximation of processes that operate in the real, i.e. stochastic, world? What significant insights are gained from a more complex analysis that calculates additional descriptive quantities of population growth?
- The consequences of structure on results of demographic and micro-evolutionary analysis: do individuals of similar state have similar performance?
- The role and influence of individual heterogeneity on population growth: under what circumstances do individual responses to unpredictable and predictable stochasticity alter individual performance and consequently population growth?

It was hypothesised that structure and stochasticity will interact and affect individual performance and consequently population growth:

- Individuals of different (st)age will exhibit differing performance due to differing ability to cope with predictable and unpredictable stochasticity;
- Deterministic and stochastic methods will diverge, dependent upon the amount of variation in demography and how the environment changes over time;
- Individual heterogeneity will be large.

1.7 OUTLINE OF THESIS

The predominant focus is on matrix models (Caswell 2001), which provide a flexible yet tractable framework to assess the focal interaction. Matrix models with and without observed variation showed marked differences between individuals of different breeding experience (chapter 2) and within, between and across diverse habitats (chapter 5). These conclusions were consistent for a wide range of scaling and definition criteria to account for mathematical dependence and biological realism (chapters 3 and 6). Calculation of multiple quantities that address various caveats of matrix projection analysis revealed differences in strength of the link between demographic rates and population growth (chapter 3). Spatial structure was more influential than age-structure in the case of predation events (chapter 4). Incorporation of age-structure significantly altered the strength and direction of selection gradients of age-dependent phenotypes over timeframes reflective of the continuous nature of micro-evolutionary change (chapter 7).

For ease of exposition, each chapter is treated as a unitary treatise. Overall conclusions are drawn in chapter 8.

CHAPTER 2

THE CONTRIBUTIONS OF AGE AND SEX TO VARIATION IN COMMON TERN POPULATION GROWTH RATE[1]

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2.1 ABSTRACT

The decomposition of population growth rate into contributions from different demographic rates has many applications ranging from evolutionary biology to conservation and management. Demographic rates with low variance may be pivotal for population persistence, but variable rates can have a dramatic influence on population growth rate. In this study, the mean and variance in population growth rate (λ) is decomposed into contributions from different ages and demographic rates using prospective and retrospective matrix analyses for male and female components of an increasing common tern (*Sterna hirundo*) population. Three main results emerged: (1) subadult return was highly influential in prospective and retrospective analyses; (2) different age-classes made different contributions to variation in λ: older age classes consistently produced offspring whereas young adults performed well only in high quality years; and (3) demographic rate covariation explained a significant proportion of variation in both sexes. A large contribution to λ did not imply a large contribution to its variation. This decomposition strengthens the argument that the relationship between variation in demographic rates and variation in λ is complex. Understanding this relationship and its consequences for population persistence and evolutionary change demands closer examination of the lives, and deaths, of the individuals within populations within species.

2.2 INTRODUCTION

Any temporal change in population size is the result of multiple stochastic and deterministic processes, which can affect individuals of different sex and age in contrasting ways (Leirs et al. 1997, Coulson et al. 2001). In order to understand such temporal changes it is necessary to identify the link between demographic rates and population dynamics as the role of environmental stochasticity, density and age-structure can vary between populations and species (Coulson et al. 2005). This link enables investigation of selection on quantitative (van Tienderen 2000) and life-history traits (Tuljapurkar et al. 2003) or identification of potential conservation management targets (Caswell 2000). Research into demographic rates of long-lived avian species has typically assumed that adults capable of reproduction have uniform survival and reproductive success regardless of age (e.g. Sæther and Bakke 2000, Doherty et al. 2004, Reid et al. 2004). Although some studies have failed to find evidence against this assumption for survival (e.g. Nichols et al. 1997, Nisbet and Cam 2002), this is not the case for reproductive success as it is widely accepted that breeding performance increases with age in birds, most notably in long-lived ones (Forslund and Pärt 1995). The assumption of uniform rates of reproductive success for all adults therefore contradicts accepted avian life-history theory. In this study, the effects of changing breeding performance with age and inter-sex differences in an increasing population of common terns (*Sterna hirundo*) are investigated by decomposing mean population growth rate and the variation within it.

For reasons of data availability, matrix analyses frequently employ the female component of a population (Sæther and Bakke 2000, Reid et al. 2004, Coulson et al. 2005, Jenouvrier et al. 2005a). There is, however, no guarantee that the demographic rates critical to population growth rate in the female component will also be critical for males because individuals of different age and sex behave, and therefore respond, differently to environmental and demographic pressures (Coulson et al. 2001). In this respect, the common tern is an interesting species: it is a monomorphic, long-lived seabird reaching more than 20 years of age (Becker and Ludwigs 2004). Adults usually start breeding after 3 or 4 years, improve breeding output with age, but show no reproductive senescence (Nisbet et al. 2002). Age-specific mortality rates are not sex-specific (Nisbet and Cam 2002), but many aspects of life are. Males feed the offspring; females brood the chicks. Consequently, males may require more foraging skills than females, and as such often recruit when one year older (Ludwigs and Becker 2002). Hatching and fledging sex ratio are female biased (Fletcher and Hamer 2004, González-Solís et al. 2005) and sons, which fledge with higher body mass than daughters (Becker and Wink 2003), tend to be more difficult to rear. Young female adults are more likely than young male adults to prospect other colonies and to emigrate (Dittmann et al. 2005). Incorporation of such sex-specific subtleties could make analyses of population growth more informative as variation in total population growth rate necessarily consists of variation in both the female and male components.

The effect of temporal variation in demographic rates on variation in asymptotic population growth rate (λ_0) are frequently investigated by perturbation analysis, which consists of two distinct branches: prospective and retrospective analysis (Caswell 2000). Prospective analysis quantifies the response of mean λ_0 to theoretical changes in one or more demographic rates; retrospective analysis explores the contribution of variation in observed demographic rates on variation in λ. Elasticity analysis identifies the relationship between a matrix element (demographic rate) and λ and is a form of prospective analysis. If a proportional change in a demographic rate has a large effect on λ_0, then it has a large elasticity. Prospective analysis requires only an average demographic rate and ignores the variation observed in rate expression; retrospective analysis incorporates this variation. There is no guarantee of a strong correlation between prospective and retrospective analyses as the results of a retrospective analysis are specific to the observed variation; the comparison is motivated as the potential benefit to λ_0 may be greatest by attempts to change a certain rate, but the observed variation around it may suggest it is unrealizable (Caswell 2000). In a comparative retrospective analysis of avian populations, Sæther and Bakke (2000) found that traits important in the prospective analysis retained their importance, albeit at a reduced level, when temporal variation was analyzed in their retrospective analysis.

Many methods exist to investigate the causes of variation in population growth, of which Structured Accounting of the Variance of Demographic Change (SDA) is the most accurate and completely decomposes variation in population growth rate into contributions from demographic rates (Brown and Alexander 1991). Despite the restrictive assumption of density-independent growth and ignorance of fluctuations in age structure, the retrospective matrix approach is generally a good approximation of the more complex SDA method (Coulson et al. 2005). In this study, it is applied to the Banter See common tern colony, whose individuals are followed throughout life through an automatic detection system that reads transponder codes in each bird (Becker et al. 2001). The aim is identification of the demographic rates of pivotal importance to changes in λ_0 and its variation for both the male and female components of the colony.

2.3 METHODS

2.3.1 Study Population

All data were collected at the Banter See common tern colony (53°27'N, 08°07'E) within the harbour area of Wilhelmshaven on the German North Sea coast. This mono-specific colony is the subject of a long-term population study (Becker et al. 2001). The colony site consists of six rectangular concrete islands of equal size. Each island is 0.9m from the neighbouring one, measures 10.7*4.6 metres, is surrounded by a 60cm wall. Walls are equipped with 44 elevated platforms for terns to land and rest on. Breeding territories are considered to be homogeneous.

Common Terns have been ringed since 1980 in Wilhelmshaven and 1984 at the study site (ringing centre "Vogelwarte Helgoland"). All fledglings have been ringed and marked with transponders (TROVAN ID 100) since 1992 and 101 breeders were caught whilst incubating and tagged between 1992 and 1995. Each elevated platform has an antenna, which can read the 10 digit alphanumeric code of each individual at a distance not greater than 11cm. In addition, an antenna is placed at each incubated clutch during the breeding season. Each clutch is checked every 2-3 days during the breeding season and offspring are therefore assigned to parents. All individuals marked since 1998 have had their sex determined by molecular sexing, and before 1998 breeders were sexed by behavioural observation. Further details of this automatic detection system, which minimizes anthropogenic interference by preventing the need for trapping, are presented in Becker & Wendeln (1997).

2.3.2 Population Dynamics

For the purpose of this study, population size is defined as all individuals marked with transponders at the colony site. As recapture probabilities are almost 1 (Ludwigs and Becker 2002), analysis is performed without the use of a mark-recapture framework. Reliable information on both male and female components of the study population enables construction of matrices for both sexes; "both components" refers to statements applicable to male and female matrices. Individuals born after 1992 are only included in the calculations if their life histories are traceable to a marked individual present in the colony in 1992 (i.e. with known lineage). 27 female and 23 male breeders tagged between 1992 and 1995 were of unknown exact age; in these cases estimated minimum age (3 years old when caught) was used. In total 218 females and 174 males were used in the analyses.

Pre-1998 chicks were of unknown sex; sex-specific fledgling rate was calculated using the average proportions observed since molecular sexing of chicks began in 1998. Common terns spend winter months in Western Africa and juveniles spend at least 18 months away from the colony; no reliable information on survival rates during this period is known. "Subadult" is defined as a pre-breeding individual that has returned to its natal colony site and "subadult return rate" (*ret*), which incorporates survival from fledgling to age 1, survival from age 1 to 2 and return to the natal colony site, as $\sum$ (returned subadults) / $\sum$ (fledglings). Recruitment rate of subadults into the breeding colony (*rec*) is defined as $\sum$ (recruits) / $\sum$ (returned subadults). Local return rate is assumed to be local survival rate, which is likely to underestimate real survival due to emigration (Martin et al. 1995).

Birds were grouped into subadults, young adults (3-6 year-old individuals), middle-aged adults (7-11), and old adults (older than 11) to incorporate different reproductive performance between age classes (Ludwigs and Becker 2002, González-Solís et al. 2004, Becker unpub. data). The associated demographic rates are: *ret* – subadult return rate; *rec* – recruitment into the breeding population; *sYA*- survival of young adults; *sMA* - survival of middle-aged adults; *sOA* - survival of old individuals; *fYA* – same-sex fledgling rate of young adults; *fMA* – same-sex fledgling rate of young adults; *fOA* – same-sex fledgling rate of young adults. Annual demographic rates for each class were calculated.

2.3.3 Prospective Matrix Analysis

Analysis is carried out from 1993 as sufficient individuals occupied all age classes from this date. Annual transition matrices were calculated from year t to year t+1 with information on subadult return from year t-1 and recruitment from year t-2. The first transition is 1995 to 1996 with subadult return from individuals born in 1994 and recruitment from 1993. All calculations and statistics (simple linear regression of elasticity against variance for the demographic rates) were performed using the R environment version 2.1.1. (R Development Core Team 2006). Mean values of annual demographic rates were calculated and used to construct single-sex post-breeding Leslie matrices (Caswell 2001) for the male (male offspring from male birds) and female components of the population. The matrices are of the form:

$$\begin{bmatrix}
0 & 0 & fYA & fYA & fYA & fYA & fMA & fMA & fMA & fMA & fOA \\
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & ret & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & rec & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & sYA & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & sYA & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & sYA & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & sMA & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & sMA & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & sMA & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & sMA & sOA
\end{bmatrix}$$

Figure 2.1 shows the associated life-cycle graph. **T** was used to calculate elasticities of population growth rate (N_{t+1}/N_t) for each demographic rate independently. Elasticities of mean population growth ($\partial \ln \lambda_0 / \partial \ln a_{ij}$) are the proportional change in λ_0 resulting from a proportional change in a demographic rate. Cell [2, 1] contains 1 as *ret* [cell 3, 2] contains demographic rate information for both cells (see “Population Dynamics” above). The elasticities of cells [2,1] and [3,2] were

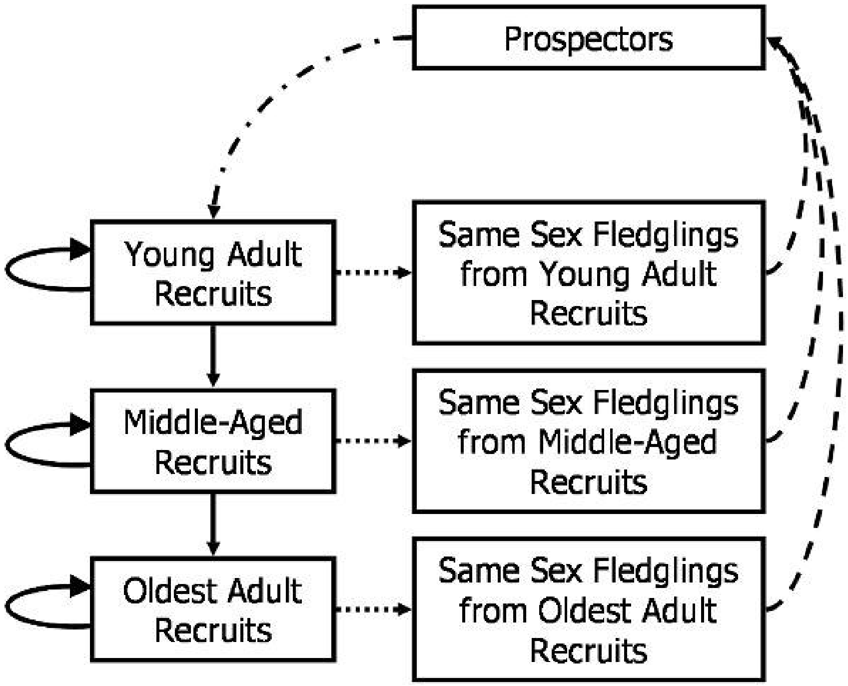

Figure 2.1. Life-cycle graph of matrix T. Solid lines are survival rate; dashed & two-dots: fledgling rate; dashed: subadult return rate; dashed and one-dot: recruitment rate.

summed for subadult return as were appropriate elasticities for young, middle-aged and old adults to generate a single elasticity per demographic rate (Caswell 2001).

2.3.4 Retrospective Matrix Analysis

The association between variation in a demographic rate and variation in λ_0 is estimated by $e_i^2 * cv_i^2$, where e_i is the elasticity of mean population growth to demographic rate r_i and cv_i is the coefficient of variation of r_i. Identical results can be obtained by using the square of the sensitivity of a demographic rate multiplied by the variance in the associated demographic rate (Horvitz et al. 1997).

As demographic rates seldom vary independently, their covariation is incorporated. A negative covariance represents rates that vary in opposing directions. The association between the covariation of two demographic rates (r_i and r_j) and variation in λ_0 can be estimated by $e_i * cv_i * e_j * cv_j * cor(r_i, r_j)$, where $cor(r_i, r_j)$ is the parametric correlation between r_i and r_j. These associations are defined as elasticities of variation in λ_0 to demographic (Coulson et al. 2005); these are presented as contributions to variation

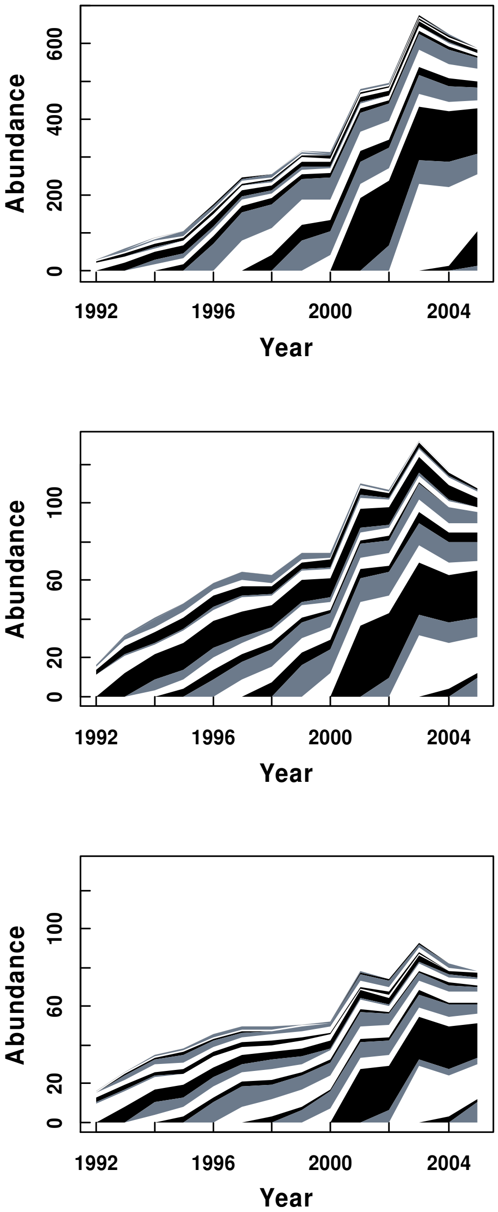

Figure 2.2. Dynamics of (top) the entire marked common tern population, (middle) the female and (bottom) the male components of the population used in the analyses. The peak of a spike is population size in the corresponding year. Each diagonal stripe represents a cohort. "Year" refers to year of attendance in the colony. Wide stripes represent cohorts, which constitute a large proportion of the population. As birds spend their first years around the over-wintering site in Western Africa, the foot of the spike originates one year after birth. More females are present as more adult females were caught and marked between 1992 and 1995.

in λ_0 when re-scaled as percentages. A negative percentage represents covariation between variations in two demographic rates that decreases variation in λ_0.

2.4 RESULTS

2.4.1 Population Dynamics

The population of common terns at the Banter See colony site has increased dramatically since 1992. The total number of marked individuals breeding at the colony site has increased from 53 in 1993 to 368 in 2005; the number of breeding pairs (marked and unmarked) has increased from 98 to 490 over the same period. The abundance of population components used here also increased (see "Contribution to Mean"), although not as strongly because individuals used in this analysis born after 1992 have known lineages (Figure 2.2) and immigrants are therefore excluded.

2.4.2 Contribution to Mean Population Growth

Mean values with associated standard deviations and elasticities of demographic rates of **T** are in Table 2.1. λ_0 was 1.061 for the female component and 1.042 for the male component. Elasticities are similar in both sexes: subadult return (0.237 female, 0.239 male) and survival of young-adults (0.231 female, 0.231 male) made the

	Female Component			**Male Component**		
Demographic Rate	**Mean**	**Standard Deviation**	**Elasticity**	**Mean**	**Standard Deviation**	**Elasticity**
ret	0.330	0.128	0.237	0.373	0.167	0.239
rec	0.717	0.287	0.100	0.736	0.261	0.101
sYA	0.902	0.051	0.231	0.909	0.085	0.231
sMA	0.924	0.048	0.179	0.835	0.077	0.167
sOA	0.848	0.136	0.134	0.859	0.140	0.144
fYA	0.575	0.426	0.052	0.471	0.385	0.053
fMA	0.747	0.338	0.033	0.658	0.324	0.036
fOA	0.870	0.462	0.034	0.715	0.314	0.031

Table 2.1. Means, standard deviations and elasticities for the eight demographic rates used in the matrix analysis for female and male components. The rates are: *ret* – subadult return rate; *rec* – recruitment into the breeding population; *sYA*- survival of young adults; *sMA* - survival of middle-aged adults; *sOA* - survival of old individuals; *fYA* – same-sex fledgling rate of young adults; *fMA* – same-sex fledgling rate of young adults; *fOA* – same-sex fledgling rate of young adults.

greatest contribution to λ_0 (Table 2.1). Elasticities and sensitivities gave qualitatively similar results. Elasticities of survival decreased as expected with age and were greater than the corresponding fledgling rate elasticities (Table 2.1).

a)

ret	1							
rec	0.256	1						
sYA	-0.039	0.331	1					
sMA	0.11	0.665	0.546	1				
sOA	-0.382	0.493	0.356	0.259	1			
fYA	-0.216	0.509	0.429	0.785	0.392	1		
fMA	0.009	0.203	0.297	0.64	-0.092	0.846	1	
fOA	0.035	0.403	0.687	0.815	0.381	0.817	0.697	1
	ret	**rec**	**sYA**	**sMA**	**sOA**	**fYA**	**fMA**	**fOA**

b)

ret	1							
rec	0.39	1						
sYA	-0.636	-0.02	1					
sMA	-0.545	0.179	0.626	1				
sOA	0.263	0.859	0.283	0.205	1			
fYA	0.264	0.414	0.419	0.105	0.605	1		
fMA	0.29	0.368	0.074	-0.005	0.596	0.66	1	
fOA	0.382	0.529	0.236	0.155	0.69	0.856	0.81	1
	ret	**rec**	**sYA**	**sMA**	**sOA**	**fYA**	**fMA**	**fOA**

Table 2.2. The variance-covariance matrix for the female (a) and male (b) components of the analysis. A negative covariance represents rates that vary in different ways. For descriptions of demographic rate codes, see Table 2.1.

2.4.3 Contribution to Variation in Population Growth

The variance-covariance matrices are in Table 2.2. The decomposition of variation in λ_0 for male and female components of the population is given in tables 5.2a and 5.2b. Subadult return, which directly explains 49.4% of the total variation in λ_0 for females and 48.3% for males, explained the most variation in λ_0 (Table 2.3).

Covariation between different demographic rates (25.5% in females; 31.0% in males), fledgling rate of young adults (females: 8.5%; males: 7.9%) and recruitment (females: 9.3%; males: 5.4%) also explained significant amounts of variation (Table 2.3).

a)

ret	49.4							
rec	5.5	9.3						
sYA	-0.3	1.0	1.0					
sMA	0.6	1.4	0.4	0.5				
sOA	-4.4	2.5	0.6	0.3	2.7			
fYA	-4.4	4.5	1.3	1.6	1.9	8.4		
fMA	0.1	0.7	0.3	0.5	-0.2	2.8	1.3	
fOA	0.3	1.7	0.9	0.8	0.9	3.2	1.1	1.9
	ret	***rec***	***sYA***	***sMA***	***sOA***	***fYA***	***fMA***	***fOA***

b)

ret	48.3							
rec	6.3	5.4						
sYA	-6.2	-0.1	2.0					
sMA	-3.8	0.4	0.9	1.0				
sOA	2.8	3.1	0.6	0.3	2.3			
fYA	5.2	2.7	1.7	0.3	2.6	7.9		
fMA	2.3	1.0	0.1	-0.0	1.0	2.1	1.3	
fOA	2.3	1.1	0.3	0.1	0.9	2.1	0.8	0.8
	ret	***rec***	***sYA***	***sMA***	***sOA***	***fYA***	***fMA***	***fOA***

Table 2.3. The retrospective matrix approximation of a decomposition of variation in population growth rate for (a) the female component and (b) the male component of the population. Values on the main diagonal represent the percentage contribution of each demographic rate to variation in population growth and values beneath the main diagonal represent the pairwise covariation between demographic rates. For descriptions of demographic rate codes, see Table 2.1.

2.4.4 Contributions to Mean and Variation in Population Growth

There was a significant negative relationship between a demographic rate elasticity and the rate's variance (female: $F_{1,6} = 18.75$, $p<0.01$, adjusted $R^2 = 0.72$; male: $F_{1,6} = 15.95$, $p<0.01$, adjusted $R^2 = 0.68$). A large contribution to λ_0 does not imply a large contribution to variation within it: markedly different contributions to λ_0 made similar contributions to its variation (Figure 2.3).

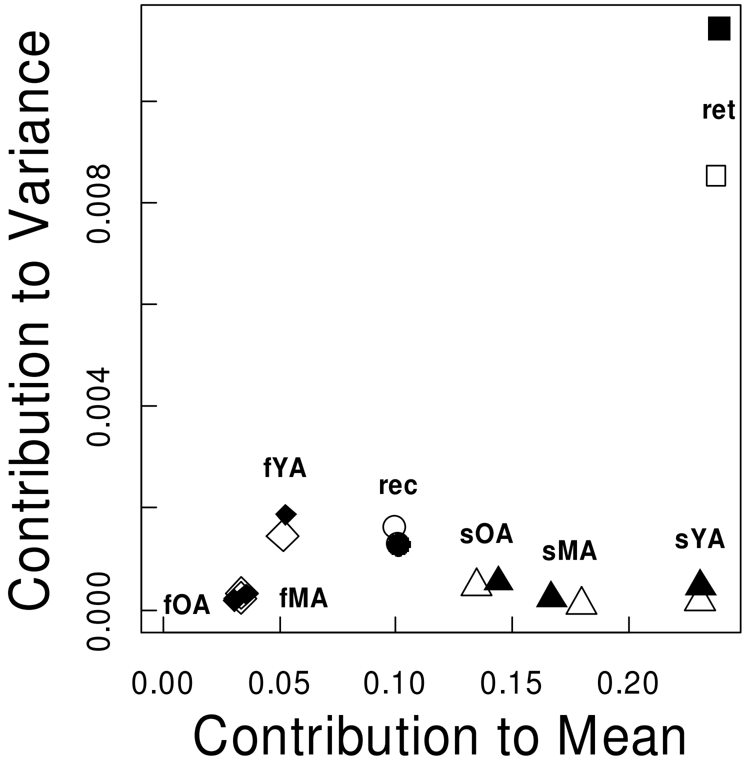

Figure 2.3. The relative contributions of demographic rates to λ and its variation for male (solid symbols) and female (open symbols) components. For descriptions of demographic rate codes, see Table 2.1

2.5 DISCUSSION

Three main results emerged from prospective and retrospective analyses: (1) subadult return was highly influential on population growth in prospective and retrospective analyses; (2) different age-classes made different contributions to variation in λ_0: older age classes consistently produced offspring whereas young adults performed well only in high quality years; and (3) demographic rate covariation explained a significant proportion of variation in both components. As observed previously, no strong correlation between prospective and retrospective analyses was found (figure 3, Caswell 2000) and there was a significant negative relationship between the elasticity of a demographic rate and its variance (Pfister 1998, Gaillard et al. 2000, Sæther and Bakke 2000). Sex-specific differences were present, although some processes affected both components similarly (Table 2.3).

Comparative studies have placed bird species on a “slow-fast continuum”, where species with high fecundity rates but low rates of survival are considered “fast” (Sæther et al. 1996). The contribution of survival to λ_0 was found in a comparative prospective analysis to be greatest amongst long-lived species at the slow end of this continuum (Sæther and Bakke 2000). The results of this prospective analysis on the Banter See colony concurred: if the elasticities of survival were summed across all age classes, as in Sæther & Bakke’s (2000) analysis, survival would have the largest elasticity of λ_0, which can be interpreted as the largest relative contribution to λ_0. The elasticity of survival for young adults makes a similar relative contribution to λ_0 as subadult return in both components.

Despite sex-specific differences in demographic rates, the patterns of the prospective analysis are very similar in both population components (Table 2.1, Figure 2.3). Female population growth was greater than male population growth in the matrices presented here, a pattern not observed in another analysis on this colony using data from 1998 on (Becker et al., unpubl. ms.). Although the employed subsets differ slightly, demographic rates are qualitatively similar when that analysis was repeated using the known-lineage subset employed here. λ_0 was greater for the female matrix due to increased female natal recruitment in earlier years of the study.

As in other long-lived birds, subadult return rates are more variable than survival rates, because they cover a longer time period and because subadults are more strongly affected by environmental conditions during migration and overwintering than adults (e.g. Schaub et al. 2005). The retrospective analysis revealed that subadult return explained almost half the variation in λ_0 in both components (Table 2.3), supporting the argument that female recruitment is more variable than male recruitment (Dittmann et al. 2005). In contrast to the prospective analysis, survival was the least influential demographic rate on variation in λ_0, which contradicts the results of a comparative avian retrospective analysis that found survival to be the dominant demographic rate in prospective and retrospective comparative analyses of avian populations (Sæther and Bakke 2000). The difference may result from matrix construction, although the importance of subadult return in an increasing population was not unexpected as recruitment dominated a retrospective analysis for an increasing ungulate population (Coulson and Hudson 2003) and a life-table response experiment on lesser snow geese (Cooch et al. 2001). Subadult return as defined here includes survival during the first two years of life, which supports Gaillard et al.'s (2000) claims that juvenile survival is the demographic rate with highest influence on variation in population growth. Without detailed data on survival of juvenile common terns during migration and at overwintering grounds, it will prove difficult to prise apart the relative importance of first and second year survival.

Older birds contributed importantly to λ_0 in both components (Table 2.3), which reinforces the argument that older individuals are important for population development for long-lived seabirds. Mean fledgling rate increased with age in both components (Table 2.1) and fledgling rate of middle-aged and old adults made a smaller contribution to variation in λ than young adults (Table 2.3, Figure 2.3). This suggests that the old birds, frequently the highest quality individuals (Wendeln and Becker 1999b), produced offspring at a consistent rate. Young adults had a more variable output, presumably as they lacked the knowledge required to forage efficiently and to co-ordinate sufficient parental care with the partner, especially during years of low environmental quality. Younger age-classes also include individuals of lower quality (Forslund and Pärt 1995). The variation in λ_0 due to fledgling production is therefore not due to older adults, who consistently produce offspring, but rather young adults, which have high reproductive success only in years of high environmental quality.

A significant proportion of total variation was the result of covariation between different demographic rates (Table 2.3), a pattern also observed in ungulates

(Coulson et al. 2005). Such covariation is unsurprising, because an environmentally favourable year may increase survival and reproductive rates without detectable costs (Tavecchia et al. 2005); good quality years when subadult return was high were also years of high recruitment, and vice versa (Table 2.3). Subtle sex specific differences existed: recruitment explained 70% more variation in female λ_0 than its male equivalent (Table 2.3). Subadult return co-varied positively with fledgling rate of young adults in the male component, but negatively in the female component: high return rates are followed by lower female, but higher male, fledging rate in young adults (Table 2.3). This might suggest that returning birds in good condition or high quality years, indicated by high subadult return, are able to produce more sons: son mortality was higher in two-chick broods originating from younger or lower quality parents (González-Solís et al. 2004). Why, however, does survival of young adults covary negatively with subadult return in the female component but not the male (Table 2.2)? A greater understanding of the covariance between demographic rates is critical if misleading conclusions are not to be drawn from analyses.

This decomposition of variation in population growth adds weight to the argument presented by Coulson et al. (2005) that the relationship between variation in a demographic rate and variation in λ_0 is a complex one. The conjecture that the source of environmental variation in demographic rates is potentially more influential on fluctuations in population growth than distance from carrying capacity appears to be borne out here. Although the causes of variation in demographic rates are not explored in this study, the quality of the year as determined by environmental conditions, specifically the abundance and availability of food, appears to cycle every two years. The increase in size of the Banter See colony has mostly been achieved by three large ‘jumps’ (e.g. 2000 to 2001; Figure 2.2) following years producing strong cohorts. Increases in abundance were not however automatic despite population size being a considerable distance from carrying capacity (e.g. 1999 to 2000; Figure 2.2). Understanding this variation and its consequences for species’ persistence and evolutionary change demands closer examination of the lives, and deaths, of the individuals within populations within specie

s.

CHAPTER 3[2]

ON THE PERTURBING ISSUES OF SCALE IN MATRIX PROJECTION ANALYSIS.

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[2] This chapter will form the basis of Gaillard, Ezard & Coulson, which is a manuscript in preparation for Ecological Monographs. This chapter is my own work, but the submitted version will incorporate different life-histories and will have Gaillard as lead author. I will contribute directly the R library, which I developed whilst writing this chapter, do the analysis and write the methods and results sections.

3.1 ABSTRACT

Population biologists aim to characterize the link between patterns of variability in demographic rates with patterns of variability in population growth. A major cause of heterogeneity in demographic rates is differences in developmental (st)age; another is temporal change in the environment a population experiences. Matrix modelling is frequently used for populations where individuals of different (st)age show variation in performance, i.e. show variation in demographic rates. Perturbation analysis aims to determine which demographic rate has the greatest impact on population growth. Sensitivity and elasticity are popular perturbations. Many more, which differ in methodological assumptions and/or perturbation scale, exist. This study focuses on the biological interpretation of the wide array of quantities: how does biological inference from each of them differ? Correlations between quantities with similar data requirements were frequently high, although the rank importance of sub-dominant elements was not. The incorporation of variation in demographic rates generated weaker correlations, especially when considering individual heterogeneity and a dynamic population structure. Given that different assumptions and scales, which describe aspects of population growth from different perspectives, accompany each method this is perhaps unsurprising. There is clearly no one “correct” method to address all biological questions. The appropriate scale for analysis is therefore dependent upon the question asked, the species studied and information available.

3.2 INTRODUCTION

Matrix projection analysis is a flexible yet tractable tool to incorporate the life-history of an organism into a structured model (Caswell 2001). Its use in elucidating the association between demographic processes and population dynamics has proven especially influential in evolutionary ecology (e.g. Lande 1982, van Tienderen 2000, Coulson et al. 2003, Tuljapurkar et al. 2003) and conservation biology (e.g. Benton and Grant 1999a, Heppell et al. 2000, Wisdom et al. 2000, Morris and Doak 2002). Both types of investigation hinge on identifying the association between patterns of variability in population growth and patterns of variability in demographic rates such as survival, recruitment and dispersal (also referred to as vital rates, Caswell 2001). The asymptotic growth rate λ_0 is a critical parameter in conservation biology. $\lambda_0>1$ reveals that the population will increase under the assumptions of asymptotic analysis; $\lambda_0<1$ reveals that the population will decline to extinction. From an evolutionary perspective, λ_0 is mean fitness of individuals in a population with overlapping generations (Fisher 1958).

Much interest has focussed on how robust a population is to changes in particular demographic rates (Caswell 2001). If $\lambda_0<1$ for a population of high conservation priority, then modelling may aim to identify the primary target for management action (e.g. Morris and Doak 2002). Perturbation analysis probes aspects of the relationship between demographic rates and population growth. They provide a measure of the influence of a demographic rate on population growth. Sensitivities of λ_0 to a_{ij} are the change in λ_0 from an absolute change in a_{ij}; elasticities of λ_0 to a_{ij} are the proportional change in λ_0 from a proportional change in a_{ij}. In long-lived species, survival rates tend to have higher elasticity than reproductive rates; the converse is true in faster life-histories (Gaillard et al. 1998, Gaillard et al. 2000, Heppell et al. 2000, Sæther and Bakke 2000). A frequently asked question is: to which demographic rate is population growth most sensitive? A valid question is: sensitivity to what (Caswell 2007)? Different quantities address different questions. Comparisons between them can, potentially, confuse biological meaning. Many quantities differ by definition, yet are often interpreted as addressing the same question. By considering the interpretation of these quantities in the light of their assumptions, multiple measures that use alternative scales can provide a more complete description of the focal system. In a system that shows little temporal variation, the mean matrix may provide a representative model of population dynamics. If population dynamics are characterized by large fluctuations (such that the mean matrix is an inadequate descriptor of dynamics) variation in demographic rates might prove more informative. A decomposition of observed population growth concluded that variation in demographic rates was the reason for contrasting results between two distinct populations of bighorn sheep (*Ovis canadensis*) separated by approximately 300 kilometres in northern Canada (Coulson et al. 2005).

The appropriate scale for analysis is dependent upon the question asked, the species studied and information available. This is likely to change between life-histories, populations and environmental conditions. There is clearly no one "correct" method to address all biological questions, hence the development of multiple measures that describe different aspects of the system (Table 3.1). This array of measures is discussed more comprehensively in the following section.

3.3 ASSUMPTIONS AND THEORETICAL DEVELOPMENT

Construction of a population projection matrix requires demographic data over at least one time-step. This time-step is frequently annual, although seasonal survival may also be relevant in certain circumstances. Data across one time-step enable deterministic analysis. Data across multiple timesteps enables analyses that incorporate variation in demographic rates.

3.3.1 Perturbations to One (Mean) Matrix

Sensitivities of asymptotic growth rate λ_0 to a matrix element a_{ij} are the change in λ_0 resulting from an absolute change in a_{ij}; elasticities of λ_0 to a_{ij} are the proportional change in λ_0 from a proportional change in a_{ij}. Elasticities of λ_0 to a_{ij} therefore sum to 1. λ_0 is the dominant eigenvalue of a population projection matrix (p 83, Caswell 2001). For ease of expression, use of "sensitivity" or "elasticity" from here on refers to these quantities. Sensitivities and elasticities can be calculated analytically (Caswell 2001) or numerically (Fox and Gurrevitch 2000). Whilst it is straightforward to compare sensitivities of two rates, it is problematic to compare the sensitivity of a rate with the sensitivity of a quantity: survival and fecundity in polytocous species are not bound by the same upper limit. Elasticities (proportional sensitivities) were developed to resolve this problem. Nichols and Hines (2002) and Heppel *et al.* (2000) argued that, despite their appealing unitlessness, conclusions drawn exclusively from elasticity analysis should be treated with suspicion. For example, an elasticity analysis might suggest that some desired λ_0 is realizable via a 10% increase in survival. If survival was already 0.933, then the correct interpretation of "prospective" (Caswell 2000) analysis would discuss the consequences of a survival rate of 1.026, which has no biological relevance. The approach "happily and quite correctly [gives] the results of changes in the vital rates that are biologically impossible" (p. 277, Caswell 2001). Sensitivities and elasticities are based upon infinitesimal perturbations to matrix elements, yet extrapolation such as that above remain common. Conclusions must be drawn with consideration of methodological scale and assumptions. Without this, the key issue of biological relevance is compromised.

Consider the relative biological relevance of survival and death. One advantage of working with mortality is the ability to partition it into various causes (Owens 2002). Olesiuk et al. (1990) concluded for killer whales (*Orcinus orca*) that λ_0 was more sensitive to changes in reproductive parameters than changes in mortality, whereas Brault & Caswell (1993) concluded – from the same data on the same population – that λ_0 was more sensitive to changes in survival than reproduction. Rather than considering difference from 0 (as in survival analysis), the difference from 1 is taken in analyses of mortality. Mean killer whale survival was 0.98. As a scaling measure it is perhaps unsurprising that results of elasticity analysis were different using this value rather than 0.02. The scale of perturbation is key to ensure biologically relevant application of any analysis. Link & Doherty Jr. (2002) argued that results should be consistent whether survival or mortality is used and suggested that scaling "may be reasonably guided by thinking about mean-variance relations" (p. 3301, Link and Doherty Jr. 2002). Elasticities might be considered as log-scaled sensitivities. Employment of arc-sin scaled sensitivities found some qualitative (rank-importance) changes in arc-sin scaled sensitivities compared to elasticities, although both were conducted on very long-lived species with high annual survival (red-tailed tropicbirds [Phaethon rubricauda], Doherty et al. 2004, Emperor penguins [Aptenodytes forsteri] and Snow Petrel [Pagodroma nivea], Jenouvrier et al. 2005b). An extension of this survival/mortality argument might consider the difference from maximum achievable fitness – survival plus fecundity – over one time-step. This quantity was defined by Watson & Galton (1874) as individual performance.

There are inevitably methodological assumptions regardless of scale. Three common (Table 3.1) assumptions are a stable-age distribution and independent, linear perturbations. Concomitant to the progression of λ_0 to its asymptotic value, the associated eigenvector also reaches an asymptote at this point, after which it remains static. The eigenvector denotes the population structure and once static is defined as the stable-age distribution (p. 87, Caswell 2001). Elasticities are defined on the basis of infinitesimal change and therefore assume independent linear perturbations. It is doubtful whether any change required for management action would remain linear (Hodgson and Townley 2006). Non-linearity has the potential to alter the magnitude of change in demographic rates required to achieve some desired level of population growth or incorrectly estimate the strength of selection on a given demographic rate. One potential cause of non-linearity is changes in the (st)age structure of a population, which has the potential to affect population dynamics (Coulson et al. 2001). A dynamic population structure can be incorporated using the observed age-structure rather than the stable age distribution (Fox and Gurrevitch 2000, Coulson et al. 2004a). Its implementation requires data over multiple seasons however, which implies the possibility to conduct stochastic analysis.

3.3.2 Perturbations to Matrices with Variation in Demographic Rates

Any required perturbation to a demographic rate may be theoretically achievable, yet unlikely to be realizable due to environmental canalization (Stearns and Kawecki 1994, Gaillard and Yoccoz 2003). As a consequence numerous attempts have been made to link demographic rates to statistics describing fluctuating populations, the first of which concerned the Northern Spotted Owl (*Strix occidenntalis caurina*, Lande 1988). Lande's (1988) methods enabled estimates of variation in λ_0 due to population patterns and sampling error as well as assessment of the relative contribution of demographic rates to observed changes in λ_0. The latter approach has been termed a life-table response experiment, although analysis of natural populations rarely incorporate experimental changes (Caswell 1989, ch. 10, Caswell 2001). This analysis can be applied to any observed pattern of variation, including those generated through simulation.

Elasticities of variation in λ_0 to variation in a_{ij} (Lande 1988) did not consider covariation in demographic rates, although the possibility was there to do so. Potential causes of covariation include trade-offs between survival and fecundity (Stearns 1992) or similar responses to environmental conditions, which can be consistent across diverse taxa (Walther et al. 2002). Horvitz *et al.* (1997) were the first to incorporate covariation in the method, which has since been found to be influential for population growth across diverse taxa and life-history (Horvitz et al. 1997, Coulson et al. 2005, Ezard et al. 2006). Integrated elasticities were developed to address life-cycle trade-offs (van Tienderen 1995) and quantify the total effect of variability in a given demographic rate on population growth using direct and indirect contributions. There are occasions when covariation is crucial. There are others when it is not. Examples of the latter include a management scenario that destroys eggs or shoots adult birds. These quantities are, however, still based on deterministic elasticities that assume asymptotic growth and a stable population structure (Table 3.1). The influence of covariation can be biological and/or mathematical: there exists a correlation between variation in vital rates and elasticity, such that the elasticity is biased upwards by positive correlation, and vice versa (Doak et al. 2005).

A key result of stochastic perturbation analysis has been the pattern of decreased variability in vital rates with higher elasticity (Pfister 1998). When most correlations between vital rates are positive, due to, say, environmental variation, the negative effects of variation can be greater previously considered: Doak et al. (2005) derived stochastic sensitivities that “correctly [estimate] how environmental stochasticity influences fitness and population growth” from the long-run stochastic growth rate assuming small noise in demographic rates (Tuljapurkar 1990).

In sufficiently large populations, the effect of environmental variation is greater than the effect of variation between individuals (Lande et al. 2003). There are however inevitable differences between individuals that are not adequately explained by (st)age. Conditions early in life can have long-term fitness consequences (Cam et al. 2003), which generate cohort effects that influence population dynamics (Lindström and Kokko 2002, Beckerman et al. 2003). There may therefore be differences in individual performance that are not predictable solely by considering differences between (st)ages. Alternative causes of individual heterogeneity have been acknowledged as an issue in matrix projection analysis (Pfister and Stevens 2003). The issue can be addressed using alternative scaling measures (Coulson et al.

2006b). In small populations, when a conservation and management applications may be paramount, individual heterogeneity is likely to be of great importance.

3.3.3 Which Measure to Use When?

In summary, which quantity should be used to answer the fundamental question: which demographic rate is the most influential on population growth? This general question encompasses several specific questions that address different aspects of population growth. Different questions require different measures (Table 3.1). Any choice should be made in the knowledge of the consequences of the scale adopted and on the question asked. Different quantities address different questions. If results are to have real world relevance they need to be achieved using methods as simple as possible, but no simpler. Calculation of multiple quantities informs on multiple aspects of a focal system and hence provides a more complete description. The recent focus on stochastic elasticities of population projection in Markovian environments (Tuljapurkar et al. 2003) is dealt with elsewhere (chapters 4 & 5).

3.4 METHODS

3.4.1 Study Population

Long-term individual-based data have been collected since 1985 from the population of Soay sheep living in Village Bay on the island of Hirta (57º49' 8º34') in the St Kilda archipelago. An identical data collection protocol has been followed throughout. Three trips are made annually to collect data: during the birth pulse (late March - early May), an annual catch (August) and during the rut (October - November). In addition, approximately 30 censuses a year and regular mortality searches are carried out. The population experiences irregular yet frequent crashes in population size, when up to 70% of the population may die (Clutton-Brock and Pemberton 2004). Population size is defined here as the number of sheep alive on August 1st each year; a "sheep year" is considered to begin and end in August, such that a lamb is defined as an individual that survives until the August of the year of its birth, a yearling as an individual that survives until the August following the year of its birth, and so on. Full details of the data collection protocol and population history are available in Clutton-Brock and Pemberton (2004).

3.4.2 Population Model

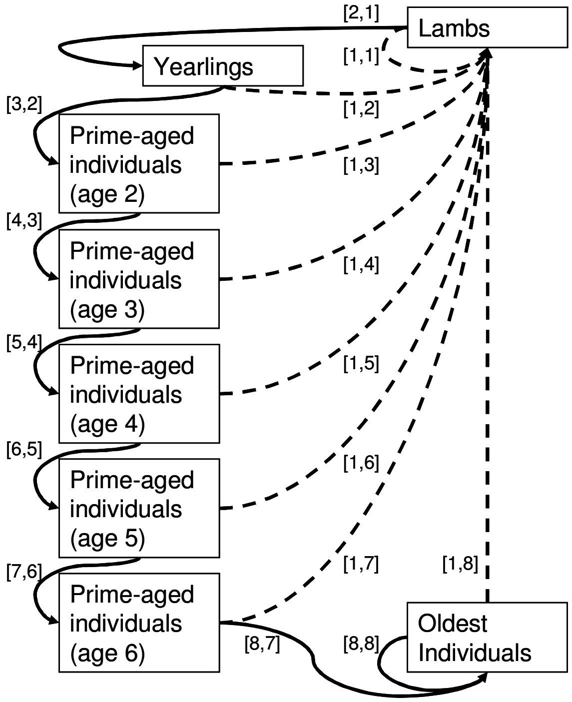

Figure 3.1. Life-cycle graph for the post-breeding Leslie matrix model **A**. Solid lines are survival; dashed lines are fecundity. Values in square brackets are matrix elements ([row, column]).

Data to construct matrices were used from 1985 to 2006 inclusive save for 2001, which was omitted because of foot and mouth disease on the mainland that restricted opportunities to collect data. Only females were considered. Four age-classes have been identified as the most parsimonious age-structure for female Soay sheep (Catchpole *et al.* 2000): lambs(L), yearlings (Y), prime-aged (P, 2-6 years old) and older (O, >6 years old). A post-breeding age-structured Leslie matrix model (Caswell 2001) **A** was constructed with 8 age-classes where sub-diagonal elements are survival rates (s, August to August) and top row elements are fecundity rates (f, lambs born from individuals that survive from August in the pre-focal year until the focal year birth pulse):

$$\mathbf{A} = \begin{vmatrix} fL & fY & fP & fP & fP & fP & fP & fO \\ sL & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP & sO \end{vmatrix}$$

The corresponding life-cycle graph is given in Figure 3.1. In the deterministic case, one matrix is calculated from mean rates from the nineteen available transitions. In the stochastic case, nineteen annual transition matrices are calculated and variation incorporated from the demographic rates that generate each matrix.

3.4.3 Perturbation Analysis of One (Mean) Matrix

Formulae for all elasticities discussed, associated assumptions and key references are given in Table 3.1. Sensitivities of λ_0 to a_{ij} and elasticities λ_0 to a_{ij} were calculated analytically. Link & Doherty Jr. (2002) noted that arcsin transformed sensitivities and logit transformed sensitivities are both variance-stabilizing transforms for data bounded by 0 and 1 and could be used in conjunction with log-scaled sensitivities that additionally control for the maximum coefficient of variation (k_{max}) for fecundity data. Logit-transformed sensitivities were used for survival data, and log-transformed sensitivities for fecundity data, where k_{max} was set at 2.6 - the maximum observed coefficient of variation in fecundity. This is the first application of variance-stabilized sensitivities for data not bounded between 0 and 1.

All of the quantities discussed thus far use a_{ij} – i.e. difference from zero – as the reference scale. It might be informative to consider the difference from maximum achievable fitness over a time-step, i.e. survival plus fecundity. This is referred to as the life-history limit. Perturbations from this limit are presented here for the first time. Female Soay sheep have a maximum of two offspring per year, such that the life-history limit is survival plus two offspring.

Instead of perturbing a demographic rate a_{ij} and seeing resultant change in λ_0, the inverse occurs to assess non-linear perturbations using transfer function analysis (Hodgson and Townley 2006). λ_0 is perturbed (λ_{pert}) and the value of a_{ij} to obtain λ_{pert} whilst holding others constant is recorded. One approach is to consider some target λ_{pert} and then compare sensitivities to critical values of a_{ij} to obtain λ_{pert} (Hodgson and Townley 2006). To obtain a general view of the inaccuracy of tangential linear extrapolation, λ_0 was compared to λ_{pert} over the observed range of λ_t (defined as the one-step population growth $\lambda_t = \frac{N_{t+1}}{N_t}$ where N is population size at time t) during the individual-based study at increments of 0.02. The non-parametric spearman rank correlation coefficient between the change required to obtain λ_{pert} and elasticity was used to assess the accuracy of the linear perturbation assumption. Hodgson & Townley's (2006) demonstration– based on Doak et al.'s (1994) desert tortoise (*Gopherus agassizii* Cooper) matrix – had a λ_0=0.958 and λ_{pert}=1.00.

Table 3.1. Perturbation measures calculated to assess the impact of demographic rates on various measures of population growth. Each quantity is presented with its definition, abbreviation used in figures and text, examples of potential uses, associated assumptions and an introductory reference.

Measure	**Definition**	**Code**	**Scaling**	**Use**	**Assumptions**	**Example reference**
Equilibrium sensitivity of the deterministic population growth rate to a matrix element	$\frac{\partial \lambda}{\partial a_{ij}}$	S_{ij}^{D}	Value of a_{ij}	Linear approximation of the association between a matrix element and population growth calculated using the observed measurement scale. Comparison across matrices	Linearity, and hence infinitesimal perturbation Stable age or stage structure	Caswell (2001)
Equilibrium elasticity of the deterministic population growth rate to a matrix element	$\frac{\partial \log \lambda}{\partial \log a_{ij}}$	E_{ij}^{D}	Proportional (elasticities of all matrix elements sum to unity)	Linear approximation of the association between a matrix element and population growth on a relative scale – direct comparisons between matrix elements within a matrix. Comparison across matrices.	Linearity, and hence infinitesimal perturbation Stable age or stage structure	Caswell (2001)
Non-equilibrium elasticity of the deterministic population growth rate to a matrix element	$\frac{\partial \log(N(t+1)/N(t))}{\partial \log a_{ij}(t)}$	E_{ij}^{nEQ}	Proportional (elasticities of all matrix elements sum to unity)	The association between a matrix element and population growth on a relative scale – direct comparisons between matrix elements within a matrix.	Population not at equilibrium	Coulson (2004)

1

Transfer function	$\mathbf{c}(z\mathbf{I}-\mathbf{A})^{-1}\mathbf{b}$ Where z is the dominant eigenvalue of the perturbed matrix, **I** is the identity matrix, **b** & **c** column and row vectors respectively and **A** the population projection matrix.	$G(z)$	Value of a_{ij}	Exact association between a matrix element and population growth calculated using the observed measurement scale. Comparison across matrices	Stable age or stage structure	Hodgson and Townley (2004)
Variance stabilised sensitivities of the deterministic population growth rate to a matrix element	$\frac{\partial\lambda}{\partial a_{ij}}\frac{1}{\lambda q'(a_{ij})}$ *q'* is a variance stabilising transformation for a_{ij}	S_{ij}^{VS}	Variance of a_{ij}	The association between a matrix element and population growth independent of the mean.	Linearity, and hence infinitesimal perturbation Stable age or stage structure	Link and Doherty (2002)
Life history limit sensitivities or elasticities of deterministic population growth to a matrix element	$\frac{\max(\lambda)-\lambda}{\max(a_{ij})-a_{ij}}$ $\frac{\log(\max(\lambda)-\lambda)}{\log(\max(a_{ij})-a_{ij})}$ Max(a_{ij}) is the maximum value of a_{ij} that the life history permits Max(λ) is the maximum possible value of λ given the life history	E_{ij}^{LHL}	Distance between maximum achievable population growth and realised growth	Comparison of population performance between years and life histories	The life history limit is measurable Same as the assumptions used in the calculation of sensitivities and elasticities.	This paper
Integrated sensitivities and elasticities of deterministic population growth to a quantitative trait	$\sum_i E_i\rho_{ij}\frac{CV_i}{CV_x}$ Where E_i the equilibrium elasticity of λ_1 to rate i, ρ_{ij} is the correlation between rates i and j and CV_i the coefficient of variation of rate i.	IE_{ij}			Same as the assumptions used in the calculation of sensitivities and elasticities.	Van Tienderen (1995)

De-lifing	$\frac{s_i(t)-\bar{s}(t)}{N(t)-1}+\frac{f_i(t)-\bar{f}(t)}{N(t)-1}$ s = survival f = reproduction N = population size t = time i = individual	$p_{t(i)}$	Individual performance scaled by mean survival and reproduction, and population size.	Individual contributions to population growth	Individuals have to been recognisable	Coulson et al. (2006b)
Retrospective sensitivities and elasticities of the variance in population growth rate to variation in a matrix element (LTRE)	$\left(\frac{\partial \lambda}{\partial a_{ij}}\right)^2 \mathrm{var}(a_{ij})$ $\frac{\partial \log \lambda}{\partial \log a_{ij}}^2 CV(a_{ij})^2$ Where CV is the coefficient of variation	E_{ij}^{R}	Temporal variance in a_{ij}	The relative contribution of the observed variation of a matrix element to variation in population growth	Linearity, and hence infinitesimal perturbation Stable age or stage structure (appropriate for small fluctuations in age-structure)	Horvitz et al. (1997) Lande et al. (1988)
Stochastic sensitivities that correctly incorporates correlation between elements	$\frac{\partial(\log \hat{\lambda}_s)}{\partial \sigma_v} \approx \frac{-1}{\bar{\lambda}_1^2}\left(\bar{S}_{vi}^2 \sigma_{vi} + \sum_{j \neq 1} \bar{S}_{vi} \bar{S}_{vj} \sigma_{vj} \rho_{vi,vj}\right)$ Where λ_1 is asymptotic growth rate, $\bar{S}_{vi}^2$ the equilibrium sensitivity of λ_1 to rate i, c_{vi} the standard deviation of rate i and $\rho_{vi,vj}$ the correlation between rates i and j.	E_{ij}^{RC}	Variance or correlations between elements	The contribution of matrix elements with observed covariation to stochastic population growth.	Small noise	Doak et al. (2005)

3.4.4 Perturbation Analysis of Matrices with Variation in Demographic Rates

Formulae for all elasticities discussed, associated assumptions and key references are given in Table 3.1. The observed population structure was used instead of the stable age distribution as weights in non-equilibrium elasticity calculations. This assessed the consequences of non-constant population structure (Fox and Gurrevitch 2000, Coulson et al. 2004a).

Variation in demographic rates, denoted here $\sigma(a_{ij})$, is matched to variation in population growth, denoted here $\sigma(\lambda_0)$, in many ways. Lande (1988) multiplied the elasticity squared by the coefficient of variation in a_{ij} squared. Identical results can be obtained when sensitivity squared is multiplied by variance in a_{ij} (Fox and Gurrevitch 2000). Covariation between demographic rates can be incorporated using correlation coefficients of two focal demographic rates. Elasticities of variation in population growth to demographic rates, $\sigma(\lambda_0)$ to $\sigma(a_{ij})$ (Coulson et al. 2005), consider correlations between specific pairs of elasticity and are presented re-scaled as percentages. A negative percentage represents covariation between variation in two demographic rates that decreases $\sigma(\lambda_0)$, and vice versa. This quantity returns one value per pair of demographic rates if covariation is incorporated or one per demographic rate if covariation is neglected. Van Tienderen (1995) developed the integrated elasticity, which measures the change in $\ln(\lambda_0)$ with a proportional change in a_{ij} by its direct and indirect effects, where ln denotes the natural logarithm. The integrated elasticity returns one value per demographic rate. Doak et al. (2005) derived the "correct expression" for these sensitivities, which is based upon Tuljapurkar's small noise approximation (Tuljapurkar 1990), but which uses λ_0 as a scaling measure and decomposes elasticity of λ_S to variance of a_{ij} into direct, i.e. from the focal rate, and indirect, i.e. from correlations between vital rates, contributions (Doak et al. 2005). Again this quantity returns one value per demographic rate.

Individual heterogeneity can be investigated by "de-lifing" a population to calculate individual contributions to population growth ($p_{t(i)}$, Coulson et al. 2006b). The logic behind the method is to consider population growth with and without a focal individual i, and repeat this for all individuals across some time-step t. $p_{t(i)}$ can therefore be partitioned into contributions from survival and fecundity. These contributions can be summed across age-classes to generate contributions of age-classes to population growth (Coulson et al. 2006b). Absolute values of $p_{t(i)}$, denoted $|p_{t(i)}|$, were used as difference from zero is analogous to the directionless nature of all other quantities calculated. When comparing this to other quantities from the mean matrix, $|p_{t(i)}|$ was summed across all individuals in all years; when comparing to other quantities that incorporate variation in demographic rates, $|p_{t(i)}|$ was summed across all individuals in each year.

3.4.5 Statistical Analysis

Generalized linear models (GLMs) were used to assess the correlations between different quantities. A quasi error distribution (Gaussian error with deviance parameter not fixed at 1 to account for overdispersion, p. 530 Crawley 2002) with identity link function was used. Significance (p-value) and proportion of variation explained (p. 235, Crawley 2002) were used to assess the strength of the correlation between the elasticities. Diagnostic plots (Crawley 2002) were assessed for each comparison to determine whether assumptions were valid and therefore whether alternative link functions or variance structures (p. 545, Crawley 2002) were required. Where applicable, these alternative link functions and variance structures are given at the appropriate juncture in the results section. Due to the low number of data points (demographic rates), there is potential for one point to dominate the regression fit. Therefore in addition to the above criteria, Cook's distance – a measure of influence of each point on a regression fit (p. 197, Fox 2002) – was calculated. If the Cook's distance of a point was greater than 4/(n-k-1) (p. 198, Fox 2002), where n is the number of data points and k the number of parameters in the model, then the model was re-fitted without the point of large influence.

The amount of non-linearity was assessed by fitting a quadratic regression of λ_{pert} against the magnitude of the perturbation required to achieve λ_{pert} squared. This generated an equation of the form $y=Ax^2$, which was then differentiated with respect to x: $dy/dx=2Ax$. Lower values of A indicate "more linear", or less curved, lines. A is defined as the differential of the non-linear gradient.

Changes in age-structure were assessed by fitting a multinomial model in the package nnet (version 7.2-34, Venables and Ripley 1999). Multinomial model fit was assessed using the Akaike's Information Criterion (AIC, Burnham and Anderson 2002), which provides a compromise between number of parameters used and explained deviance. The model with the lowest AIC is considered the minimum adequate, but models within 4 AIC values – the lower bound of Burnham & Anderson's (2002) recommendation – are considered equivalent. Amongst equivalent models, that with the smallest number of parameters is the minimum adequate.

All correlations to assess the maintenance of rank importance in the perturbation measures were assessed with non-parametric spearman rank correlation coefficients. All population projection, perturbation analysis and statistical analysis were achieved in the R environment (R Development Core Team 2007).

3.5 RESULTS

The mean Leslie post-breeding matrix had an asymptotic growth rate λ_0 of 1.06, with a stable age-distribution (left, scaled to sum to 1, see also figure 4) and reproductive value (right, scaled relative to first element)

:

$$\begin{vmatrix} 0.292 \\ 0.148 \\ 0.114 \\ 0.096 \\ 0.080 \\ 0.067 \\ 0.056 \\ 0.146 \end{vmatrix} \qquad \begin{vmatrix} 1.000 \\ 1.773 \\ 2.008 \\ 1.917 \\ 1.809 \\ 1.679 \\ 1.525 \\ 1.341 \end{vmatrix}$$

3.5.1 Deterministic Analyses

Sensitivities of λ_0 to a_{ij} (S_{ij}^{D}) and elasticities of λ_0 to a_{ij} (E_{ij}^{D}) were highly correlated (Figure 3.2a; β=0.952, s.e.=0.195, p<0.01, r=0.799). Rank importance of demographic rates is largely conserved between the two measures (Table 3.2). S_{ij}^{D} did not covary significantly with variance-stabilized sensitivities (S_{ij}^{VS}) (β=1.883, s.e.=0.782, p>0.05, r=0.492), but E_{ij}^{D} did (Figure 3.2b; β=2.673, s.e.=0.415, p<0.001, r=0.873) and rank correlation of demographic rates was high (Table 3.2). Life-history limit elasticities (E_{ij}^{LHL}) did not covary significantly with E_{ij}^{D} (Figure 3.2c; β=-8.561, s.e.=8.544, p>0.05, r=0.143) or S_{ij}^{D} (β=-3.591, s.e.=8.553, p>0.05, r=0.028) or S_{ij}^{VS} (β=-4.079, s.e.=2.764, p>0.05, r=0.267) and rank correlations were moderate (Table 3.2). Diagnostic plots of these regressions were acceptable, but *sP* had large influence on the regressions of S_{ij}^{VS} on S_{ij}^{D} (Cook's distance=3.46) and E_{ij}^{D} (Cook's distance=4.34). When these regressions were re-fitted without this point, proportion of variation explained dropped to 0.001 for S_{ij}^{VS} on S_{ij}^{D} (β=0.045, s.e.=0.698, p>0.05) and to 0.438 for S_{ij}^{VS} on E_{ij}^{D} (β=1.548, s.e.=0.784, p>0.05).

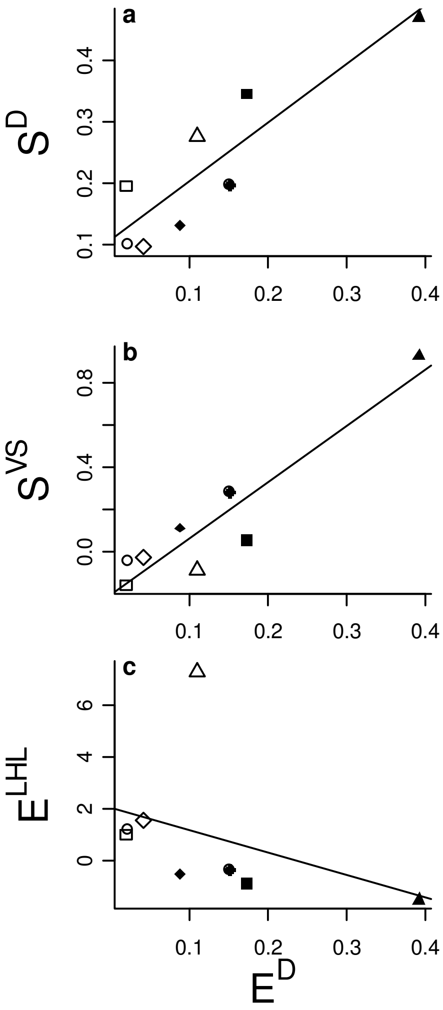

Figure 3.2. Elasticities of λ_0 to a_{ij} (E_{ij}^{D}) are highly correlated with corresponding sensitivities of λ_0 to a_{ij} (S_{ij}^{D}, black) and variance-stabilized sensitivities (S_{ij}^{VS}, light gray). Life-history limit elasticities (E_{ij}^{LHL}, dark gray) are not significantly correlated with anything. Solid symbols are survival, open symbols fecundity. Squares relate to lambs, circles to yearlings, triangles to prime-aged individuals and diamonds to oldest individuals.

The amount of bias caused by the linear approximation differs for different demographic rates. The amount of non-linearity significantly correlated with E_{ij}^{D} (Figure 3.3b; β=-1.461, s.e.=0.156, p<0.001, r=0.848). The correlation coefficient was at least 0.6 for perturbations within 5% of the observed λ_0 for this population (Figure 3.3b), suggesting that the linear approximation retains a large proportion of the rank importance of demographic rates for sizeable perturbation sizes.

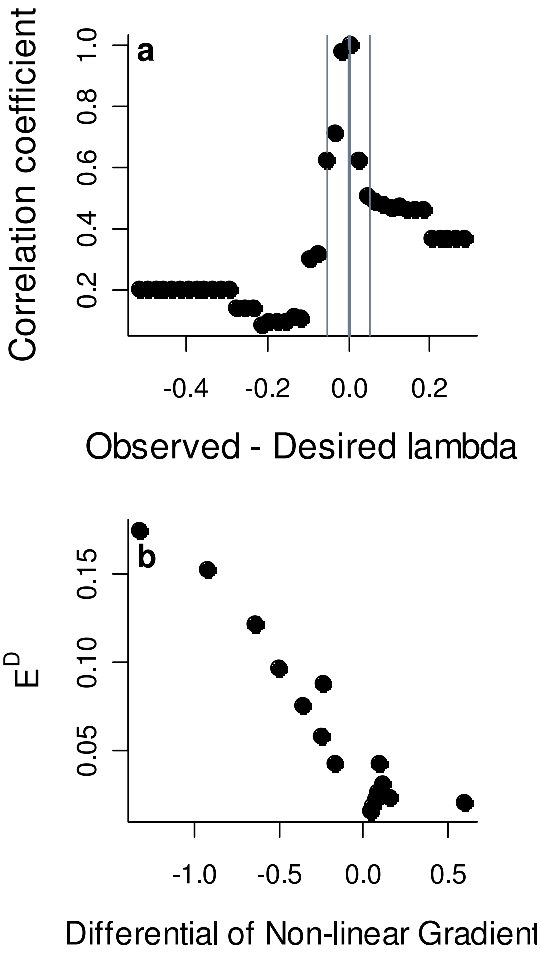

Figure 3.3. Sensitivity predictions are based on tangential extrapolation, whereas transfer function predictions capture the nonlinear relationship between changes to the transition rates and the resulting dominant eigenvalue of **A**. The non-parametric rank correlation coefficient is greater than 0.6 between a transfer function and deterministic analysis when perturbations are within 95% of observed λ_0 indicated by vertical lines (a). As E_{ij}^{D} increases, non-linearity decreases significantly over unit intervals (b). Each point is a matrix element in **A**.

3.5.2 Stochastic Analyses

Significant fluctuations in the age-structure were detected (Figure 3.4): a model that considered age-structure as a constant performed significantly worse (AIC= 11464) than one that treated year as a continuous variable (AIC= 11453), one that treated year as a categorical variable (AIC=11290) and one that separated crash from non-crash years (AIC=11423). The correlation between E_{ij}^{D} and non-equilibrium elasticities of λ_0 to a_{ij} (E_{ij}^{nEQ}, from a quasi GLM with identity link function and mu^2 variance function to account for the increased variation with the mean) was high but variance explained low (Figure 3.5a; β=0.401, s.e. =0.073, p<0.001, r=0.158). This correlation between E_{ij}^{D} and absolute individual contribution to population growth $|p_{t(i)}|$ was similar (Figure 3.5b; β=0.078, s.e.=0.021, p<0.001, r=0.084); E_{ij}^{nEQ} and $|p_{t(i)}|$ were more strongly correlated (Figure 3.5c; β=0.146, s.e.=0.025, p<0.001, r=0.190). Demographic rates occupy similar areas of the plots, but the variation around them is not consistent in both directions: variation in E_{ij}^{nEQ} was much greater than E_{ij}^{D} (Figure 3.5).

S_{ij}^{D}	1							
E_{ij}^{D}	**0.810**	1						
S_{ij}^{VS}	0.381	**0.762**	1					
E_{ij}^{LHL}	-0.571	-0.619	-0.738	1				
E_{ij}^{R}	0.667	0.738	0.690	-0.881	1			
E_{ij}^{RC}	-0.762	-0.714	-0.595	0.905	**-0.905**	1		
IE_{ij}	0.619	**0.667**	**0.619**	-0.381	0.286	-0.429	1	
$\|p_{t(i)}\|$	**0.952**	0.667	0.167	-0.524	**0.643**	**-0.762**	0.381	1
	S_{ij}^{D}	E_{ij}^{D}	S_{ij}^{VS}	E_{ij}^{LHL}	E_{ij}^{R}	E_{ij}^{RC}	IE_{ij}	$\|p_{t(i)}\|$

Table 3.2. Spearman rank-correlation coefficients between different perturbation analyses. The first four quantities are based on one (mean) matrix; the latter four incorporate observed stochasticity over the 19 transition matrices available from the data. Large values in bold are when the regression between the two quantities is significant at the 99% level, i.e. p<0.01; bold values indicate that the regression between the two quantities is significant at the 95% level, i.e. p<0.05. For perturbation quantity codes, see Table 3.1. $|p_{t(i)}|$ is summed across all years.

Elasticities of variation in λ_0 to variation in a_{ij} (E_{ij}^{R}) were highly correlated with the refinement based on the small-noise approximation (E_{ij}^{RC},Figure 3.6a; β=-1.924, s.e. =0.255, p<0.001, r=0.904). The correlation was also significant between E_{ij}^{R} and $|p_{t(i)}|$ (Figure 3.6b; β=5.674, s.e. =2.008, p<0.05, r=0.571) and between

E_{ij}^{RC} and $|p_{t(i)}|$ (Figure 3.6c; β=-2.964, s.e. =0.912, $p<0.05$, r=0.638). Rank correlation was maintained (Table 3.2). The Cook's distance of *sL* was very large in one comparison: $|p_{t(i)}|$ (13.3) against E_{ij}^{R}. When this regression was re-fitted without *sL*, the correlation between E_{ij}^{R} and $|p_{t(i)}|$ became (marginally) non-significant (β=15.304, s.e. =6.480, $p>0.05$, r=0.527).

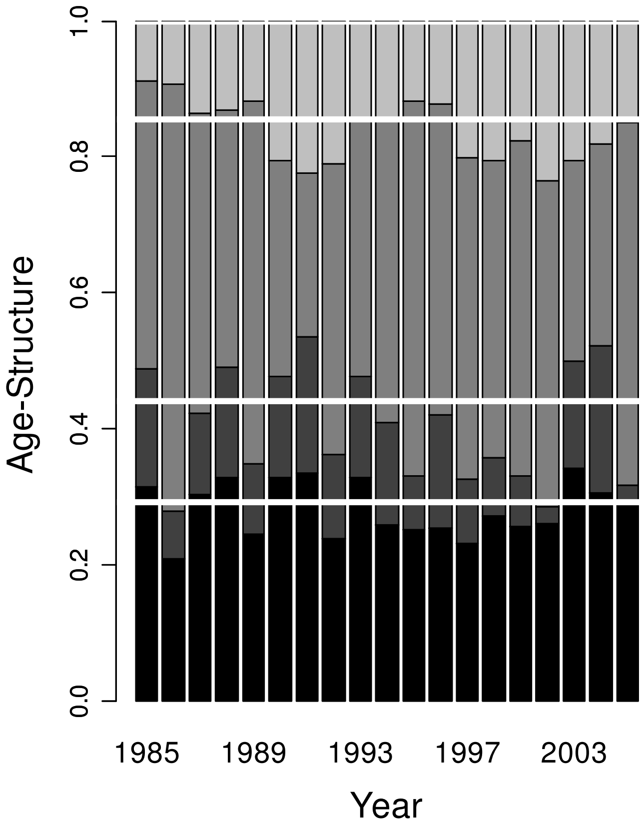

Figure 3.4. The age-structure of the Soay sheep population on St Kilda is neither constant nor at the asymptotic stable-age distribution (denoted in thick white lines; the age-classes of prime-aged and oldest individuals have been pooled for clarity), which are assumptions of deterministic analysis. Year represents survival from the focal to the post-focal.

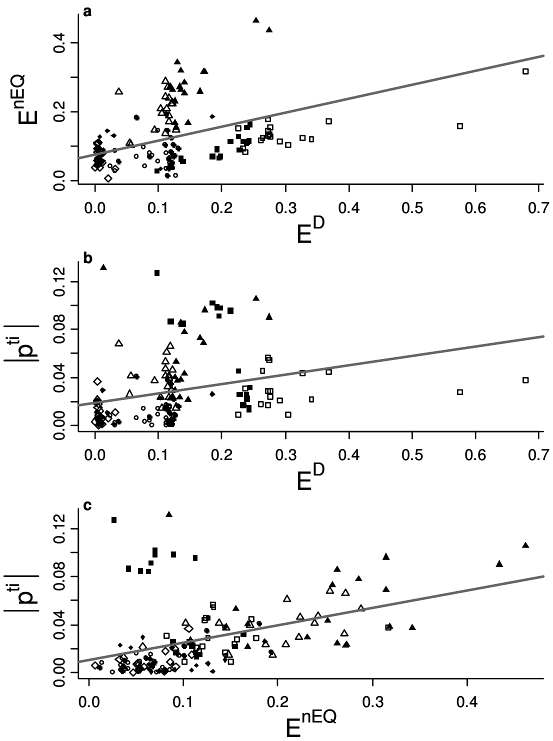

Figure 3.5. The deterministic elasticity of λ_0 to a_{ij} (E_{ij}^{D}), which assumes the stable-age distribution, is highly correlated with non-equilibrium elasticities of λ_0 to a_{ij}, (E_{ij}^{NQ}) which do not (a). Both of these quantities are correlated with the absolute value of the individual contribution to population growth $|p_{t(i)}|$ (b and c). For symbol codes, see Figure 3.2. Each symbol represents the elasticity in one of the 19 transition matrices.

The largest contribution of E_{ij}^{R} when covariation between demographic rates was incorporated was covariation. The rank of E_{ij}^{D} of *sP* was first (Figure 3.2), whereas when covariation was incorporated it was third (Figure 3.7). Integrated Elasticities (IE_{ij}) were significantly correlated with E_{ij}^{D} (Figure 3.7b; β=2.61, s.e.=0.780, p<0.05, r=0.640, Table 3.2).

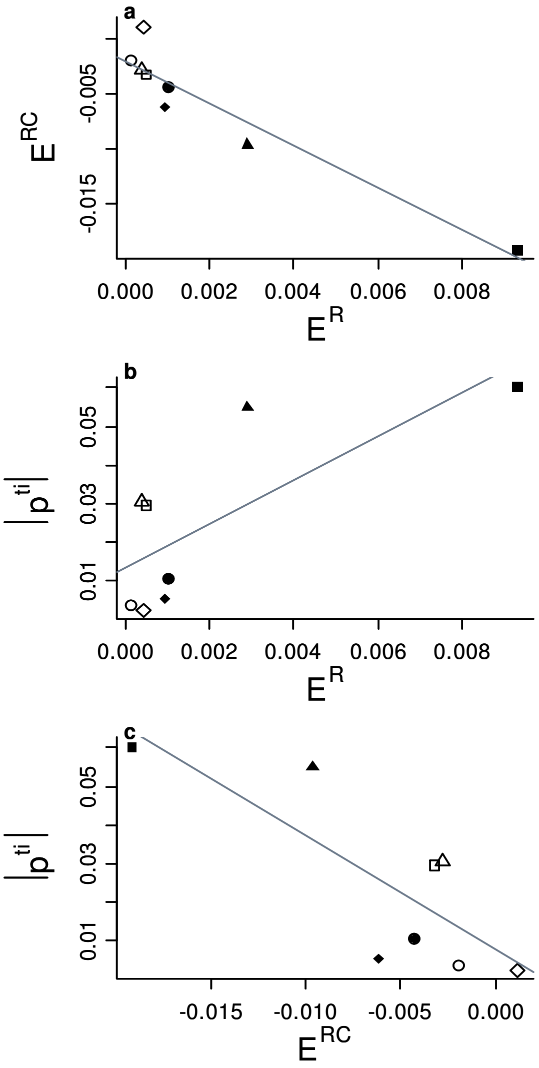

Figure 3.6. Retrospective elasticities (Lande 1988) are highly correlated with Doak *et al.'s* (2005) rescaling (a). The absolute value of the individual contribution to population growth $|p_{t(i)}|$ is significantly correlated with retrospective elasticities of σ(λ) to σ(a_{ij}) (b) and Doak et al.'s (2005) rescaling (c). For symbol codes, see Figure 3.2. Note the high influence of *sL* in (a) and (b) however, suggesting that these relationships are overtly dependent upon this rate.

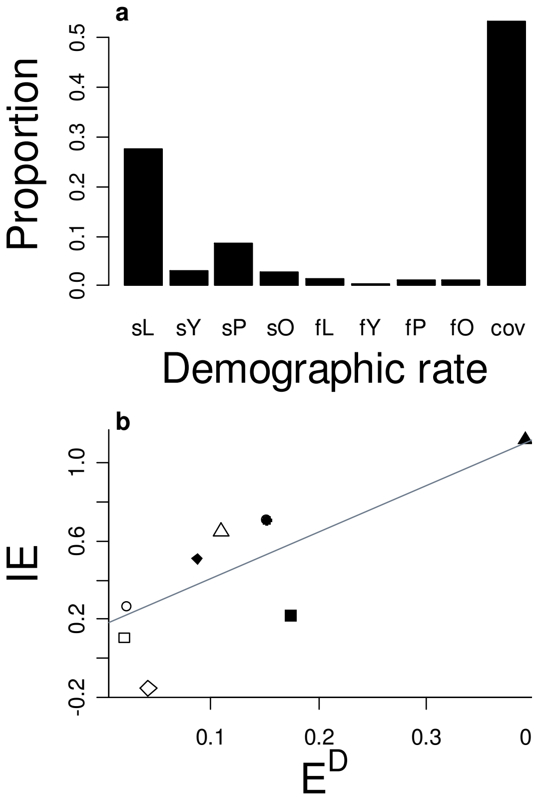

Figure 3.7. Covariation between demographic rates explains significant proportions of observed variation (a). Although integrated elasticities (IE) were correlated with E_{ij}^{D}, some changes in rank correlation were evident (b). For symbol codes, see Figure 3.2; cov indicates the covariance term.

Correlations between deterministic and stochastic measures were largely non-significant, although there were some notable exceptions: S_{ij}^{D} of the mean matrix and $|p_{t(i)}|$ summed across all seasons were highly correlated (β= 0.164, s.e.=0.028, p<0.01, r=0.851, Table 3.2, Figure 3.8a). The correlation when S_{ij}^{D} and $|p_{t(i)}|$ were calculated annually was also significant, although marked variation was noticeable in $|p_{t(i)}|$ (β= 0.066, s.e.=0.008, p<0.001, r=0.315, Figure 3.8b). Other significant correlations between measures with and without variation were detected between E_{ij}^{D} and IE_{ij} (see above) as well as S_{ij}^{VS} and IE_{ij} (β= 0.903, s.e.=0.285, p<0.05, r=0.625, Table 3.2).

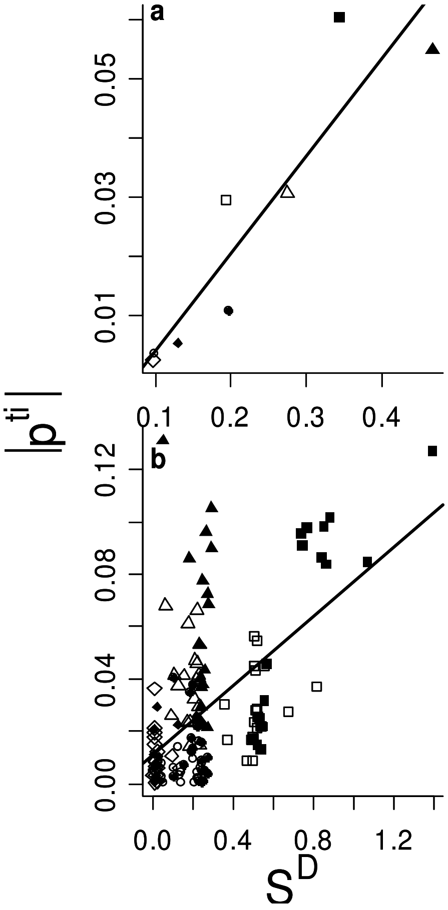

Figure 5. The correlation between $|p_{t(i)}|$ summed across all years and sensitivities of the mean matrix are highly correlated with consistent rank of elements (a) despite large annual differences when these quantities are calculated annually (b). For symbol codes, see Figure 3.2.

3.6 DISCUSSION

Significant differences were detected for some comparisons, but there was often a high correlation between perturbation measures on different scales (Table 3.2). Lower correlations were common between a measure that incorporated variation and one that did not (Table 3.2). Different perturbation measures address different biological questions: in effect they quantify different aspects of the system. Caswell (p. 295, 2001) argued that "elasticities have their place, but it is not in evolutionary calculations". Van Tienderen (2000) scaled selection gradients to be on the same scale as elasticities and demonstrated how selection gradients can be linked to elasticities to estimate the strength of selection, and that identical results can be obtained using sensitivities provided selection gradients are appropriately scaled. Whilst this argument appears to make issues of scale in current evolutionary applications redundant, it does not resolve the difficulties when attempting to quantify the importance of different demographic rates on population growth. There are sufficient differences between rank importance of elasticities (Table 3.2) – especially when the assumptions of perturbation analysis are relaxed – that it appears unlikely that a comprehensive understanding of any system is achievable without calculation of multiple quantities.

Perturbation analysis aims to determine the demographic rate with the largest influence on population growth, frequently assumed to be λ_0 (Caswell 2001). A large absolute change (S_{ij}^{D}) has a disproportionate impact if demographic rates are bound by different limits. These issues have been considered problematic (Link and Doherty Jr. 2002), but differences between quantities can be interpreted as answering different biological and mathematical questions. Variance-stabilized sensitivities S_{ij}^{VS} might be considered analogous to GLMs in their attempts to control for non-normal errors, but Link and Doherty Jr. (2002) concede that accurate knowledge of k_{max} is of pivotal importance for the accuracy of the method when fecundity is not bounded by the same limits as survival. In monotocous species, the bounds for survival and fecundity are the same and the problems of different scale do not apply for S_{ij}^{D}. The life-history of an organism is a key factor in determining the appropriateness of each method, although even identical life-histories can generate different results if different life-cycles are assumed (Royama 1992).

One hypothesis for these high correlations (Table 3.2) is that many of the quantities summarized in Table 3.1 use the matrix element as a scaling reference. The difference is taken from 0 and neglects different potential for change in polytocous species. This is precisely what life-history limit elasticities (E_{ij}^{LHL}) calculate. In more fecund species than Soay sheep, the difference between E_{ij}^{LHL} and other quantities might be greater. Or vice versa. Survival rates of long-lived species are frequently higher than offspring production, which implies greater potential for change in the recruitment rates further from their theoretical limit. Considering the difference from what can theoretically be achieved rather than 0 yields distinctly different patterns because the potential for change is often greater: rank correlations between E_{ij}^{LHL} and measures that incorporate variation were high. This method is not without caveats however: Soay sheep are unusual for their life-history as they can become pregnant during their first year of life although they – in contrast to other age-classes – have never been recorded as producing twins (Clutton-Brock and Pemberton 2004). This is what E_{ij}^{LHL} base their comparison on. Interpretation of the difference from the theoretical limit therefore needs to be considered concomitantly with the biological limit (Deines et al. 2007). Accurate parameterization of the biological limit may be problematic.

Frequently applied methods, which purport to incorporate stochasticity, are still based on deterministic elasticities in the density-independent case. Sæther & Bakke (2000) presented integrated elasticities (van Tienderen 1995) and found that rank importance was consistent between prospective and retrospective elasticities; Coulson et al. (2005) and Ezard et al. (2006) partitioned retrospective elasticities into contributions from pairs of elasticities and found the opposite. In this case, survival maintained its importance in both forms (Figure 3.7), which contradicts results on another ungulate population of similar life-history as analyzed by Coulson et al. (2005). Rather than being life-history speed dependent, patterns may differ due to variable effects of environmental stochasticity between populations. If this population-dependence holds, then accurate knowledge of the dominant processes within each population is critical. If population dynamics are characterized by large fluctuations (such that the mean matrix is an inadequate descriptor of dynamics) variation in demographic rates might prove more informative. A decomposition of observed population growth concluded that variation in demographic rates was the reason for contrasting results between two distinct populations of bighorn sheep (*Ovis canadensis*) separated by approximately 300 kilometres in northern Canada (Coulson et al. 2005). Long-term studies have a critical role to play in this regard and should aim to document a representative frequency of the environments that a population experiences.

There was marked variation in population age-structure (Figure 3.4). Neglect of a dynamic population structure influences the accuracy of predictions much more than non-linear perturbations (Figure 3.3), which is consistent with previous research (Caswell et al. 2004). This is perhaps unsurprising since demographic rates with higher E_{ij}^{D} will require a smaller perturbation to achieve λ_{pert} than rates with lower E_{ij}^{D}. Incorporation of the observed rather than asymptotic population structure generated patterns of variation in E_{ij}^{D}, non-equilibrium elasticities of λ_0 to a_{ij} (E_{ij}^{nEQ}) and contributions to population growth $|p_{t(i)}|$ that were inconsistent in direction (Figure 3.5). $|p_{t(i)}|$ were poorly predicted by either E_{ij}^{D} or E_{ij}^{nEQ}. sL – most frequently the key demographic rate – was always underestimated by E_{ij}^{D} compared to E_{ij}^{nEQ} (Figure 3.5). Given the importance of cohort effects (Lindström and Kokko 2002, Beckerman et al. 2003) and the importance of early conditions on individual quality (Kruuk et al. 1999, Cam et al. 2003), assumption of a stable population structure and uniform performance of age-classes is likely to be violated frequently. $|p_{t(i)}|$ is the only quantity calculated that considers simultaneous relaxation of multiple assumptions. When summed over all years, $|p_{t(i)}|$ was however strongly correlated with S_{ij}^{D} (Table 3.2, Figure 3.8a) despite its calculation of the exact contribution to population growth and that it assumes neither the stable-age distribution nor linear approximation (Coulson et al. 2006b). Averaging away variation neglects fluctuating strengths, paths and targets of selection, which, in part, reconciles observed and predicted micro-evolutionary change in natural populations (Coulson et al. 2003). An individual's (hypothetical) response to the mean environment may bear little resemblance to its response to the variation encountered.

The low correlation between analysis with and without variation in demographic rates is not a new result (Caswell 2000). Its inclusion emphasizes the importance of considering which demographic rates are more likely to change and which are not (Stearns and Kawecki 1994, Gaillard and Yoccoz 2003). The high rank correlation between E_{ij}^{R}, E_{ij}^{RC} and E_{ij}^{LHL} (Table 3.2) suggests that considering the potential of rates to vary might may predict patterns of observed variation more accurately when data on rate variability is unavailable. Populations are dynamic structures, and accurate prediction of their change over time requires consideration of multiple aspects. Asymptotic measures do not measure short-term differences in population dynamics, which depend upon changes in vital rates and in population structure (Haridas and Tuljapurkar 2007). In populations rarely at mean population size with fluctuating dynamics – due to over-compensatory density-dependence for the Soay sheep on Hirta (Clutton-Brock et al. 1997) – and a dynamic population structure (Figure 3.4), the accuracy of short-term predictions based on asymptotic analysis of the mean matrix is likely to be limited. S_{ij}^{D} of the mean matrix were highly correlated with $|p_{t(i)}|$ summed across all years, but predictive power over a year was low (Figure 3.8). In analogous fashion, λ_0 can be considered as mean fitness in an evolutionary context (Fisher 1958) but is likely to be limited in value when predicting annual realised fitness of individuals, whose demographic rates determine population growth of their population. Both measures are correct from an analytical perspective, but answer different biological questions.

There are many aspects to observed patterns of variability in population dynamics, which is reflected in the diversity of quantities that aim to describe them (Table 3.1). Conclusions may be correct from an analytical perspective, but which are relevant biologically? Management recommendations might calculate multiple quantities to obtain more comprehensive knowledge or multiple aspects of the system. For example, S_{ij}^{D}, or E_{ij}^{D}, would indicate the rates that have contributed to mean population growth but not necessarily those that are likely to respond to management action. To identify rates with a greater theoretical potential for change, E_{ij}^{LHL} might be illuminating. If data have been collected over more than one season, analyses incorporating observed variation could provide some validation of which demographic rates contributed most to the observed pattern of variation, which might then be considered in the light of previous and expected future environments to determine how to best construct a coherent management strategy that considers multiple aspects of the demography of a particular system.

Caswell (2001) remarked that different questions require different measures. This chapter argues that the abundance of perturbations cannot simply be partitioned into prospective or retrospective analysis. There is no right or wrong measure *per se*. The choice is dependent on the focal question. The appropriate scale for analysis is dependent upon the question asked, the species studied and information available. The population dynamics and environmental conditions are likely to be critical. An integrated approach provides a more complete description of the focal system, which is the aim of any demographic analysis. Extension to multiple life-histories across a range of environments could prove illuminating in determining whether the conclusions drawn here reveal part of a wider pattern or are just an isolated case for an isolated population.

CHAPTER 4

INDIVIDUAL AND POPULATION RESPONSES TO DISTURBING PREDATION[3]

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[3] This chapter has been submitted to Journal of Animal Ecology under the authorship of Ezard, T.H.G., Braasch, A., Becker, P.H. and T. Coulson

4.1 ABSTRACT

Predation affects demographic rates, which in turn determine population growth. How surviving, non-dispersing individuals respond to predation has fundamental consequences for local population dynamics. The Banter See common tern (*Sterna hirundo*) colony was predated heavily by a brown rat (*Rattus norvegicus*) in 1993 and a long-eared owl (*Asio otus*) in each of 1998 and 2005. The predators affected individual life-history decisions, colony composition and individual fitness. Significant spatial variation in chick predation across the colony was detected, but significant spatial variation in subsequent divorce and inter-island dispersal was not. Individuals that divorced or dispersed within the colony commenced breeding later in post-predation breeding seasons. Individuals that dispersed to another island within the colony had reduced fledgling production in those post-predation breeding seasons; this effect was as strong as typical determinants of individual quality. These results highlight how a single predator can disturb seabird colonies and elucidate how individuals and populations might respond to stochastic events.

4.2 INTRODUCTION

Population growth is a function of deterministic and stochastic processes (Bjornstad and Grenfell 2001, Lande et al. 2003). Predator attack is one of many unpredictable stochastic processes that influences demography and population dynamics (Hanski et al. 1991, Oro et al. 1999, Festa-Bianchet et al. 2006, Oro et al. 2006). It furthermore has the potential to alter the behaviour of surviving individuals that choose not to disperse (Pelletier et al. 2006). Fitness consequences of life-history decisions in response to disturbance in their environment is the focus here: how does predatory removal of chicks affect reproductive decisions, and consequently fitness among individuals, in a common tern (*Sterna hirundo*) breeding colony?

A population is a group of individuals living within a certain region. Population growth is determined by the demographic rates of individuals (survival, recruitment and dispersal), which are in turn determined by some combination of phenotypic, morphological and behavioural traits (Ricklefs and Wikelski 2002, Coulson et al. 2006a). Individual heterogeneity, both past and present, influences population dynamics in a non-trivial manner due to disparate responses of individuals to their surroundings (Benton et al. 2006). Life-history decisions depend on an individual's perception of its environment: great tits (*Parus major*), for example, attempt to time the hatching of their chicks to the period of maximum food availability (Stevenson and Bryant 2000). Inadvertently or otherwise, individuals gain information on local conditions from their neighbours (Danchin et al. 2004, Dall et al. 2005). The success, or failure, of a nest's hinterland can override personal circumstances: if a black-legged kittiwake (*Rissa tridactyla*) considered itself to have a high-quality site it remained there in defiance of poor individual performance (Danchin et al. 1998). Colonial living can benefit the individual as the probability of losing its offspring is diluted (Fernández et al. 2003) and collective vigilance increased (Pays et al. 2007). Groups of different size respond differently to perceived risk. Common terns in the centre of colonies had higher breeding success than those on the periphery in years of herring gull (*Larus argentatus*) predation (Becker 1995). Individual vigilance was greater when grey partridges (*Perdix perdix*) were in small groups, areas with tall vegetation or of high predation risk (Watson et al. 2007). Small groups of Audouin's gulls (Larus audouinii, Oro et al. 2006) and common terns (Hernández-Matías et al. 2003) were unable to protect their nests against predation by yellow-legged gulls (*Larus michahellis*): prey fecundity was most affected by predators when predators outnumbered their prey (Oro et al. 2006). On the other hand, high nest density of common terns. European badger (*Meles meles*) predation of Audouin gull chicks provoked increased dispersal (Oro et al. 1999) whereas fox predation on adults provoked neither nest abandonment within the season nor increased dispersal following it (Cam et al. 2004b). Responses to predators therefore vary and can influence demographic rates. For these reasons, how surviving, non-dispersing individuals respond to disturbance clearly influences local population dynamics.

Chicks at the Banter See common tern colony were predated heavily by a brown rat (*Rattus norvegicus*) in 1993 and by a long-eared owl (*Asio otus*) in each of 1998 and 2005, which provoked the question: what consequences, if any, do predator disturbances have on life-history decisions, individual performance and colony composition in the subsequent breeding season? Chick losses by predation were greater and varied significantly between sub-colonies in years of predator presence, which correlated with increased rates of divorce and inter-island dispersal. Individuals that dispersed within the colony had reduced fledgling production in post-predation seasons.

4.3 METHODS

4.3.1 Study Area and Population

All data were collected at the Banter See common tern colony (53^{o}30’N, 08^{o}06’E) in Wilhelmshaven, Germany, which is the subject of a long-term individual-based study (Becker et al. 2001). The colony has increased in size from 90 to 470 nests and from 33 to 523 marked individuals from 1992 to 2006. Its site consists of six rectangular concrete islands of equal size, arranged linearly with island A nearest land and island F furthest from it. Each island is 0.9m from the neighbouring one, measures 10.7*4.6 metres and is surrounded by a 60cm wall. Breeding habitat is considered to be homogeneous.

Individuals have been ringed since 1980 in Wilhelmshaven and 1984 at the Banter See (ringing centre “Vogelwarte Helgoland”). All fledglings have been ringed and marked with transponders (TROVAN ID 100) since 1992. Antennae, which read the 10 digit alphanumeric code of each individual at a distance not greater than 11cm, are located on each of 44 elevated platforms on the surrounding walls of each island during the breeding season and temporarily around each incubated clutch to assign individuals to nests. Fewer antennae and balances were available in the early years of the study, when rotation ensured complete colony coverage. Further details of this automatic detection system are presented in Becker & Wendeln (1997). Additionally, each nest is checked every 2-3 days throughout the breeding season to determine the fate (alive, dead, absent) of each individual.

4.3.2 Definitions

Chick loss by predation is defined as chicks no longer found alive at the colony site or chicks found dead and wounded or partly eaten by a specific predator (Sudmann et al. 1994). Divorce is defined as a change in breeding partner between consecutive breeding seasons, given that both birds have returned to the colony site. Only breeding pairs with two marked birds are eligible for divorce, as there is no way of identifying if an unmarked partner is the same from one season to the next. Inter-island dispersal is defined as a change in island within the Banter See colony between consecutive breeding seasons. If more than one breeding attempt was made during the previous season, the comparison is made to the partner and island during the first attempt. To avoid pseudoreplication (Crawley 2002), the nest rather than the individual is considered the replicate (the partners are not independent: if one divorces, the other must). Local return rate is defined as local survival rate, which is likely to underestimate real survival due to emigration (Martin et al. 1995). A fledgling is a bird, which reaches 18 days of age, leaves the colony site and is not recorded as dead within the same season; fledging rate is the number of fledged chicks per clutch. Age-corrected laying date is defined as the residual from a generalized additive mixed-effect model (Wood 2006) of laying date (date of discovery of first egg) against age as a smooth function and individual as a random effect (Ezard et al. 2007).

4.3.3 Statistical Analyses

Mixed effect models consist of fixed and random effects. Fixed effects describe population level patterns whereas random effects describe how subjects deviate from these (Pinheiro and Bates 2000). They provide “a flexible and powerful tool for the analysis of grouped data” (Preface, Pinheiro and Bates 2000), which includes longitudinal data analysis. Diggle *et al.* (2002) partitioned longitudinal data analysis into two groups: (1) those where the regression of a variable onto another is the scientific focus and the number of experimental subjects is much greater than the number of observations per unit and (2) those where correlation within subjects is the focus, or where the number of experimental subjects is small. Pinheiro & Bates (p. 254, 2002) argued likewise that a mixed effect model may not be the most appropriate method if a hierarchical structure is neither present nor relevant, and the regression parameters are of more interest. In this instance, the number of experimental subjects (597 individuals) is much greater than the number of observations per subject (mean=3.85), and the correlation within and among subjects is not of specific interest or value. Following Diggle *et al.*’s (2002) criteria, generalized linear mixed models (GLMMs) might not be the most appropriate. All analyses were conducted using GLMMs and generalized linear models (GLMs). GLMMs were fitted in identical fashion to the descriptions for appropriate GLMs as described below, except that GLMMs incorporated additionally individual as a random effect.

Chick loss by predation was assessed by fitting quasipoisson GLMs, which account for overdispersion (p. 543, Crawley 2002), for all years and for years when predators were present. The number of chicks taken per nest with at least one marked adult individual was regressed against year, island and their interaction. Both explanatory variables were categorical, and there were 505 nests for 371 individuals during years when predators were observed and 2444 nests for 635 individuals during all years. Terms were removed sequentially in a reverse stepwise procedure (ch. 25, Crawley 2002) according to F tests. When only significant factors remained, these factor levels were collapsed into each other (p. 455, Crawley 2002).

Divorce and changes in island usage rates were assessed by fitting binomial GLMs, including all years. The year with mean closest to the overall mean was taken as the intercept; any year with $p>0.2$ was collapsed into this intercept. The new categorization was then re-examined, and the most parsimonious year grouping obtained by collapsing levels according to the Akaike’s Information Criterion (AIC, Burnham and Anderson 2002), which provides a compromise between model deviance and the number of parameters used. Models within 4 AIC values, the lower bound of Burnham and Anderson’s (2002) recommendation, are considered equivalent; among equivalent models the one with fewest parameters is preferred as the minimal adequate. If the number of parameters was identical, the minimal adequate model had the lowest AIC. This two-step process prevented over-fitting. Fledgling production and age in the previous season was controlled for during both stages. Divorce or inter-island dispersal was the binary response variable. Year grouping and island during the previous breeding season were categorical explanatory variables, fledgling production in that previous season and age were continuous. All main effects, two- and three-way interactions were fitted. The minimal adequate model used the complementary log-log link function, as this minimized the residual deviance in both cases (Crawley 2002).

Consequences of disturbance in the colony on laying date were assessed using a quasi GLM for age-corrected laying date regressed against year, inter-island dispersal and divorce as categorical explanatory variables. Differences in survival by fitting four models with year as the sole explanatory variable as (1) a categorical variable with one level per year, (2) as a categorical variable with predation years distinct from others (four levels), (3) as a continuous variable and (4) as a constant. The dispersion parameter was 1.00 to two decimal places, and therefore AIC was used to obtain the minimum adequate. Fitness consequences were assessed using GLMs for fledgling production regressed against year, divorce, inter-island dispersal, age and age-corrected laying date. All explanatory variables were categorical except for age and age-corrected laying date, which were continuous. Only post-predation years were considered, which ensued 541 data points for 458 individuals. GLMMs were not fitted for this analysis as median and mode number of data points per individual was 1. All explanatory variables and two-way interactions were fitted in both cases and minimal adequate models obtained using F tests. The correlation between divorce and inter-island dispersal was 0.203, which is sufficiently low to suggest that results are not biased by it. As a quasipoisson model with logistic link function did not produce acceptable diagnostic plots for the fitness consequences, other link functions and variance structures were tested (p. 545, Crawley 2002). A quasi error structure with inverse link function and constant variance was adopted for the final model on this basis. The GLM for age-corrected laying date used the identity link function and constant variance.

All analyses were conducted in the R environment version 2.5.1 (R Development Core Team 2007) using the mgcv package (version 1.3-1.22) to fit the generalized additive mixed effect model and the lme4 package (version 0.9975-13, function lmer) to fit GLMMs, which used the Laplacian approximation to maximum likelihood. All coefficients are from GLMs and presented on the scale of the link function.

4.4 RESULTS

The Banter See colony was predated in 1993 by a Norwegian rat and by long-eared owls in 1998 and 2005. Chick losses by predation were greater and varied significantly between sub-colonies in years of predator presence. In post-predation seasons, colony composition was disturbed as divorce and inter-island dispersal was greater. Individuals that dispersed within the colony had reduced fledgling production in post-predation seasons.

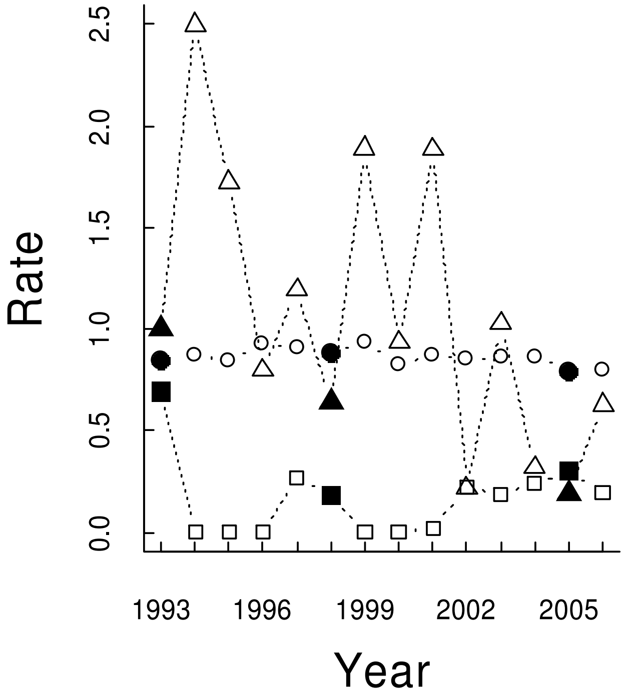

Figure 4.1. Local survival (circles), fledging (triangles) and chick loss by predation (squares) rates. Chick loss by predation rates were greater in these years when predators were present (solid symbols) and since 2001 (Table 1). Symbols are survival to the focal year (e.g. values for 1993 represent fledging and chick loss by predation rates in 1993 and survival from 1992 to 1993). The minimum adequate model treated survival as constant (AIC=935.5, 1 parameter), rather than fully categorical (944.3, 13), predation distinct (939.6, 5) or continuous (931.5, 2).

Year		**Island**					
		A	**B**	**C**	**D**	**E**	**F**
Early	n	86	90	120	106	127	156
	μ	0.02	0	0	0	0.01	0
1993	**n**	**1**	**5**	**7**	**4**	**7**	**12**
	μ	**0**	**1.40**	**1.00**	**0.75**	**0.86**	**0.17**
1997	n	4	17	21	19	19	21
	μ	0	0.29	0.90	0.37	0.11	0
1998	**n**	**16**	**21**	**30**	**20**	**29**	**31**
	μ	**0**	**0**	**0.53**	**0**	**0.03**	**0.10**
2005	**n**	**53**	**48**	**58**	**51**	**45**	**67**
	μ	**0.26**	**0.27**	**0.26**	**0.25**	**0.24**	**0.45**
Late	n	166	165	174	202	198	226
	μ	0.23	0.14	0.16	0.14	0.22	0.21

Table 4.1. Number of (n) and mean (μ) chick loss by predation per nest per island. The colony was predated in 1993 by a brown rat and 1998 and 2005 by long-eared owls (**bold**). Chick loss by predation has been significantly higher since 2001 (late) than before it (early); 1998 did not suffer significantly higher chick loss by predation than these 'late' years and 1997 and 2005 were not significantly different according to the minimal adequate model. See also Figure 4.1. Shaded cells denote significantly greater values on those islands compared to the rest of the colony in that season.

4.4.1 Chick Predation

The number of chicks, which were not found during the breeding season, has increased in recent years of the individual-based study (Figure 4.1; Table 4.1). Years were divided into groups of early (before 2001, β=-4.482, s.e. =0.387, $p<0.001$) and late (2001 and after, β=-2.642 s.e. =0.394, $p<0.001$). Four years were unusual: 1993 (β=-4.034, s.e. =0.449, $p<0.001$), 1997 and 2005 (β=-3.126, s.e. =0.401, $p<0.001$) and 1998 (as late, non-predation years). In real terms, average chick loss by predation per nest was 0.01 in early years, 0.16 in late years and 1998, 0.26 in 1997 and 2005 and

Year Grouping	**Degrees of Freedom**	**AIC**	
		Divorce	**Inter-island dispersal**
All Years Individually	16	1684.2	1582.9
1993; 1994; 1995; 1999; 2001; 2003; 2005; 2006	9	1674.0	
(1993, 1994, 1995, 1999, 2003, 2005 and 2006); 2001	4	1666.7	
(1993, 1994, 1995, 1999, 2001, 2003, 2005 and 2006)	**3**	**1669.4**	
Post-Predation Years	3	1691.2	1599.5
Good and Bad Years	3	1690.8	1600.5
Before 2001; after and including 2001	3	1688.3	1590.9
(1993, 1994, 1995, 1998, 1999 and 2006)	4		1578.4
(1994, 1998, 1999 and 2006); (1993 and 1995);	**5**		**1570.2**
(1994, 1995, 1998, 1999 and 2006); 1993	5		1574.7

Table 4.2. Year groupings as determined by the Akaike's Information Criterion under various hypotheses. The most parsimonious set is denoted in bold; for rationale see Methods section. Good and bad years are split by mean fledgling production being greater than or equal to 1 or less than 1, respectively. Previous fledgling production was only significant for inter-island dispersal; age was significant in both cases (Table 4.3).

0.64 in 1993. This model explained 16.9% of the residual deviance. No spatial differences were detected.

If years when predators were present were compared to those when predators were absent (comparing 1993, 1998 and 2005 individually to all other years), significant spatial variation in chick loss by predation was detected (see shaded cells in Table 4.1): predation was significantly greater on island C in 1998 (β=3.473, s.e. =1.158, p<0.01) but not 1993 (β=0.182, s.e. =0.466, p>0.5) or 2005 (β=-0.0477, s.e. =0.556, p>0.05). On island F, predation was significantly greater in 1998 (β=4.794, s.e. =1.533, p<0.01) and 2005 (β=2.689, s.e. =0.303, p<0.05) and significantly lower in 1993 (β=-2.216, s.e. =1.051, p<0.05). This model explained 16.6% of the residual deviance, of which 6.5% was explained by year, 1.7% by island and 8.3% by their interaction

4.4.2 Divorce and Inter-Island Dispersal

Divorce rate did not vary significantly with fledgling production, and was found to be significantly higher than average in the following years: 1994, 1999, 2001, 2003, 2005 and 2006, which did not differ significantly from each other (Table 4.2). Age covaried significantly and negatively with divorce (Table 4.3). In real terms, mean divorce rate was 0.23 in the six years mentioned above and 0.16 in all others (Figure 4.2a).

Inter-island dispersal covaried negatively with fledgling production and age (Table 4.3). It was significantly higher in 1993 and 1995 as well as 1994, 1998, 1999 and 2006; these groups were significantly different from each other (Table 4.2). In real terms,

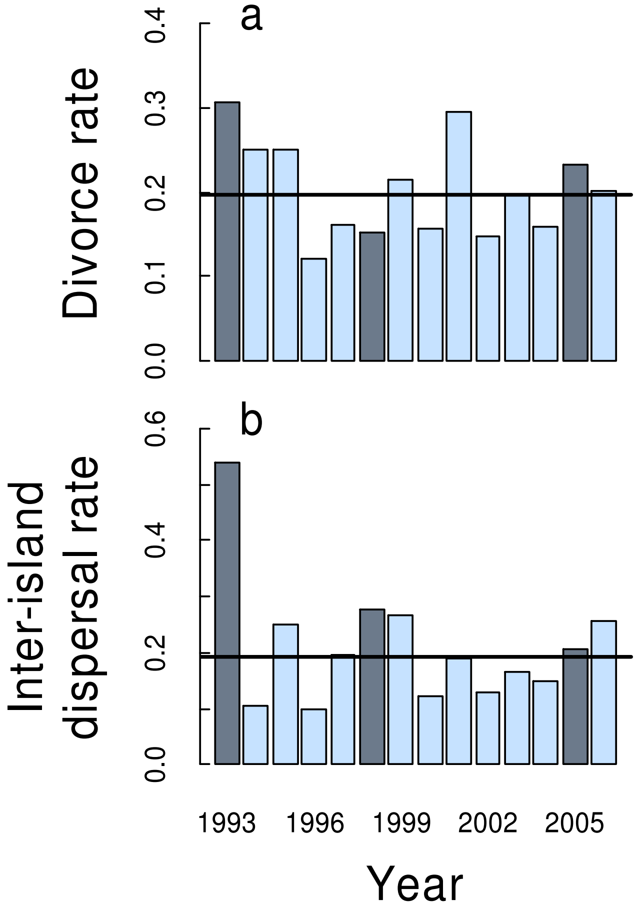

Figure 4.2. Divorce (a) and inter-island dispersal (b) rates, with overall mean rates as horizontal bars. Dark grey bars are years when predators were present (1993 brown rat, 1999 and 2005 long-eared owls). Each bar is the rate to the focal year from the previous one (e.g. divorce in 1993 is divorce between 1992 and 1993). Note differences in sample size between different years (Table 4.1).

inter-island dispersal rate was 0.32 in 1993 and 1995, 0.25 in 1994, 1998, 1999 and 2006 and 0.16 in all other years (Figure 4.2b).

Differences between GLM and GLMM model fits were not substantial since coefficients of a GLM are within one standard error of the corresponding coefficient from the GLMM, and vice versa (Table 3). Proportions of explained variation were similar between coefficients of either model, although GLMMs explained more, which was due in part to the random intercept (Table 4.3). Fitting models with random slopes and intercepts (divorce: AIC=1667.8 for 6 parameters; inter-island dispersal: AIC=1584.3 for 8 parameters) compared to those with just random intercepts (divorce: AIC=1663.8 for 4 parameters; inter-island dispersal: AIC=1579.6 for 6 parameters) did not improve model fit.

4.4.3 Phenotype and Fitness Consequences

Divorce (β=4.820, s.e. =1.021, $p<0.001$) and inter-island dispersal (β=3.542, s.e. =0.967, $p<0.001$) significantly increased age-corrected laying date. 1999 and 2006 were significantly different from 1994 and each other (1999: β=5.199, s.e. =1.715, $p<0.01$; 2006: β=9.926, s.e. =1.623, $p<0.001$). This model explained 19.6% of residual deviance, of which 4.1% was due to inter-island dispersal, 4.2% to divorce and 11.3% to year.

Year explained 49.7% of the variance in fledgling production during post-predation breeding seasons: 2006 (β=1.128, s.e. = 0.108, $p<0.001$) and 1999 (β=0.098, s.e. = 0.033, $p<0.01$) were significantly worse in real terms than 1994 (Fig.ure 7.1). Inter-island dispersal had a significant negative impact on fledgling production in real terms (β= 0.119, s.e. = 0.042, $p<0.001$, deviance explained=2.3%). As individuals became older, fledgling production increased in real terms (β=-0.013, s.e. =0.004, $p<0.001$, deviance explained=2.2%) but any significant advantage of early laying was detected only in 2006 (1994: β=0.004, s.e. =0.003, $p>0.05$; 1999: β=0.001, s.e. =0.004, $p>0.05$; 2006: β=0.045, s.e. =0.012, $p<0.001$, deviance explained as main effect=0.7%, as interaction=2.2%). In total, the minimal adequate model explained 57.0% of the residual deviance. Divorce was not significant.

Coefficient	Divorce				Inter-island dispersal			
	GLM		GLMM		GLM		GLMM	
	β (s.e.)	% residual variance	β (s.e.)	% residual variance	β (s.e.)	% residual variance	β (s.e.)	% residual variance
Previous Fledgling Production					-0.412 (0.781) ***	2.5	-0.429 (0.086)	1.8
Age	-0.063 (0.019) **	0.7	-0.076 (0.023)	0.5	-0.054 (0.021) **	0.4	-0.067 (0.024)	0.5
Years (1994, 1999,2001, 2003, 2005 and 2006)	0.381 (0.115) ***	0.7	0.413 (0.133)	0.6				
Years (1994, 1998, 1999 and 2006)					0.372 (0.121) ***	1.6	0.405 (0.130)	1.5
Years (1993 and 1995)					1.355 (0.269) ***		1.400 (0.303)	
Random Effect				0.6				2.1
Total		1.4		1.7		4.5		6.7

Table 4.3. Differences between GLM and GLMM model fits were not substantial since coefficients (β) of a GLM are within one standard error (s.e) of the corresponding coefficient from the GLMM, and vice versa. *** indicates $p<0.001$, ** $p<0.01$ and * $p<0.05$. P values are not presented for GLMMs because no "correct" denominator degrees of freedom exists (Bates 2005).

4.5 DISCUSSION

A single predator can reduce population growth (Festa-Bianchet et al. 2006) and its underlying demographic rates (Oro et al. 1999). Here, predation by a solitary predator was not uniform across the colony, but responses of individuals were. Colony composition was disturbed in post-predation seasons: divorce and inter-island dispersal increased. Despite this disturbance, no significant variation in local survival was evident (Figure 4.1), which for adult birds are within 95% confidence intervals estimated using a capture-mark-recapture framework (Appendix 1). This suggests that results can be interpreted without fear of excessive bias caused by emigration. Individuals that dispersed within the colony had reduced fledgling production in post-predation seasons.

The long-eared owls predated island F – the furthest from the mainland and most densely populated – to a significantly greater degree in 1998 and 2005, but the consequences were felt across the entire colony. Any conclusions of the difference of effects between the brown rat and long-eared owl are compromised because the number of marked adults increased from 33 individuals in 1992 to 523 in 2006. Chick loss by predation across the entire colony in 1993 was less than on any one island in 2005 (Table 4.1). Nocturnal predation caused deaths of more chicks than just those killed by the predator: many (predominantly young) chicks died from a lack of care when their parents abandoned the colony site (Sudmann et al. 1994, Wendeln and Becker 1999a). Quantifying the exact causes of all chick disappearances is difficult as not all are observed, and indeed predation is one of many possible causes of disturbance.

Divorce and inter-island dispersal were significantly higher in post-predation breeding seasons than the average, but not exclusively so (Table 4.2, Figure 4.2). Divorce was more likely in recent years (Figure 4.2a), which may be a consequence of increased chick mortality due to intraspecific aggression (Sudmann 1998) during this period of greater population density and decreased fledgling production (Figure 4.1). Divorce was not significantly correlated with fledgling production in the subsequent season, which is consistent with the argument that divorce is not adaptive but a consequence of asynchronous arrival (Gonzalez-Solis et al. 1999), but inter-island dispersal was. Individuals, which dispersed within the colony site, produced fewer fledglings and laid their eggs later in the subsequent season. The cause of this reduction is unclear: is the delay in (age-corrected) laying date responsible? A delay of four days is unlikely to be costly in itself because of the low amount of variation explained by laying date on individual contributions to population growth (Ezard et al. 2007). Furthermore, divorce had at least as much an effect on laying date and did not significantly affect fledgling production. The most productive areas within a kittiwake colony were also the most populated (Danchin et al. 1998). An individual gains information from its neighbours (Danchin et al. 2004, Dall et al. 2005), which, if inaccurate, might decrease its performance (Giraldeau et al. 2002). Although there is no guarantee that the population influences any individual decision, coloniality provides a hypothesis for the similarity between the results of GLMs and GLMMs: “individual error is suppressed by group cohesion” (Diggle et al. 2002). The lack of hierarchical structure did not substantially alter results (Table 4.3). This should not, however, be confused with a lack of individual differences, but rather implies that operating processes are consistent across individuals and that individuals follow similar strategies to their neighbours: entire colonies, for example, were deserted in the presence of nocturnal predators (Sudmann et al. 1994, Wendeln and Becker 1999a). The amount of unexplained variation was however high; the possibility remains that some unmeasured personal circumstance prompts these life-history decisions.

The predators affected individual life-history decisions, which affected colony composition, which affected individual fitness. The consequences of predation during three of fourteen breeding seasons highlight the importance of stochasticity on population growth. The behavioural responses investigated explained similar proportions of variation as age and laying date, which are frequently considered key determinants of fledgling production (Perrins 1970, Forslund and Pärt 1995). Further work is required to investigate the fitness consequences of responses to disparate disturbance, which may help to explain the often high amounts of heterogeneity in individual performance. Individual responses to unpredictable changes in their environment are, according to these results, influential in determining how populations respond to a changing and uncertain world.

CHAPTER 5

HABITAT DEPENDENCE AND CORRELATIONS BETWEEN ELASTICITIES OF LONG-TERM GROWTH RATES[4]

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[4] This chapter is in review at American Naturalist under the authorship of Ezard, T.H.G., Gaillard, J.-M., Crawley, M.J. and T. Coulson

5.1 ABSTRACT

In population biology elasticity is a measure of the importance of a demographic rate on population growth. A relatively small amount of stochasticity can impact substantially the dynamics of a population, whose growth is a function of deterministic and stochastic processes. Analyses of natural populations frequently neglect the latter. Even in a population that fluctuates substantially with time, the results of a deterministic perturbation analysis correlated strongly with results of an analysis of the long-run stochastic growth rate. Population growth was however not uniformly sensitive to demographic rates across different environmental conditions. The overall correlation between deterministic and stochastic perturbation analysis may be high, but environmental variability can alter dramatically the contributions of demographic rates in different environmental conditions. This potentially informative detail is neglected by deterministic analysis, yet highlights one potential difficulty when extrapolating results from long-term deterministic or stochastic analysis to shorter-term environmental change.

5.2 INTRODUCTION

If individuals of different (st)ages are affected by their environment in different ways (Leirs et al. 1997, Coulson et al. 2001), then matrix models are a flexible tool to examine the link between demographic rates and population dynamics (Caswell 2001). The relative importance of these different classes and rates can be investigated using perturbation analysis, i.e. some measure of sensitivity or elasticity, which aims to identify the importance of demographic rates on some measure of population performance (Caswell 2001). Analysis of the asymptotic population growth rate λ_0 predicts the eventual behaviour of a system described by some model. Often however, there is little correlation between elasticities of λ_0 to a matrix element (frequently a demographic or vital rate, Caswell 2001) a_{ij} and elasticities of observed variation in a_{ij} on variation in λ_0 for diverse long-lived taxa (Coulson et al. 2005, Ezard et al. 2006). Potential therefore appears to exist for stochastic models to quantify how demographic rates determine population growth more accurately.

Deterministic and stochastic processes affect survival and recruitment, which conjointly determine population growth (Bjornstad and Grenfell 2001, Lande et al. 2003). The dynamical consequences of stochasticity depend furthermore on the population structure: populations of different (st)age-structure but similar size and environments can exhibit contrasting short-term dynamics (Benton et al. 2001). Despite the important role of stochasticity in population dynamics, perturbation analyses on natural populations frequently assume density-independent growth, a stable age-distribution and a constant environment (Caswell 2001), i.e. are deterministic. Given the considerable interest in population dynamics in variable environments, recent research (Tuljapurkar et al. 2003, Haridas and Tuljapurkar 2005, Horvitz et al. 2005, Morris et al. 2006, Tuljapurkar and Haridas 2006) has relaxed Tuljapurkar's (1982) small noise approximation, which only permits demographic rates to vary by small amounts. This suite of work uses sequences of discrete habitat states – generated using Markov chains – to model environmental change. It has produced a comprehensive array of quantities that describe diverse aspects of the long-run stochastic growth rate λ_S. The influence on λ_S of a change in the distribution of a_{ij} – the elasticity of λ_S to a_{ij} – is frequently considered the analogue of the deterministic elasticity of λ_0 to a_{ij}. Increasing a_{ij} by a small amount in the stochastic case perturbs the mean and variance of a_{ij} (denoted here μ_{ij} and σ_{ij} respectively) such that the coefficient of variation of a_{ij} remains constant. In the deterministic case however, only μ_{ij} is perturbed (Tuljapurkar et al. 2003). Acknowledging that simultaneous perturbations to μ_{ij} and σ_{ij} are difficult to interpret in natural populations, Tuljapurkar *et al.* (2003) partitioned the stochastic elasticity of λ_S to a_{ij} into contributions from μ_{ij} and σ_{ij}. Such a partition treats all environmental conditions as equal, whereas there is no guarantee that the importance of certain processes in one habitat state will persist in another (Horvitz et al. 2005). The calculation of elasticities of λ_S to μ_{ij} and σ_{ij} is more challenging than the calculation of the elasticity of λ_0 to a_{ij}. It has also been argued that, for many systems, a_{ij} and μ_{ij} will be similar with σ_{ij} small. The theory has been demonstrated on an understory shrub population in a sequential, disturbance-prone system (see Tuljapurkar et al. 2003). Does analysis of λ_S provide insight, which is unobtainable from analysis of λ_0, into determinants of population growth in disparate systems influenced by stochastic processes?

Soay sheep (*Ovis aries*) are the only vertebrate herbivores on the island of Hirta in the St Kilda archipelago (Clutton-Brock and Pemberton 2004). The dynamics of this population are characterized by over-compensatory density-dependence (Clutton-Brock *et al.* 1997) yet are known to be influenced by stochastic processes: food limitation is the primary cause of winter mortality (Crawley *et al.* 2004), although winter weather, age- and sex-structure also contribute significantly (Coulson *et al.* 2001). This contradicts the assumptions of deterministic analysis. This note addresses three principle questions: (1) does use of λ_S – rather than λ_0 – alter qualitatively predictions of the key demographic rate for population growth; (2) is relative importance of demographic rates consistent for perturbations to μ_{ij} and σ_{ij}; and (3) how does the relative importance of demographic rates vary between habitat states?

5.3 METHODS

5.3.1 Study Population

Individual-based data have been collected under an identical protocol since 1985 from the population of Soay sheep living in Village Bay on Hirta (57º49' 8º34') in the St Kilda archipelago. Three trips are made annually to collect data: during the birth pulse (late March - early May), an annual catch (August) and during the rut (October - November). Full details of the data collection protocol and population history are available in Clutton-Brock and Pemberton (2004). Population size is defined here as the number of sheep alive on August 1st each year.

5.3.2 Population Model and the Markov Chain

Demographic and environmental data were available from 1991 to 2006 inclusive (except 2001 due to foot and mouth disease on the mainland). Only females were considered, for which the most parsimonious age-structure has four age-classes (Catchpole et al. 2000): lambs (*L*), yearlings (*Y*), prime-aged (*P*, 2-6 years old) and older (*O*, >6 years old). A post-breeding Leslie matrix (Caswell 2001) **A** was constructed with 8 age-classes (for matrix and life-cycle graph, see Appendix A2). The population model is $\mathbf{P}(t) = \mathbf{A}(t)\mathbf{P}(t-1)$, where $\mathbf{P}(t)$ is the population vector at time t and $\mathbf{A}(t)$ a transition matrix at time t chosen according to the probabilities defined by a Markov chain.

The Markov chain of habitat states (Tuljapurkar *et al.* 2003) was generated using mean sward height in March, mean station-based North Atlantic Oscillation (NAO, Hurrell 1995) between December and March and adult: lamb ratio. Sward height is a measure of vegetation and is dependent not only on the number of sheep but also plant biomass over each growing season (Crawley et al. 2004, Jones et al. 2006). NAO is a broad proxy for weather conditions, with higher values indicating more winter storms and harsher conditions in northern Scotland. Adult: lamb ratio approximates the population structure, which can fluctuate independently of total abundance and significantly affects population growth (Coulson et al. 2001). Tree regression, which generates discrete classes of explanatory variables (Venables and Ripley 1999), indicated that sward height should be split at approximately 3.5 (range: 2.02 to 5.24) and that adult: lamb ratio should be split at approximately 3 (range 1.52 to 3.32). In an additive model containing all terms, NAO was consistently subdominant except for a small change in fecundity of prime-aged individuals. This rate is – compared to other demographic rates – relatively invariant to environmental change (Coulson *et al.* 2001) and thus disregarded. Two classes were adopted for each of sward height and adult: lamb ratio, thus producing four habitat states when combined. No years were classified as low sward and low adult: lamb ratio, which left three habitat states (Figure 5.1). There were five years in state 1 (low sward height; the lowest quality habitat with λ_0 for the mean matrix of all years in that habitat of 0.91), three in intermediate state 2 (high sward and low adult: lamb ratio; λ_0

of mean matrix = 0.99) and five in the highest quality habitat state 3 (high sward and high adult: lamb ratio; λ_0 of mean matrix = 1.22).

The habitat transition probabilities were obtained using observed rates of transition after defining the three habitat states (Figure 5.1a; for habitat transition matrix **H** see appendix A2). The habitat state at time t+1 is probabilistically dependent upon the habitat state at time t. The process was iterated to generate one Markov chain of length 100,000 (with an initial transient of length 10,000 discarded). The sequence determined the habitat state that the population experienced at each timestep. Feedback between population growth, demographic rates and environmental variables in the sequence of habitat states is extrapolated from the feedback observed within the study period (Figure 5.1b). Each **A**(t) was obtained in the following manner: (1) obtain the habitat state at time t from the Markov chain; (2) randomly select a year when the population was in that habitat state (Figure 5.1); (3) fill **A**(t) using the observed demographic rates for that year. These processes generate a transition matrix at each time, which was stored with associated vectors of population structure and reproductive value for perturbation analysis (Tuljapurkar et al. 2003). Note that

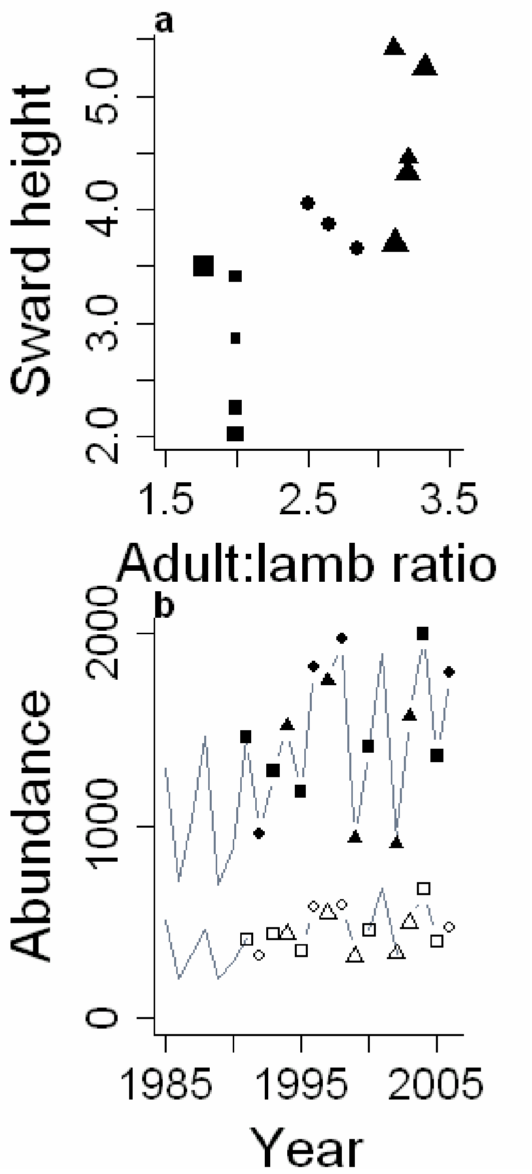

Figure 5.1. Figure 1. (a) the three habitat states (squares indicate habitat state 1, the lowest quality state; circles state 2; and triangles state 3, the highest quality state) with symbol size proportional to λ_0 in the observed year; and (b) the time-series from 1985 to 2006 of abundance of Soay sheep for Hirta (open symbols) and the Village Bay study population (solid symbols). Data used in this study was collected between 1991 and 2006; annual population growth varied from 0.61 to 1.34 over these years.

simulated – not asymptotic – sequences of population structure and reproductive value were stored, i.e. the population structure does not converge to the stable-age distribution.

5.3.3 Perturbation Analysis

Elasticities of asymptotic growth λ_0 to a matrix element a_{ij} (here a demographic rate) are the proportional change in λ_0 from a proportional change in μ_{ij} (mean a_{ij}) over all 100,000 time steps. This quantity was calculated and is denoted E_{ij}^{D}.

The long-run stochastic growth rate λ_S was calculated over all 100,000 time steps and defined as log (λ_S) = $\lim_{t\to\infty}(1/t)\log[P(t)/P(0)]$. The stochastic elasticity (denoted E_{ij}^{S}) of λ_S with respect to element a_{ij} is the proportional change in λ_S for a proportional change in a_{ij}, such that the coefficient of variation of a_{ij} does not change (Tuljapurkar et al. 2003). The elasticity of λ_S with respect to μ_{ij} (denoted $E_{ij}^{S\mu}$) is the proportional change in λ_S for a proportional change in μ_{ij}, which is the same perturbation as in E_{ij}^{D}, but to λ_S not λ_0 (Tuljapurkar et al. 2003). The elasticity of λ_S with respect to variation in a_{ij} (σ_{ij}, denoted $E_{ij}^{S\sigma}$) is the proportional change in λ_S for a proportional change in σ_{ij} (Tuljapurkar et al. 2003).

These quantities perturb every matrix in the simulated sequence and do not consider habitat-dependence. The habitat-stage elasticity (denoted $E_{ij\beta}$) of λ_S with respect to a_{ij} and habitat state β does. $E_{ij\beta}$ is the proportional change in λ_S for a proportional change in a_{ij} if and only if the environment is in habitat state β (Horvitz *et al.* 2005). This quantity is in part dependent upon the frequency of the habitat state in the Markov chain (Horvitz et al. 2005). It is therefore presented as the contribution of each a_{ij} to $E_{ij\beta}$ ($E_{ij\beta}\big/\sum E_{ij\beta}$, Horvitz et al. 2005).

Calculations were performed in R version 2.4.1 (R Development Core Team 2007). Tree regression employed the tree package (version 1.0-1.25, Venables and Ripley 1999). Source code is available on request. After calculation, elasticities were summed to quantify the impact on λ_S or λ_0 of each rate per age class.

5.4 RESULTS

λ_S was 1.037 and λ_0 1.062. Even in a dynamic system rarely at mean population size (Figure 5.1b), E_{ij}^{D} (deterministic elasticities of λ_0 to a_{ij}) were highly correlated with E_{ij}^{S} (stochastic elasticities of λ_S to a_{ij}) and $E_{ij}^{S\mu}$ (elasticities of λ_S to μ_{ij}, Figure 5.2). E_{ij}^{D}, E_{ij}^{S} and $E_{ij}^{S\mu}$ were not strongly correlated with $E_{ij}^{S\sigma}$ (elasticities of λ_S to σ_{ij}, Fig. 2).

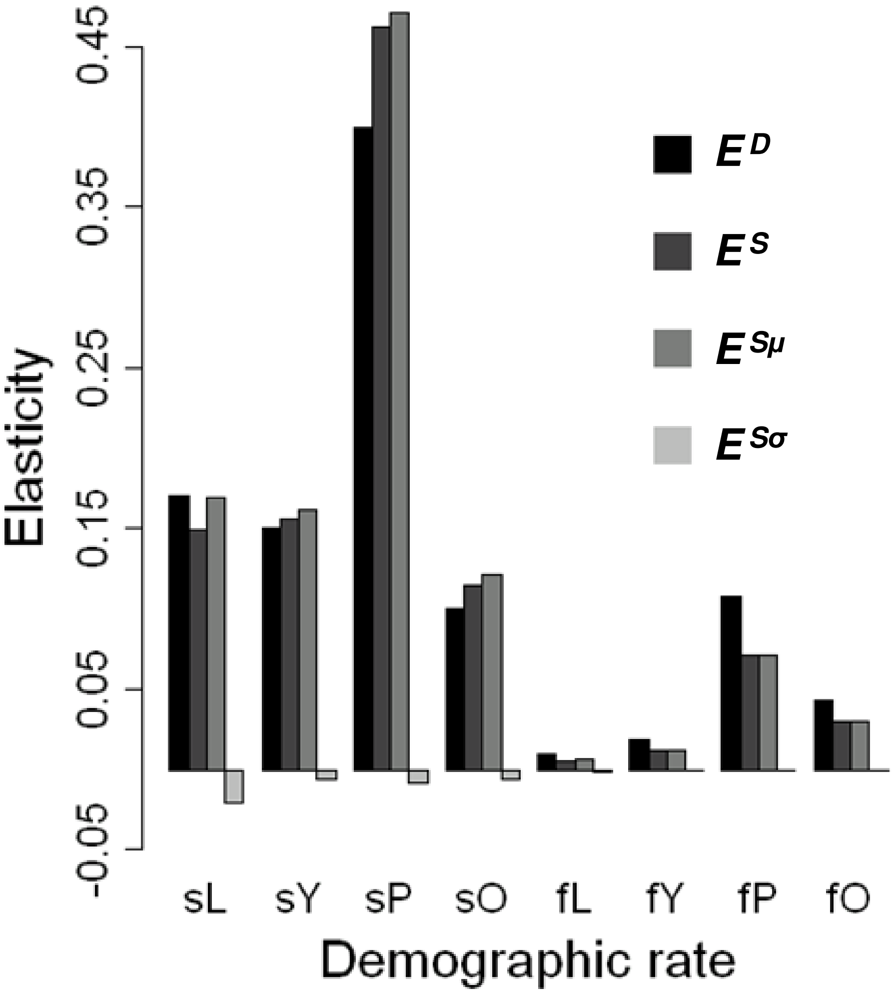

Figure 5.2. Elasticities of asymptotic growth to matrix elements a_{ij} (E_{ij}^{D}) and of long-run stochastic growth to matrix elements a_{ij} (E_{ij}^{S}), to overall mean a_{ij} ($E_{ij}^{S\mu}$) and to overall variation in a_{ij} ($E_{ij}^{S\sigma}$). E_{ij}^{D} were strongly correlated with E_{ij}^{S} (r=0.842) and $E_{ij}^{S\mu}$ (r=0.991), as were E_{ij}^{S} and $E_{ij}^{S\mu}$ (r=0.997). $E_{ij}^{S\sigma}$ were not strongly correlated with either E_{ij}^{D}, E_{ij}^{S} or $E_{ij}^{S\mu}$ (r=0.131, 0.124, 0.161 respectively). The eight demographic rates are composites of: *s* survival; *f* fecundity; *L* lambs; *Y* yearlings; *P* prime-aged individuals; *O* oldest individuals.

Contributions to habitat-stage elasticities to λ_S differed across different habitat states, although the overall contribution of survival was relatively constant approximately 0.8 (Figure 5.3). Age-class contributions of survival and fecundity differed. Lamb survival contributed 0.122 in the lowest quality habitat but 0.203 in the highest. Survival of oldest individuals contributed 0.198 in the lowest quality habitat but 0.126 in the highest (Figure 5.3). Yearlings (0.162 with survival and fecundity pooled) made their greatest contribution in the lowest quality habitat, whereas lambs contributed most to λ_S in the highest quality habitat (0.225 when pooled).

The habitat-stage elasticity (Figure 5.4a) $E_{ij\beta}$ reflected the Markov Chain frequency. Contributions to habitat-stage elasticities $E_{ij\beta} \big/ \sum E_{ij\beta}$ were different in the different habitat states defined (Figure 5.4). The contribution of survival to habitat-stage elasticity was consistently greater than that of fecundity and relatively constant

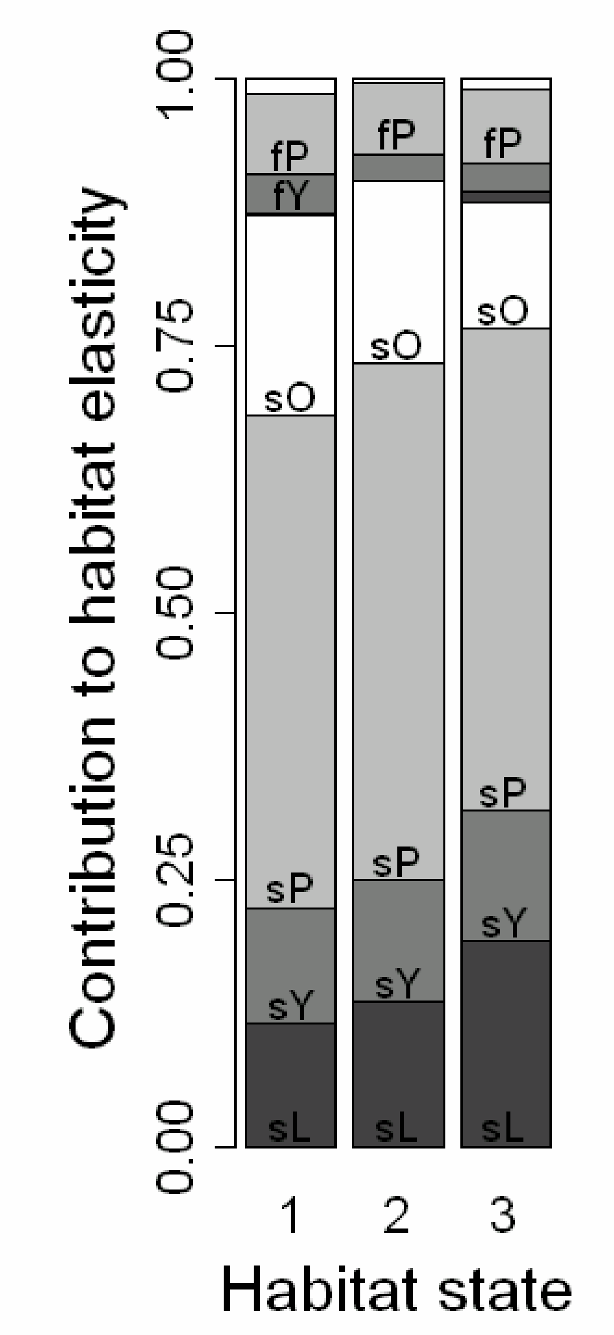

Figure 5.3. The contribution to habitat elasticity $E_{ij\beta} \big/ \sum E_{ij\beta}$ of each demographic rate per age-class. The eight demographic rates are composites of: *s* survival; *f* fecundity; *L* lambs; *Y* yearlings; *P* prime-aged individuals; *O* oldest individuals. The demographic rate is indicated by letters only if the contribution is greater than 3%. *L* are shaded black; *Y*: dark grey: *P*: light grey and *O*: white, such that the stacked elasticities are (from bottom to top) in the order *sL*, *sY*, *sP*, *sO*, *fL*, *fY*, *fP* and *fO*.

5.5 DISCUSSION

Stochasticity has long been recognised by ecologists as playing a pivotal role in population dynamics (Andrewartha and Birch 1954). The food-limited Soay sheep population on Hirta experiences irregular yet frequent crashes in population size (Clutton-Brock and Pemberton 2004, see also Figure 5.1b). Even in a population that fluctuates dramatically in size and whose annual growth is poorly described by mean population growth, E_{ij}^{D} , E_{ij}^{S} and $E_{ij}^{S\mu}$ were all strongly correlated (Figure 5.2). The age-classes contributed variably to λ_S across different habitat states however (Figure 5.3), which suggests that one quantity may be insufficient to describe how demographic rates contribute to the growth of populations exposed to variable environments.

The impact of environmental stochasticity of another ungulate population on a Hebridean island was negligible: sensitivity calculations in deterministic and stochastic environments differed by approximately 1% (Benton *et al.* 1995). Despite shorter generation times (Clutton-Brock and Pemberton 2004), an extreme example of variation in population dynamics for this life-history (Clutton-Brock *et al.* 1997) and relaxation of the small-noise approximation (see Tuljapurkar 1982) for variation in demographic rates, predictions made using density-independent methods were not altered qualitatively for the Soay sheep population considered here. Is this because of the high similarity between λ_S and λ_0? Benton *et al.* (1995) found an even greater similarity (λ_0=1.060, λ_S=1.058 when calculated assuming small noise) between these growth rates. Lande et al. (p. 164, 2003) cite Bro et al. (2000) as an example when correlations between λ_S and λ_0 are lower. Bro et al. (2000) use 250 timesteps however and not 100,000 as here and elsewhere (e.g. Tuljapurkar et al. 2003). Whether strong correlations between λ_S and λ_0 as well as E_{ij}^{D} , E_{ij}^{S} and $E_{ij}^{S\mu}$ persist across diverse life-histories and shorter time-series remains to be seen (see Benton and Grant 1996).

Transient analysis (Caswell 2007, Haridas and Tuljapurkar 2007, Townley et al. 2007) may be more appropriate for short-term applications, especially for long-lived species (Koons *et al.* 2005). In this study, the relative importance of demographic rates differed across different habitat states (Figure 5.3). The dominant demographic rate for population persistence in the short-term likely depends upon the initial habitat state and the habitat states that succeed it. The Markov chain consisted of three discrete habitat states (Figure 5.1b). λ_S was differentially sensitive to events in different habitat states (Figure 5.3). The youngest individuals are most sensitive to harsh conditions, hence their lowest contribution to habitat-stage elasticity in the lowest quality habitat, whereas older individuals are simultaneously more capable (Figure 5.3). Elasticity analysis based over, say, 5 years of data might struggle to "correctly" identify the optimal rate for management action (Heppell *et al.* 2000) or under most intense selection (van Tienderen 2000) if the frequency of and transition probabilities between habitat states is unrepresentative of the range a population experiences over longer periods.

Sensitivities are transformed elasticities (p. 295, Caswell 2001); both can be interpreted as weights in evolutionary calculations (Lande 1982, van Tienderen 2000). Altwegg *et al.* (2007) found a high correlation between sensitivities of λ_S with respect to μ_{ij} and sensitivities of λ_0 to a_{ij}. The relative importance of stochastic variables alters however from year to year, such that the dominant demographic rate for population growth is also variable (Coulson et al. 2003). The habitat-stage elasticities (Figure 5.3) indicate that perturbing demographic rates by the same amount across all years ignores these dynamic patterns in demographic rate dominance. Lande (2007) argued synonymously that for a genotype or phenotype, λ_S is not a valid measure of fitness in a fluctuating environment. Elasticities can alter markedly from one year to the next. Use of long-term measures of population growth – deterministic or stochastic – neglects these dynamic patterns, which can be revealed by, say, partitioning the environment into groups of similar state.

The models presented here link directly herbivores to their food source. The high correlation between E_{ij}^{S} and E_{ij}^{D} is consistent with earlier work on ungulate populations (Benton *et al.* 1995), but the partitioning of E_{ij}^{S} into habitat-dependent contributions (Horvitz *et al.* 2005) suggests that long-term analysis will not always yield optimal results for populations in variable environments. Whilst deterministic analyses may appear superficially acceptable, they may neglect informative detail as to how populations respond to inevitable stochasticity in their environments.

CHAPTER 6[5]

THE INFLUENCE OF THE ENVIRONMENTAL DRIVER ON ELASTICITIES OF STOCHASTIC POPULATION GROWTH.

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[5] This chapter is still in preparation for submission.

6.1 ABSTRACT

All natural populations experience temporal variation in their environments, which alters the dynamics of the population. Elasticity analysis aims to quantify the influence of a demographic rate on population growth. Results calculated in variable environments can vary noticeably from those obtained when the environment is assumed constant. One method of examining how environmental stochasticity influences population dynamics is to use Markov chains, which divide the environmental change continuum into sequences of discrete habitat states. There are numerous ways to characterize environments, but how sensitive are the results of perturbation analysis of the long-run stochastic growth rate to the discretization process? Demographic rates retained their rank importance regardless of changes in descriptive aspects of the Markovian environment. Some quantitative changes were detected for elasticities of within- and between-habitat states. Correlations between different elasticities altered significantly with changes in the accuracy of the environmental descriptor (indicated by proportion of variation in λ_t explained by habitat state definition procedure). The largest differences in these correlations were generated however by "perfect" environmental drivers. In similar systems to that employed here, results of elasticity analysis in Markovian environments appear relatively robust against changes in Markov chain construction.

6.2 INTRODUCTION

Anthropogenic-enduced climate change is predicted to result not only in altered trends of environmental conditions (IPCC 2001) but also increased variability around these trends (Giorgi et al. 2004, Watterson 2005). It is furthermore expected that such changes will impact populations (Root et al. 2003, Travis 2003, Boyce et al. 2006). The incorporation of environmental stochasticity in population projection modelling has the potential to fundamentally alter the conclusions of perturbation analysis under certain circumstances (Benton and Grant 1996, Tuljapurkar et al. 2003, Claessen 2005, Haridas and Tuljapurkar 2005). Recent research has addressed consequences of environmental variability on population growth using sequences of discrete habitat states (Tuljapurkar et al. 2003, Haridas and Tuljapurkar 2005, Horvitz et al. 2005, Morris et al. 2006, Tuljapurkar and Haridas 2006). However, in reality, habitat changes over a continuum. Although continuous changes can be modelled using transition intensities (e.g. Rudemo 1976), the recent theoretical developments in stochastic demography cited above partition this continuum when calculating quantities that describe aspects of the long-run stochastic growth rate λ_S. λ_S might be considered as geometric mean growth over a large number of time-steps. These quantities may be dependent on the classification of the discrete habitat states from the continuum of environmental stochasticity, but to what extent? In Caswellian diction: how sensitive are elasticities of λ_S with respect to statistics summarizing demographic rates to changes in the habitat discretization process?

All natural populations are subject to changes in their environment (Bjornstad and Grenfell 2001, Lande et al. 2003). Although catastrophic events such as hurricanes (Emanuel 2005) or fire (Menges and Quintana-Ascencio 2004) have by definition a (more) discrete nature, many temporal changes in habitat – such as climate change or density-dependence – are arguably best described by a continuous gradient. Use of λ_S is considered to be necessary for demographic models to incorporate the impact of environmental variability. Recent theoretical developments in stochastic demography have employed Markov chains to generate sequences of discrete habitat states that describe the environments experienced by populations (Tuljapurkar et al. 2003). This theory partitioned λ_S into contributions from various statistics, which summarize distributions of demographic rates. (At least) two factors are of importance with respect to this process: differences between the defined habitat states and differences in how habitat changes from state to state. Different demographic rates can contribute to different extents in different habitat states (Horvitz et al. 2005, see also chapter 5) because individuals respond differently to different environmental conditions: the costs of reproduction might only be identifiable - during severe weather conditions, for example (Tavecchia et al. 2005). There is no guarantee that processes that affect within-state variation will affect between-state variation in a similar fashion (Morris et al. 2006). In northern temperate zones, climate models predict increasing summer temperatures and decreasing summer precipitation concomitant to greater variability in these factors between seasons (Giorgi et al. 2004, Watterson 2005). How habitat states are defined is clearly important with respect to these matters. Any definition protocol further determines the probability of progression from state to state. Auto-correlation in the habitat states a population experiences is potentially at least as influential on λ_S as inter-annual variability (Tuljapurkar and Haridas 2006). How the habitat continuum is partitioned has evidently the potential to alter these quantities, but how?

Habitat quality is frequently defined using environmental drivers, but not all are equivalent in their ability to explain variation in population dynamics. If the environmental driver characterized perfectly the dynamics of the system, the proportion of variation in population growth explained by that driver over some time-step would be 1. This is however unlikely to occur in natural populations, so models are built that characterize statistically the association between (aspects of) population growth and the environmental driver. A univariate model might explain less variation in population growth than a multivariate one. Variation often remains unexplained, but how much effort should be devoted to reducing this amount? One method of compromise is to adopt the principle of parsimony (Young et al. 1996), such that any model is as simple as possible, but no simpler. A model with fewer habitat states may have a habitat transition matrix with more realistic habitat transition probabilities but incorrectly estimate within or between state variability. Or vice versa.

In summary, demographic inference from stochastic models is dependent on the way in which stochasticity is handled. The number of habitat states, the order of habitats and their frequency of occurrence all have the potential to affect λ_S. An important question is: how is biological inference impacted by different treatments of stochasticity in environmental variables? Using data that links directly the sole herbivores on an isolated island with their food source, climatic conditions and population structure – all of which interact to impact demographic rates and therefore population dynamics (Coulson et al. 2001) – this analysis probes the consequences of the use of multiple environmental drivers and application of the principle of parsimony in the construction of Markov chains. In general terms: how dependent are the results of stochastic perturbation analysis on construction of the Markov Chain? In specific terms: does the number of habitat states, proportion of variation in observed population growth explained by these habitat states and auto-correlation in the Markov chain influence elasticities of λ_S with respect to various statistics of demographic rates?

6.3 METHODS

6.3.1. Study Population

Individual-based data have been collected under an identical protocol since 1985 from the population of Soay sheep living in Village Bay on Hirta (57º49' 8º34') in the St Kilda archipelago. Three trips are made annually to collect data: during the birth pulse (late March - early May), an annual catch (August) and during the rut (October - November). Full details of the data collection protocol and population history are available in Clutton-Brock and Pemberton (2004). Population size is defined here as the number of sheep alive on August 1st each year.

6.3.2 Population Model and the Markov Chain

Demographic and environmental data were available from 1991 to 2006 inclusive (except 2001 due to foot and mouth disease on the mainland). Only females were considered, for which the most parsimonious age-structure has four age-classes (Catchpole et al. 2000): lambs (*L*), yearlings (*Y*), prime-aged (*P*, 2-6 years old) and older (*O*, >6 years old). A post-breeding Leslie matrix (Caswell 2001) **A** was constructed with 8 age-classes (for matrix and life-cycle graph, see Appendix A2). The population model is $\mathbf{P}(t) = \mathbf{A}(t)\mathbf{P}(t-1)$, where $\mathbf{P}(t)$ is the population vector at time t and $\mathbf{A}(t)$ a transition matrix at time t chosen according to the probabilities defined by a Markov chain.

6.3.3 The Markov Chain

Various hypotheses exist for how to combine and divide multiple explanatory variables; those tested are summarized in Table 3.1.

Method		**Number of habitat states**			
		2	**3**	**4**	**5**
λ_t ranked and split	**6**	0.656	0.849	0.966	0.980
Sward height (threshold=3.49) and adult:lamb ratio	**5**	0.517	0.604		
Sward height (threshold=3.56) and adult:lamb ratio	**4**	0.265	**0.420**		
Sward height (threshold at 3.56)	**3**	0.265	0.301	0.395	
Median and quantiles of sward height	**2**	0.079	0.517	0.588	
Mean sward height and standard deviation	**1**	0.079	0.264	0.142	

Table 6.1. Summary of hypotheses used to construct Markov chains with the R^2 of the regression of annual population growth (λ_t) against the habitat states defined according to each hypothesis/number of states combination. The hypotheses generated categories that explained from 7.9% to 98.0% of the variation in λ_t by habitat state as a categorical explanatory variable. The method that combined sward height and adult: lamb ratio created categories that featured no years in one of the four combinations. The method used in chapter 5 is denoted in **bold**.

A "perfect" environmental driver would have no overlap in population growth from one year to the next, denoted λ_t, such that the within-state deviance is minimized and proportion of explained variation in λ_t maximised. To achieve this λ_t was split visually, which enabled the use of 2, 3, 4 and 5 habitat states (method 6, in Table 6.1).

The population dynamics of the female component of the Soay sheep population are significantly affected by age-structure, population density and winter weather (Coulson et al. 2001). Multivariate models therefore describe this system ore comprehensively than a univariate alternative. Soay sheep are the sole herbivores on Hirta, and their density is affected significantly by sward height (Crawley et al. 2004). Tree regression, which divides the response variable (here, a demographic rate) into discrete classes of explanatory variables (Venables and Ripley 1999), was used to obtain the most parsimonious combination of environmental variables. Results indicated that sward height should be split between 3.49 and 3.61 (range: 2.02 to 5.24) and that adult: lamb ratio should be split at approximately 3 (range 1.52 to 3.32). In an additive model containing all terms, winter weather (approximated crudely by the mean station-based North Atlantic Oscillation between December and March) was consistently subdominant except for a small change in *fP*, which has previously been shown to be relatively invariant to environmental change (Coulson *et al.* 2001). Two classes were adopted for sward height and adult: lamb ratio, thus producing four habitat states when combined. No years were classified as low sward and low adult: lamb ratio, which left three habitat states. This method was used in chapter 5 and is method 5 here (Table 6.1). Combining the two higher quality states enabled testing of differences between 2 and 3 state models using this hypothesis.

There was one significant outlier in the tree regression (2003)[6]. Since the dominant explanatory variable was sward height and this was split between two points, the effect of choosing the lower bound as the threshold was tested. This year had λ_t=1.27, and choosing a lower bound places it into a category that increased the proportion of variation explained (c.f. methods 4 and 5 in Table 6.1). As with method 5, the two higher quality states were combined to give a 2 and 3 state model (method 4, Table 6.1).

The influence of the incorporation of multiple environmental drivers was assessed by construction of a Markov chain using sward height only (method 3, Table 6.1). Thresholds were obtained using tree regression for the 2 and 3 habitat state case. Tree regression using sward height only detected a further node at 3.79. Sward height was split visually for the four state case to ensure at least two data points per class.

An alternative method would be to split the continuum into bins defined using medians and quantiles (method 2, Table 6.1). Using this method enabled construction of 2, 3 and 4 state Markov chains. The two-state chain was less than/greater than median sward height; the four-state chain partitioned this partition using the 1st quantile, median and 3rd quantile as boundaries between states; the three-state chain sorted the states in a similar fashion, but split them into three groups of equal size.

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[6] Cook's distance is a measure of influence of data points in a regression and values above 4/(n-k-1) are considered to have overt influence, where n is the number of data points and k the number of parameters (Fox 2002). There were 13 data points and only 2003 was over this threshold (0.4) when habitat state was taken to be continuous (0.588) or categorical (0.404). Diagnostic plots (not shown) supported the argument that 2003 was atypical.

In a similar vein, splitting the distribution of sward heights using the mean and standard deviations also generated 2, 3 and 4 habitat states (method 1, Table 6.1). The 2-state chain was less than/greater than mean sward height (μ); the 4-state chain partitioned sward height using standard deviations (σ) and $\mu \pm \sigma$; 3-state chain split the distribution of mean sward height into 3 classes based on $\mu \pm (2/3)\sigma$. The lowest quality state was therefore when sward height < (μ - (2/3)σ) and the highest quality state sward height > (μ + (2/3)σ)

The habitat transition matrix **H** was therefore of variable dimension. The sub-dominant eigenvalue informs of auto-correlation in the system defined by **H**, which is dependent upon the transition probabilities that comprise it. As a consequence, different habitat state definitions to test hypotheses of the effect of the influence of the environmental driver on the elasticities generated different auto-correlation (Figure 6.1). All Markov chains satisfy the usual ergodicity conditions (Tuljapurkar *et al.* 2003)

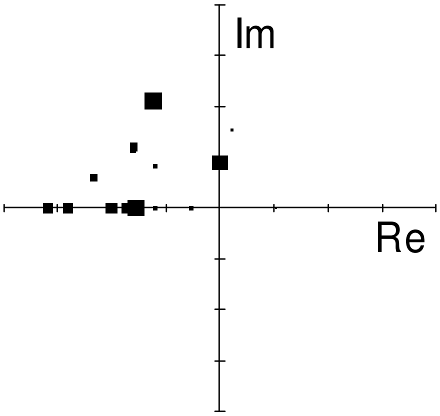

Figure 6.1. The correlation between real and imaginary parts of the sub-dominant eigenvalue was weak. Absolute distance from the origin was used in analysis, and varied between 0.04 and 0.79. Symbol size is proportional to the proportion of variation in λ_t explained by the habitat states.

6.3.4 Perturbation Analysis

Elasticities of asymptotic growth λ_0 to a matrix element a_{ij} (here a demographic rate) are the proportional change in λ_0 from a proportional change in μ_{ij} (mean a_{ij}) over all 100,000 time steps. This quantity was calculated and is denoted E^D_{ij}.

The long-run stochastic growth rate λ_S was calculated over all 100,000 time steps and defined as log (λ_S) = $\lim_{t\to\infty}(1/t)\log[P(t)/P(0)]$. The stochastic elasticity (denoted E^S_{ij}) of λ_S with respect to element a_{ij} is the proportional change in λ_S for a proportional change in a_{ij}, such that the coefficient of variation of a_{ij} does not change (Tuljapurkar et al. 2003). The elasticity of λ_S with respect to μ_{ij} (denoted $E^{S\mu}_{ij}$) is the proportional change in λ_S for a proportional change in μ_{ij}, which is the same perturbation as in E^D_{ij}, but to λ_S not λ_0 (Tuljapurkar et al. 2003). The elasticity of λ_S

with respect to variation in a_{ij} (σ_{ij}, denoted $E_{ij}^{S\sigma}$) is the proportional change in λ_S for a proportional change in σ_{ij} (Tuljapurkar et al. 2003).

These quantities perturb every matrix in the simulated sequence and do not consider habitat-dependence. Paritioning this sequence according to the habitat states determined by the Markov chain might yield further insight (Morris *et al.* 2006). The elasticity of λ_S with respect to the within-state variability of a_{ij} (denoted $E_{ij}^{\sigma W}$, Morris et al. 2006) quantifies the proportional change in λ_S for a proportional change in the variability of a_{ij} within each phase whilst keeping the means in each phase and between-phase variance fixed. Conversely, the elasticity of λ_S with respect to the between-state variability of a_{ij} (denoted $E_{ij}^{\sigma B}$, Morris et al. 2006) quantifies the proportional change in λ_S for a proportional change in the mean μ_{ij}^{β} in each phase whilst keeping the overall mean and the variability within each phase fixed. The elasticities of variability are linked (Morris *et al.* 2006): $E_{ij}^{S\sigma} = E_{ij}^{\sigma W} + E_{ij}^{\sigma B}$.

Another method of incorporating habitat dependence is habitat-stage elasticities (Horvitz et al. 2005). The habitat-stage elasticity (denoted $E_{ij\beta}$) of λ_S with respect to a_{ij} and habitat state β does. $E_{ij\beta}$ is the proportional change in λ_S for a proportional change in a_{ij} if and only if the environment is in habitat state β (Horvitz *et al.* 2005). This quantity is in part dependent upon the frequency of the habitat state in the Markov chain (Horvitz et al. 2005). It is therefore presented as the contribution of each a_{ij} to $E_{ij\beta}$ ($E_{ij\beta} \big/ \sum E_{ij\beta}$, Horvitz et al. 2005).

6.3.5 Statistical Analysis

The dependence of correlations between the elasticities defined above on aspects of Markov chain construction were analysed using generalized linear models (GLMs, ch. 27, Crawley 2002) with quasibinomial error structure that accounted for overdispersion and the logit link function. Number of states (as a three state categorical variable: 2, 3 and 4&5), sub-dominant eigenvalue of **H** (continuous variable as absolute distance from the origin) and proportion of variation in λ_t explained by the discrete habitat states (continuous, obtained from a quasi GLM with identity link function) and all interactions were fitted. A reverse stepwise procedure was used to remove insignificant terms and hence obtain the minimal adequate model;

F tests were used to test whether terms should be retained in the model (p. 530, Crawley 2002). The fit of the minimal adequate model was assessed using diagnostic plots (p. 237, Crawley 2002).

To assess variation in the elasticities defined in the previous section, GLMs were fitted with explanatory variables. Model selection was as above. For E_{ij}^{D} and E_{ij}^{S}, which are bounded by 0 and 1, a quasibinomial error structure and logit link function was used; for all others, which can be positive or negative, a quasi error structure (Gaussian errors but with the deviance parameter not fixed at 1) and identity link function was used.

Changes in contribution to habitat-stage elasticity were assessed using generalised linear mixed-models (GLMMs, Diggle et al. 2002) with a quasibinomial error structure and logit link function. Models were fitted using the proportion of variation in λ_t explained by the discrete habitat states, sub-dominant eigenvalue of $\mathbf{H}$ and their interaction as continuous fixed effects. Both explanatory variables were also nested within the number of states as a categorical random intercept to test the significance of variable slopes for different numbers of habitat states (one might hypothesise that contributions to habitat-stage elasticity of a demographic rate would change more quickly if two states rather than four were employed). Terms were removed sequentially from this full model to obtain the minimum adequate as previously.

Results are presented on the scale of the link function and given as coefficients (β) with associated standard errors (s.e.), p-values (for GLMs only as "exact" p-values do not exist for GLMMs, Bates 2005) and proportion of variation explained by each effect (r^2). All calculations and statistics were performed in R version 2.5.1 (R Development Core Team 2007), and used the tree package (version 1.0-1.25) to calculate regression trees (Venables and Ripley 1999) and the lme4 package to calculate GLMMs (version 0.99875-7, Bates 2005), which were fitted using the Laplacian approximation to maximum likelihood. Source code is available from the authors on request.

6.4 RESULTS

6.4.1 Correlations between Elasticities of λ_S

The amount of variation in population growth over a single timestep λ_t did not affect the correlation between deterministic (E_{ij}^{D}) and stochastic (E_{ij}^{S}) elasticities and between E_{ij}^{D} and elasticities to mean demographic rates ($E_{ij}^{S\mu}$) or between E_{ij}^{S} and $E_{ij}^{S\mu}$ (Table 6.2). There was a weak effect of correlation in the Markov chain on the correlation between E_{ij}^{D} and $E_{ij}^{S\mu}$; in real terms the effect was to increase the correlation from 0.94 to 1.00. The amount of variation in λ_t significantly affected the correlation between E_{ij}^{D} and elasticities to variation in demographic rates ($E_{ij}^{S\sigma}$) and between E_{ij}^{D} and elasticities to variation between phases of the disturbance cycle ($E_{ij}^{\sigma B}$). Given the high correlation between E_{ij}^{D}, E_{ij}^{S} and $E_{ij}^{S\mu}$, qualitatively identical patterns were detected when E_{ij}^{D} was replaced by either E_{ij}^{S} or $E_{ij}^{S\mu}$ (Table 6.2).

Correlations between the elasticities of variation ($E_{ij}^{S\sigma}$, $E_{ij}^{\sigma W}$ and $E_{ij}^{\sigma B}$) varied more dramatically (see R^2 figures in Table 6.2). The correlation between $E_{ij}^{S\sigma}$ and $E_{ij}^{\sigma W}$ did not covary significantly with proportion of variation in λ_t as a main effect, but did via correlation in the Markov chain and their interaction. In real terms the correlation varied from 0.998 to 0.039. A similar pattern was detected between $E_{ij}^{\sigma W}$ and $E_{ij}^{\sigma B}$, although both main effects were significant (Table 6.2, range of correlations in real terms 0.980 to 0.079). The correlation between $E_{ij}^{S\sigma}$ and $E_{ij}^{\sigma B}$ varied significantly with proportion of variation in λ_t only, and spanned a more restricted range (0.820 and 0.980) over the range of data collected.

The number of habitat states in the Markov chain affected nothing in a statistically significant manner

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Table 6.2. Correlations between elasticities of λ^S varied significantly with the proportion of variation that the habitat states explained in λ_t (R^2) and the auto-correlation in the Markov chain (AC) and their interaction (R^2:AC). Where cells are blank, no significant correlations were found. Patterns of dependence were not consistent across all comparisons however. No significant trends in correlations between elasticities and number of habitat states were detected, and are hence not included in the table. Coefficients (β, with associated standard errors in brackets) are presented on the scale of the logit link function, with significance codes (:p>0.05, *:p<0.05, **: p<0.01; ***: p<0.001) and R^2 values for the model. Elasticity codes are deterministic E_{ij}^{D}, stochastic E_{ij}^{S}, to overall mean $E_{ij}^{S\mu}$, to overall variability $E_{ij}^{S\sigma}$, of within- $E_{ii}^{\sigma W}$ and between-phase $E_{ii}^{\sigma B}$ variability.

E_{ij}^{D}																		
E_{ij}^{S}																		
$E_{ij}^{S\mu}$		β=2.75 (0.98) * r^2=.37			β=1.60 (0.58) * r^2=.37													
$E_{ij}^{S\sigma}$	β=1.92 (0.61) ** r^2=.40			β=2.31 (0.69) ** r^2=.42			β=2.09 (0.65) ** r^2=.40											
$E_{ij}^{\sigma W}$										β=2.84 (1.70)	β=12.4 (2.63) **	β=-24.6 (4.32) *** r^2=.96						
$E_{ij}^{\sigma B}$	β=1.94 (0.75) * r^2=.31			β=2.56 (0.82) ** r^2=.40			β=2.34 (0.78) ** r^2=.38			β=2.69 (0.92) ** r^2=.42			β=6.65 (1.70) **	β=14.2 (2.59) **	β=-26.5 (4.85) *** r^2=.86			
	R^2	AC	R^2:AC	R^2	AC	R^2:AC	R^2	AC	R^2:AC	R^2	AC	R^2:AC	R^2	AC	R^2:AC	R^2	AC	R^2:AC
	E_{ij}^{D}			E_{ij}^{S}			$E_{ij}^{S\mu}$			$E_{ij}^{S\sigma}$			$E_{ij}^{\sigma W}$			$E_{ij}^{\sigma B}$		

6.4.2 Elasticities of Statistics of λS

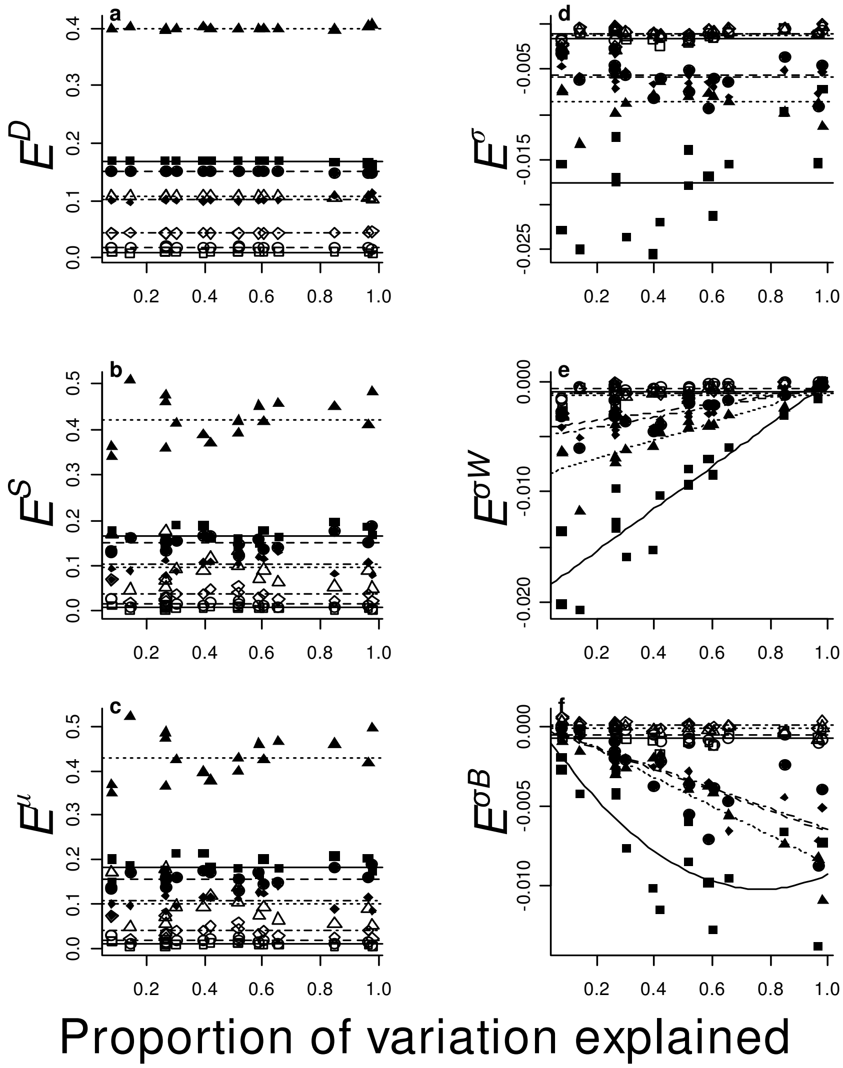

Figure 6.2. Rank importance in elasticities was maintained despite changes in the proportion of variation in λ_t explained by the habitat states. Elasticity codes: deterministic E_{ij}^{D}, stochastic E_{ij}^{S}, to overall mean $E_{ij}^{S\mu}$, to overall variability $E_{ij}^{S\sigma}$, of within-$E_{ij}^{\sigma W}$ and between-phase $E_{ij}^{\sigma B}$ variability. Large quantitative trends were evident in $E_{ij}^{\sigma W}$ (e) and $E_{ij}^{\sigma B}$ (f, where a quadratic term was necessary) however. Solid symbols are survival, open symbols fecundity. Squares and solid lines relate to lambs, circles and dotted lines to yearlings, triangles and dashed lines to prime-aged individuals and diamonds and dot-dash lines to oldest individuals.

Rank importance in the elasticities of each demographic rate was maintained (Figure 6.2). The only elasticities to show significant trends were survival elasticities of $E_{ij}^{\sigma W}$ and $E_{ij}^{\sigma B}$: all survival elasticities of $E_{ij}^{\sigma W}$ covaried positively and significantly with the proportion of variation explained in λ_t Figure 6.2e). All survival elasticities of $E_{ij}^{\sigma B}$ covaried negatively and significantly with proportion of variation explained in λ_t (Figure 6.2f). Diagnostic plots (not shown) suggested that linear regression was sufficient for all rates except for $E_{ij}^{\sigma B}$ of *sL* (Figure 6.2f), where a significant quadratic term was necessary to avoid serial correlation in residuals.

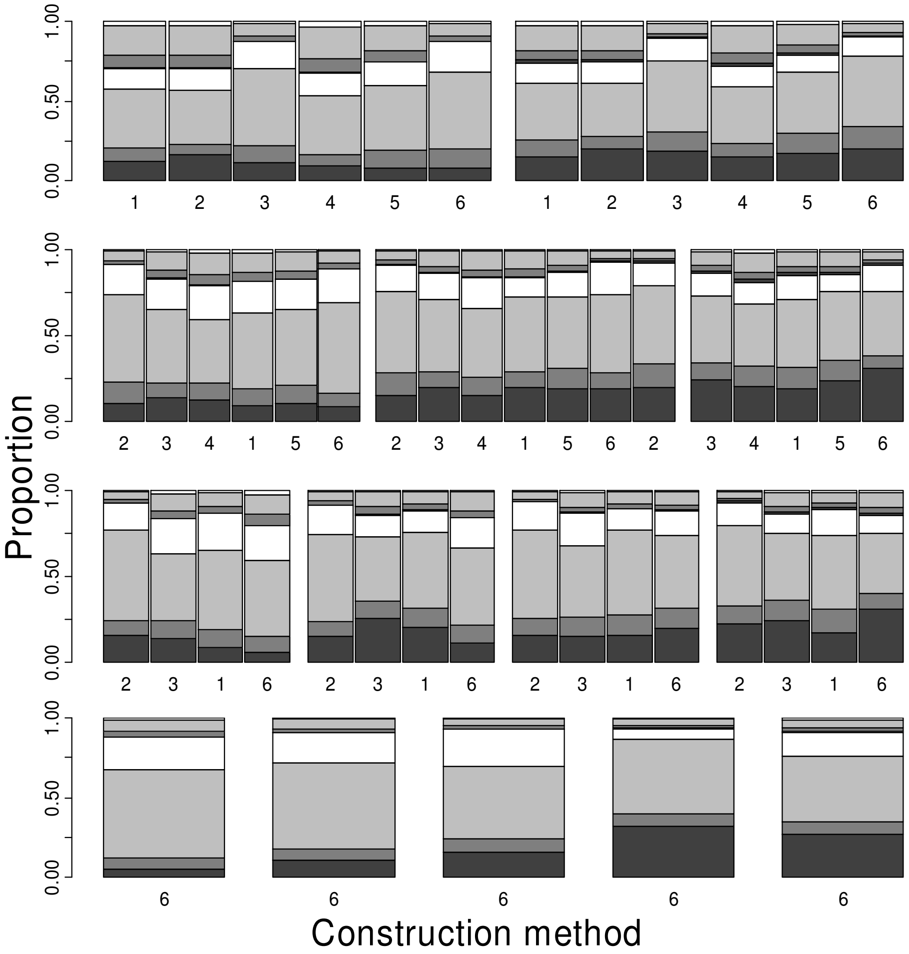

Figure 6.3. Habitat-stage elasticity changed in relation to the frequency of a given state in the Markov chain (not shown); changes in contribution to habitat stage elasticity (Horvitz et al. 2005) under the different methods of Markov chain construction (Table 6.1) showed little consistent pattern. Habitat states are ordered according to the proportion of variation explained in λ_t by that method (left to right: minimum to maximum proportion of variation in λ_t.), but do not differ significantly with proportion of variation explained, auto-correlation in the Markov chain or the number of habitat states (see table 6.1 for model number codes). $E_{ij\beta} \big/ \sum E_{ij\beta}$ for lambs are shaded black and darkness decreases with age in the same order as in figure 5.3. Survival elasticities are beneath fecundity elasticities.

Model		**AIC for models on each demographic rate**							
Fixed Effects	**Random Effects**	***sL***	***sY***	***sP***	***sO***	***fL***	***fY***	***fP***	***fO***
PV*AC	(PV|N) + (AC|N)	21.5	20.2	20.6	20.6	20.3	20.4	20.7	20.2
PV+AC	(PV|N) + (AC|N)	19.5	18.3	18.6	18.4	18.4	18.4	18.8	18.2
PV	(PV|N) + (AC|N)	17.5	16.4	16.6	16.5	16.4	16.4	16.8	16.3
AC	(PV|N) + (AC|N)	17.5	16.3	16.6	16.4	16.4	16.4	16.8	16.3
1	(PV|N) + (AC|N)	15.5	14.3	16.6	14.7	14.4	14.5	14.9	14.4
1	(AC|N)	9.5	8.2	8.6	8.5	8.3	8.4	8.9	8.2
1	(PV|N)	9.5	8.3	8.6	8.5	8.4	8.4	9.0	8.2
1	(1|N)	5.5	4.2	4.6	4.5	4.3	4.4	4.9	4.2

Table 6.3. AIC values of models under various hypotheses to test the impact of auto-correlation in the Markov chain (AC), proportion of variation in λ_t explained by habitat state (PV) and the number of habitat states (N), wher PV|N indicates that PV is nested within N. The minimum adequate model – determined using Akaike's Information Criterion –l for all demographic rates (quasibinomial GLMM) retained neither fixed nor random effects in any case. Demographic rate codes: L lambs; Y yearlings; P prime-aged individuals; O oldest individuals; s survival; f fecundity.

All slopes of demographic rates with habitat state were not significantly different, as indicated by the negligible contribution of random effects (habitat state nested within correlation in the Markov chain and proportion of variation explained), and neither fixed nor random effects were retained in minimum adequate models (Table 6.3). The contribution to habitat-stage elasticities showed some variation, although consistent trends were not obvious (Figure 6.3).

6.5 DISCUSSION

Recent research has employed discrete habitat states to characterize the impact of various statistics that summarize demographic rates on the long-run stochastic growth rate λ_S (Tuljapurkar et al. 2003, Haridas and Tuljapurkar 2005, Horvitz et al. 2005, Morris et al. 2006, Tuljapurkar and Haridas 2006). Elasticity analysis of the long-run stochastic growth rate λ_S addresses the frequently violated assumptions of density-independent growth (λ_0), one constant environment and stable population structure. It is therefore arguably surprising that correlations between elasticities of λ_S and λ_0 were so high (chapter 5). The analyses of this chapter strengthen the arguments made previously. They confirm additionally that such results are robust to changes in Markov chain construction.

Tuljapurkar *et al.* (2003) constructed Markov chains for an understory shrub population (*Ardisia escalloniodes*) that compared results using the historical hurricane frequency with a lower and higher frequency (Tuljapurkar et al. 2003). The latter of which is predicted to become increasingly likely in the future (Emanuel 2005, Katz et al. 2005). Morris et al. (2006) argued that if climate change alters only within- or between-phase variability then elasticities of overall variability may poorly estimate these effects. Implicit in this logical conjecture is accurate identification of habitat states – both number and boundaries of – and habitat frequency. Pascarella and Horvitz (1998) defined the habitat state of the system analyzed by Tuljapurkar et al. (2003) using percentage of canopy openness, i.e. light availability in the understory. In many systems one environmental driver may be insufficient to explain the dynamics if interactions are significant in predicting accurately the responses of populations to their environments (Bjornstad and Grenfell 2001). This is certainly the case for the Soay sheep on Hirta, where age- and sex-structure, population density and environmental conditions interact to influence population dynamics (Coulson et al. 2001, Coulson et al. accepted). There are intuitive advantages of methods that capture more variation in population dynamics, although it makes little impact on many quantities that describe aspects of λ_S. (Figure 6.2, Figure 6.3 & Table 6.2).

Many – often conflicting – arguments are presented on how to construct statistical models (Whittingham et al. 2006) although the trade-off between simplicity and complexity, which is the principle of parsimony or Occam's razor (Young et al. 1996), has a long history. One might argue against partitioning a general state into something more specific on the grounds of power; one might argue that a lack of power in the data is insufficient not to split processes that are, from a biological perspective, clearly distinct. All elasticities of λ_S were not significantly correlated with the number of habitat states defined, which suggests that how the environmental change continuum is divided is not of primary concern for this population.

For the quantities presented by Tuljapurkar et al. (2003), no significant trends in E_{ij}^{S}, $E_{ij}^{S\mu}$ and $E_{ij}^{S\sigma}$ were detected (Figure 6.3). Correlations between these quantities were relatively robust; the only discernible differences occurred when the environmental driver was artificially created and has greater explanatory power than most statistical analyses. For this system therefore, habitat states could be assigned at random without substantial impacts upon these quantities. The elasticities of variability are linked by a sum rule: $E_{ij}^{S\sigma} = E_{ij}^{\sigma W} + E_{ij}^{\sigma B}$ (Morris et al. 2006). Since $E_{ij}^{S\sigma}$ did not vary significantly, any changes in $E_{ij}^{\sigma W}$ and $E_{ij}^{\sigma B}$ had to be opposite or neutral. They were opposite: $E_{ij}^{\sigma W}$ covaried positively with proportion of variation explained by habitat states on λ_t and negatively for $E_{ij}^{\sigma B}$ (Figures 6.3e and 6.3f). This observed dependence of $E_{ij}^{\sigma W}$ and $E_{ij}^{\sigma B}$ on the proportion of variation explained is perhaps unsurprising: if the environment is poorly defined, then more variation will exist between the years of a particular state and the proportion of variation in λ_t explained by the habitat states will be low. Under this scenario, $E_{ij}^{\sigma W}$ will therefore be more influential on $E_{ij}^{S\sigma}$ than $E_{ij}^{\sigma B}$, because a large proportion of variation is not explained by the habitat states. Another interpretation if $| E_{ij}^{\sigma W} | > | E_{ij}^{\sigma B} |$ is that the environmental driver does not explain the majority of variation in the dynamics. The dependency in elasticities of survival was consistent across the entire range of proportion of explained variation in λ_t, suggesting that regardless of the explanatory power of the environmental driver, this dependency should be taken into account on interpretation of these elasticities of variation

The dynamics of the Soay sheep population on Hirta are characterized by strong patterns of negative auto-correlation: two successive declines in population abundance have never been observed and nor have three successive increases (Clutton-Brock and Pemberton 2004). (Tuljapurkar and Haridas 2006). A high influence of auto-correlation implies that “vital rates remember the past” (p. 333, Tuljapurkar and Haridas 2006); the consequences of this in the expectation of increasing environmental variability (Boyce et al. 2006) are clearly of importance. Ripa and Heino (1999) concluded for a non age-structured model that negative auto-correlation is more devastating than positive autocorrelation. Dependent upon the proximity of a system to the boundary of the stability region, resonance between environmental variability and population structure (system dynamics) and can increase the probability of invasion and/or extinction (Greenman and Benton 2005). Habitat state definitions vary in their ability to capture the observed negative auto-correlation of the system (Figure 6.2) but these differences were not correlated significantly with the quantities assessed here. One caveat of this analysis is however that this example does not feature auto-correlation on the levels reported for *A. escalloniodes* in a hurricane dominated system (> 0.9, Pascarella and Horvitz 1998, Tuljapurkar et al. 2003) where auto-correlation can be more influential than inter-annual variability on λ_S.

According to this study, elasticities of λ_S to statistics that summarize demographic rates retain their rank importance regardless of how environmental change is incorporated into stochastic population projection. The results of stochastic elasticity analysis for the Soay sheep population therefore appear robust against how environmental variability is incorporated. Significant quantitative changes were not detected for E_{ij}^{S}, $E_{ij}^{S\mu}$ or $E_{ij}^{S\sigma}$, but were for $E_{ij}^{\sigma W}$ and $E_{ij}^{\sigma B}$ (Figure 6.2). Powerful methods can be applied to describe how demographic rates affect λ_S. Further work extending these ideas to other systems, especially short-lived species in sequential habitats might prove instructive in determining the generality of these results.

CHAPTER 7

CORRELATIONS BETWEEN AGE, PHENOTYPE AND INDIVIDUAL CONTRIBUTION TO POPULATION GROWTH IN COMMON TERNS[7]

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[7] This paper was published by Ecology as Ezard, TH.G., Becker, P.H. and Coulson, T. (2007) Correlations between age, phenotype and individual contribution to population growth in common terns. Ecology 88 (10) 2X75-2X83.

7.1 ABSTRACT

There have been numerous reports of changes in phenology, which are frequently attributed to environmental change. Age-dependent change in phenotypic traits, fledgling production, and the timing of events in the life cycle is also widespread. This means that changes in the age structure of a population could generate changes in phenology, which may be incorrectly attributed to environmental change or microevolution. Here, estimates of selection for arrival date, arrival mass, and laying date are compared when age is and is not corrected for. This is achieved using long-term individual-based data collected from a breeding colony of Common Terns (Sterna hirundo) and a novel fitness measure: individual contributions to population growth. The failure to correct for age generated deceptive estimates of selection in eight out of nine comparisons. In six out of nine comparisons, the direction of selection differed between age-corrected and uncorrected estimates. Persistent individual differences were detected: individuals remained within the same part of the phenotype distribution throughout life. The age-corrected estimates of selection were weak and explained little variation in fitness, suggesting that arrival date, arrival mass, and laying date are not under intense selection in this population. These results also demonstrate the importance of correcting for age when identifying factors associated with changes in seabird phenology.

7.2 INTRODUCTION

Age-related improvements in reproductive success have been ubiquitously reported in avian species, especially long-lived ones (Reid 1988, Wooller et al. 1990, Weimerskirch 1992, Daunt et al. 1999, Cam and Monnat 2000, Pärt 2001, Reid et al. 2003a, González-Solís et al. 2004, Mauck et al. 2004)Potential reasons underpinning the improvements remain the subject of debate (Curio 1983, Forslund and Pärt 1995). Three hypotheses have been proposed: the selection hypothesis (Cam and Monnat 2000, Mauck et al. 2004); the increased ability hypothesis (Daunt et al. 1999, Pärt 2001) and the optimization of reproductive effort hypothesis (Reid 1988). Increased ability often has been documented as the dominant hypothesis (Forslund and Pärt 1995) due to age-related improvements in foraging ability (Daunt et al. 1999), diet choice (Rutz et al. 2006), experience with the same mate (Bradley et al. 1990), and access to better territories (Pärt 2001). The hypotheses are not mutually exclusive and a combination of all three has been adopted as a cogent explanation of age-related improvements in reproductive success in some cases (Wooller et al. 1990, Weimerskirch 1992, Barbraud and Weimerskirch 2005). High-quality birds, which breed early and successfully, are frequently also the oldest (deForest and Gaston 1996). Deceptive conclusions can be drawn from selection analyses if the correlation between age and phenotype is not considered. Here, the concurrent effects of age, reproductive success, and phenotypic trait expression are investigated for arrival date, arrival mass, and laying date in a population of the Common Tern (Sterna hirundo): a long-lived migratory seabird that shows significant age-related improvements in reproductive success (Nisbet et al. 1984, Nisbet and Cam 2002).

Heterogeneity in individual quality and its consequences for demography and life history theory have often been discussed (Vaupel et al. 1979, Wendeln and Becker 1999b), but a conclusive definition and assessment procedure remain elusive (Cam et al. 2004a). Phenotypic traits such as arrival or laying date are examples of dynamic measures of quality. Timing of breeding is often related to fledgling production (e.g. deForest and Gaston 1996, Arnold et al. 2004) and this trait has been employed as a measure of quality(Sydeman and Eddy 1995, Arnold et al. 2004). Concurrent to age-related changes in reproductive success, age-dependent phenotypic trait expression has been reported (González-Solís et al. 2004, Becker and Limmer, unpubl.). The correlations between age and timing of breeding (deForest and Gaston 1996, González-Solís et al. 2004) as well as between age and fledgling production (Curio 1983, Forslund and Pärt 1995) are potential causes of bias because older, more experienced birds commence breeding before younger ones (deForest and Gaston 1996, González-Solís et al. 2004). It is therefore problematic to tease apart the cause of increased fledgling production: are early breeders simply more experienced and therefore more capable parents, or do chicks benefit most from more developmental time before departure from the breeding site? Does the use of timing of arrival or breeding as a measure of quality suggest simply that old birds are good and young birds bad?

Date of arrival in the breeding area is hypothesized to be a key determinant of breeding success in migratory bird species. It enables selection of high-quality nesting sites (Kokko et al. 2004) and therefore mates (Alatalo et al. 1986, Ludwigs and Becker 2006). Early arrival also permits early breeding, which provides additional developmental time before departure from the breeding site (Dawson and Clark 2000). Directional selection promotes an early laying date and additive genetic variance underlying it (Sheldon et al. 2003). Environmental conditions also affect phenotype distributions: phenological responses to recent climate change have been reported in diverse taxa (Walther et al. 2002) and have ecological consequences (Stenseth et al. 2002). A population-level response, which appears to be the result of environmental or microevolutionary change, may be due solely to phenotypic plasticity: warmer winters enabled female Collared Flycatchers to lay more eggs earlier (Przybylo et al. 2000). Common Terns in good condition, as defined by body mass (Wendeln and Becker 1999b) but not necessarily by body size (Wendeln et al. 1997), breed earlier and more successfully than birds in poor condition (Wendeln and Becker 1999b). If arrival condition deteriorates however, individuals may require more time to improve condition and initiate clutches. Wendeln and Becker (1999) found evidence for a state-based life history approach by comparing masses during incubation and chick-rearing.

Phenotypic traits change over an individual's lifetime, but, until recently, measuring individual fitness over a short time step has been problematic. A generation-free approach, which compares population size at time t and time t+1 with and without focal individual i, enables calculation of an individual's contribution to population growth, $p_{t(i)}$, from one year to the next. $p_{t(i)}$ is an individual's annual realized fitness (Coulson et al. 2006b)and can be decomposed into contributions from individual survival ($s_{t(i)}$) and fecundity ($f_{t(i)}$), which facilitates identification of the fitness component under most intense selection. The Common Terns of the breeding colony ‘‘Banter See’’ are followed throughout life via an automatic detection system (Becker and Wendeln 1997), which enables investigation of temporal changes in phenotypic trait distribution at the individual level. The importance of arrival date, arrival mass, and laying date is assessed here. We address the following questions. Have changes in distributions of phenotypic traits occurred? If so, are these changes selective and driven predominantly via survival or fecundity? If not, what might be preventing expected selective changes? It is hypothesized that selection will promote earlier arrival and laying date and increased arrival mass.

7.3 METHODS

7.3.1 Study Population

All data were collected at the Banter See Common Tern colony (538300 N, 088060 E) within the harbor area of Wilhelmshaven on the German North Sea coast. This monospecific colony is the subject of a long-term population study (Becker et al. 2001). The colony site consists of six rectangular concrete islands of equal size. Each island is 0.9 m from the neighbouring one, measures 10.7 3 4.6 m, and is surrounded by a 60-cm wall. Walls are equipped with 44 elevated platforms for terns to land and rest on. Breeding habitat is considered to be homogeneous.

Common Terns overwinter in western Africa and migrate in early spring. Individuals have been ringed (banded) since 1980 in Wilhelmshaven and 1984 at the study site (ringing center ‘‘Vogelwarte Helgoland’’). All fledglings have been ringed and marked with transponders (TROVAN ID 100; TROVAN, Köln, Germany) since 1992. Antennae, which can read the 10-digit alphanumeric code of each individual at a distance <11 cm, are located on each elevated platform and temporarily around each incubated clutch during the breeding season. Of the 44 elevated resting platforms, 16 are additionally equipped with digital balances (Sartorius PT and BL series, Sartorius, Goettingen, Germany). Data are returned every five seconds throughout the breeding season. Fewer antennae and balances were available in the early years of the study, when rotation ensured complete colony coverage. Further details of this automatic detection system are presented in Becker and Wendeln (1997).

7.3.2 Data Collection, Definitions and Fitness Measures

Arrival date is defined as day of year (day 1 = 1 January) of first registration of an individual at the colony site. Arrival mass (grams) is defined as mean body mass from the first four days of colony attendance, which correlates strongly with arrival mass on arrival date (Spearman's rank correlation coefficient = 0.867) but reduces potential bias as more data points per individual exist and sample size is increased. The colony is checked for new clutches every 2–3 days throughout the breeding season; laying date (day of year) is defined as date of discovery of the first egg. Analysis is restricted to years since 1994, when the first native subadults returned to the colony.

Full details on the calculation of annual realized fitness ($p_{t(i)}$) are given in Coulson et al. (2006). Because $p_{t(i)}$ depends upon subadult return to the breeding site, we use phenotypic trait data from 1994 to 2004, with information on subadult return from 2006. Use of data between 1994 and 2003, because some subadults return for the first time at 3 years of age (Dittmann and Becker 2003), did not significantly alter the results. We calculate $S_{t(i)}$, the residual performance or contribution to $p_{t(i)}$ of survival, assuming that local return rate is local survival rate, which is likely to underestimate real survival due to emigration (Martin et al. 1995). Common Terns spend at least 18 months at wintering grounds after their initial migration; thus, $F_{t(i)}$, the contribution to $p_{t(i)}$ of fecundity, considers survival to first return. The formula is

$$p_{t(i)} = \frac{s_{t(i)} \quad \bar{s}_t}{N_t \quad 1} + \frac{f_{t(i)} \quad \bar{f}_t}{N_t \quad 1} = S_{t(i)} + F_{t(i)}$$

where $f_{t(i)}$ is fecundity of individual i at time t, $\bar{f}_t$ is the population average fecundity at time t, and N_t is the population size at time t; survival terms are defined similarly.

Of 101 adults caught and tagged during incubation between 1992 and 1995, 50 were of unknown age. Minimum age (3 years old at capture) was used instead of age for these 50 individuals only. Repeating analyses without this subset did not significantly alter the results. These criteria yielded 3445 arrival dates for 1014 individuals, 1967 arrival masses for 807 individuals, and 2230 laying dates for 660 individuals. 1130 data points with values for all three phenotypic traits existed for 514 individuals. The total number of marked individuals at the colony site has increased from 92 in 1994 to 514 in 2006; the number of breeding pairs (marked and unmarked) has increased from 90 to 470 over the same period.

7.3.3 Statistical Methods

To control for changes in phenotypic traits with age, generalized additive mixed-effect models (GAMMs) were fitted for arrival date, arrival mass, and laying date. Individual was fitted as a random effect and age as smooth function using default settings (Wood 2006). All years were pooled to enable investigation of temporal trends in phenotypic traits. Reproductive success was defined as residual fledgling production (the difference between the average fledgling rate of a given season and the number of fledglings per nest), and a GAMM was fitted as described. The residuals from each relevant model were defined as age-corrected phenotypic traits and were used for all further analyses. This two-step process ensured acceptable diagnostic plots (Wood 2006).

Temporal changes in age-corrected phenotypic trait distribution were assessed using generalized linear mixed-effect models (GLMMs) fitted using the Laplacian approximation to maximum likelihood with a quasi error distribution (to control for overdispersion), identity link function, and constant variance structure. Individual was fitted as a random effect and year as a fixed effect. Determinants of age-corrected arrival date and age-corrected arrival mass were not investigated because it is not the aim of this study to consider the impact of climatic variables, but rather conditions at the breeding site. Age-corrected laying date was regressed against age-corrected arrival date, age-corrected arrival mass, breeding experience (categorical), year (continuous, to control for temporal trend), and all two-way interactions. Terms were removed sequentially according to the Akaike's Information Criterion, AIC (Burnham and Anderson 1998), which provides a compromise between model deviance and the number of parameters used. If the AIC did not advocate further model simplification but $|t|<1$ for a fixed effect, then this fixed effect was also removed. Models within 4 AIC values, the lower bound of Burnham and Anderson's (1998) recommendation, are considered equivalent; among equivalent models, the one with the fewest parameters is preferred. No significant annual effects were detected by fitting year as a categorical variable in this analysis.

To compare effects with and without controlling for age, models of selection pressure are presented in both cases. GAMMs were used to calculate selection pressure by regressing the phenotypic trait as a smooth term against $p_{t(i)}$, $S_{t(i)}$, or $F_{t(i)}$ using a quasi-error distribution with individual as a random effect. This smooth term can be considered as analogous to the linear predictor in GLMMs (Wood 2006). To control for interactions between fixed effects and to enable model selection using AIC, selection gradients were also calculated using GLMMs by regressing phenotypic traits against $p_{t(i)}$, $S_{t(i)}$, or $F_{t(i)}$ using the Laplacian approximation, quasi error distribution and individual as a random effect. Year and stage (prospector (Dittmann and Becker 2003); recruit (Ludwigs and Becker 2002); and experienced breeder) were fitted as categorical fixed effects for analyses of age-corrected traits. Note that only recruit and experienced breeder were applicable for analyses on laying date. Stage was not fitted for analyses on uncorrected traits because the trait and stages covary positively. Model simplification was as we described previously. This permitted a comparison between GAMMs and GLMMs.

All analyses were conducted in the R environment version 2.3.1 (R Development Core Team 2007) using the mgcv (multiple generalized cross validation) package (version 1.3–1.18) to fit GAMMs and the Matrix package (version 0.995-16, function lmer) to fit GLMMs. P values are not presented for GLMMs because no ‘‘correct’’ denominator degrees of freedom exists (F tests are always approximations for these mixed models, Bates 2005). Coefficients are presented on the scale of the linear predictor (GLMMs) or smooth function (GAMMs).

7.4 RESULTS

7.4.1 Age-Related Changes in Phenotypic Trait Expression and Residual Fledgling Production

The relationship between age and phenotypic trait was significantly different from zero for all traits considered, where β are coefficients on the scale of the GAMM (for arrival date, β=-63.509, SE=9.869, df=2430, t=-6.435, P<0.001, Figure 7.1a; for arrival mass, β=7.801, SE=2.282, df=1159, t=3.419, P<0.001, Figure 7.1b; for laying date, β=-20.077, SE=6.224, df=1469, t=-3.226, P=0.0013, Figure 7.1c). Relationships had significant nonlinear components (for arrival date, estimated df=8.68, P<0.001, Fig. 1a; for arrival mass, estimated df=5.92, P<0.001, Figure 7.1b; for laying date, estimated df=8.34, P<0.001; Figure 7.1c). The adjusted r^2 of these GAMMs was 0.704 for arrival date, 0.059 for arrival mass, and 0.497 for laying date. The proportion of variance explained by individual was 0.721 for arrival date, 0.612 for arrival mass, and 0.488 for laying date.

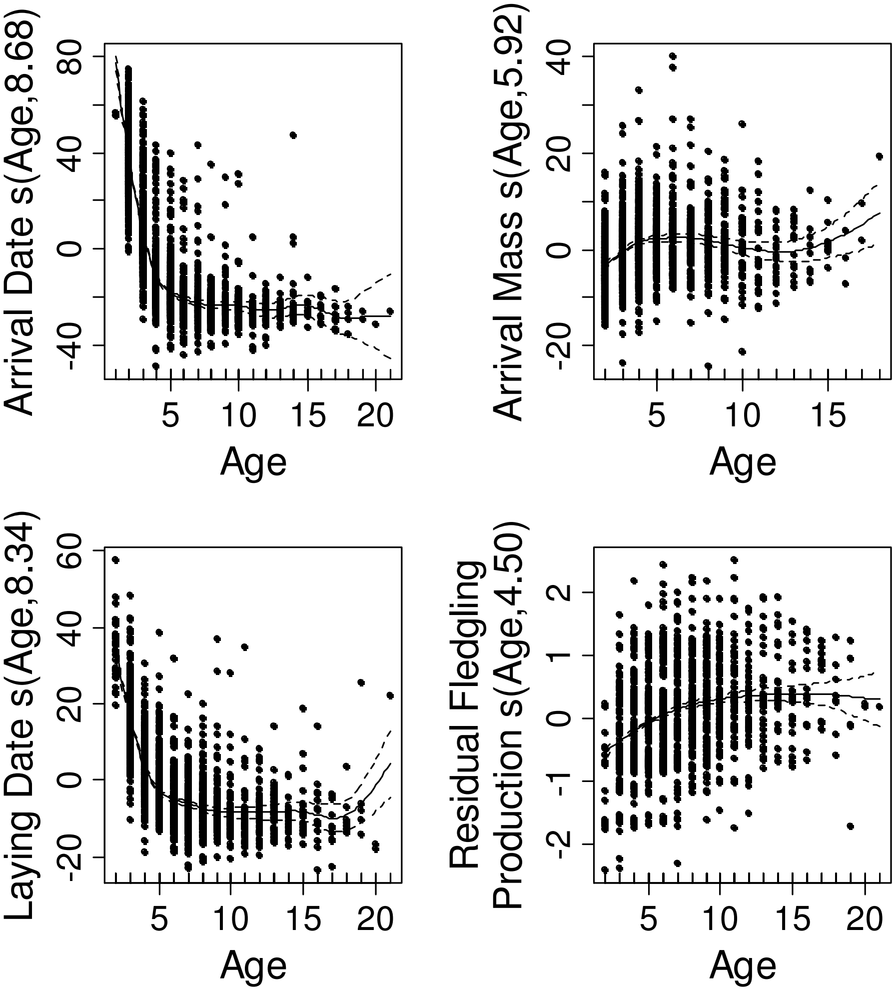

Figure 7.1. Changes in phenotypic trait expression with age for (a) arrival date, (b) arrival mass, (c) laying date, and (d) residual fledgling production (RFP, the difference between the average fledgling rate of a given season and the number of fledglings per nest). Values on the y-axis are residuals, the smooth-term coefficients (s) fitted from a generalized additive mixed model, scaled to have mean 0 across all years, where age is the smoothed explanatory variable. Numbers following age are estimated df. Dashed lines are 95% confidence intervals. For RFP, the residuals are from mean fledgling production in a given year.

Significant nonlinear age-related improvements in residual fledgling production were detected (β=0.246, SE=0.119, df=1569, t=2.060, P=0.0395; estimated df = 4.50, P , 0.001; Figure 7.1d). The adjusted r^2 was 0.114 and the proportion of variance explained by individual was 0.068.

7.4.2 Temporal Changes in Phenotypic Traits

Neither age-corrected arrival date (β=0.072, SE=0.077, t=0.940; Figure 7.2a) nor age-corrected arrival mass (β=-0.085, SE=0.060, t=-1.420; Figure 7.2b) changed significantly across the 13 years analyzed. Age-corrected laying date increased significantly (β=0.278, SE=0.063, t=4.389; Fig. 2c). In real terms, a Common Tern now lays its first egg between 3 and 4 days later than at the start of this study.

7.4.3 Determinants of Age-Corrected Laying Date (ACLD)

The minimum adequate model was:

$$ACLD_i=ACAD+ACAM+R+Y+C+\varepsilon_i$$

where C is the fixed-effect intercept (C=-731.415, SE=213.298, t=-3.429); ε_i is the random intercept. Age-corrected arrival date (ACAD) covaried positively with age-corrected laying date (ACAD=0.650, SE=0.032, t=20.371). Age-corrected arrival mass (ACAM) negatively affected age-corrected laying date (ACAM=-0.806, SE=0.031, t=-2.576). Age-corrected laying date increased across this study (year, Y=0.367, SE=0.107, t=3.446). Recruits laid later than experienced breeders (R=3.293, SE=0.519, t=6.340).

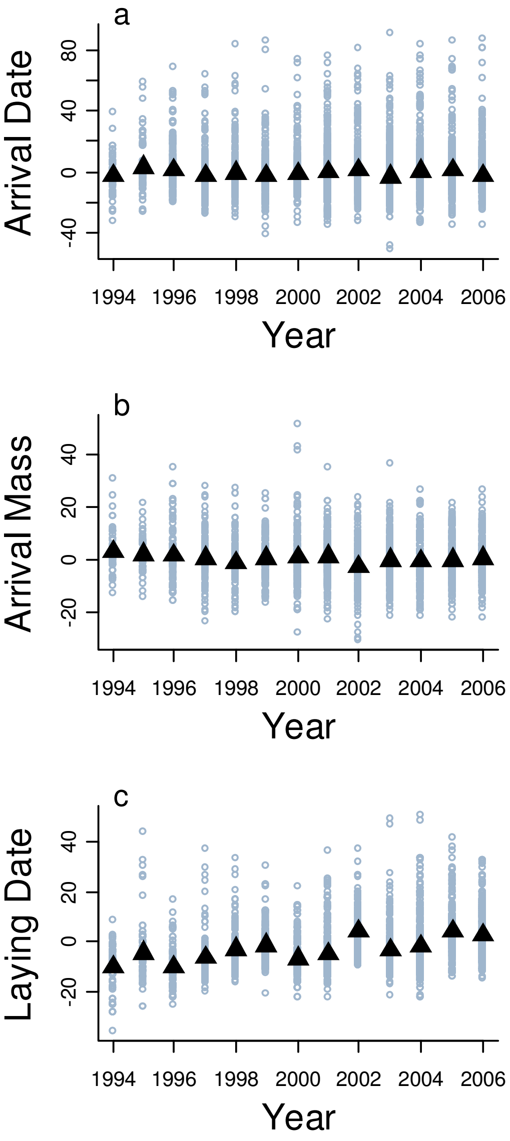

Figure 7.2. Temporal changes in age-corrected phenotypic traits from 1994 to 2006. Solid triangles show mean age-corrected phenotypic trait values. Values on the y-axis are residuals, scaled to have mean 0 across all years. The only significant relationship was for laying date (GLMM, b=0.278, SE=0.063, t=4.389).

Table 7.1. Selection gradients (β, with associated standard error in bracket) on annual realized fitness ($p_{t(i)}$), and the contributions of survival ($s_{t(i)}$) and fecundity ($f_{t(i)}$) to it. Values for age-corrected (AC) and uncorrected (UC) phenotypic traits calculated using Generalized Linear Mixed Models (GLMM) and Generalized Additive Mixed Models (GAMM) and associated t-values (t) are shown. β and s.e. have been transformed by 10^5. r^2 values are given where effects are significant (either non-linear or directional); r^2 is the adjusted r^2 from GAMMs or the proportion of variation explained by fixed effects for GLMMs.

			$p_{t(i)}$			$s_{t(i)}$			$f_{t(i)}$		
			β (s.e.)	t	r^2	β (s.e.)	t	r^2	β (s.e.)	t	r^2
Arrival Date	A	GLMM	-1.131 (0.154)	-7.17	0.015	-0.540 (0.114)	-4.76	0.007	-0.566 (0.105)	-5.37	0.008
	C	GAMM	3.112 (2.342)	1.33	0.026	-0.629 (0.184)	-3.42	0.000	0.945 (1.942)	0.49	0.022
	U	GLMM	-1.200 (0.082)	-14.6	0.059	-0.310 (0.062)	-5.01	0.007	-0.891 (0.055)	-16.1	0.069
	C	GAMM	-2.959 (0.727)	-4.07	0.059	1.197 (0.174)	6.89	0.000	-2.474 (0.809)	-3.06	0.073
Arrival Mass	A	GLMM	0.721 (0.381)	1.89		0.467 (0.272)	1.72		0.254 (0.291)	0.87	
	C	GAMM	0.505 (0.339)	1.49		0.435 (0.242)	1.80		0.117 (0.256)	0.46	
	U	GLMM	1.406 (0.367)	3.83	0.008	0.563 (0.263)	2.14	0.002	0.843 (0.282)	2.99	0.005
	C	GAMM	1.083 (0.337)	3.21	0.006	0.164 (0.241)	0.68		0.650 (0.255)	2.55	0.003
Laying Date	A	GLMM	-1.387 (0.354)	-3.88	0.007	-0.183 (0.236)	-0.78		-1.183 (0.283)	-4.18	0.008
	C	GAMM	-1.157 (0.348)	-3.32	0.006	0.347 (0.166)	-2.10	0.000	1.090 (0.279)	-3.88	0.000
	U	GLMM	-1.551 (0.281)	-6.25	0.017	-0.188 (0.167)	-1.13		-1.363 (0.199)	-6.85	0.021
	C	GAMM	-1.487 (0.775)	-1.92	0.017	1.161 (0.229)	5.07	0.000	-1.681 (0.761)	-2.21	0.022

7.4.4 Selection Gradients

Selection gradients are given in Table 4.1 and GAMMs for age-corrected and uncorrected phenotypic traits are given in Figure 7.3. If age was not corrected for, early arrival was selected for via annual realized fitness ($pt(i)$, Figure 7.3a) and the contribution of fecundity to $pt(i)$ ($Ft(i)$, Figure 7.3c), but later arrival was selected for via the contribution of survival to $p_{t(i)}$ ($S_{t(i)}$; Figure 7.3b). Similarly, early laying date was selected for via $p_{t(i)}$ (Figure 7.3g) and $F_{t(i)}$ (Figure 7.3i), but later laying date via $S_{t(i)}$ (Figure 7.3h). Heavier arrival mass was selected for via $p_{t(i)}$ (Figure 7.3d) and $F_{t(i)}$ (Figure 7.3f), but no significant gradient was detected via $S_{t(i)}$ (Figure 7.3e). GAMMs returned qualitatively similar results. If age was corrected for, GLMMs detected significant selection for early arrival via all three fitness measures; however, GAMMs found that the relationships between age-corrected arrival date and $p_{t(i)}$ and $F_{t(i)}$ were not significant (Figure 7.3a, c), but had significant nonlinear components (for $p_{t(i)}$, estimated df=5.12, $P<0.001$; Figure 7.3a; for $F_{t(i)}$, estimated df=5.71, $P<0.001$; Figure 7.3c). No significant selection gradient was detected on age-corrected arrival mass (Figures 10.3d–f). Earlier laying date was favoured by $p_{t(i)}$, $S_{t(i)}$, and $F_{t(i)}$ (Figures 10.3g–i). Excluding a slight nonlinear component on age-corrected laying date against $S_{t(i)}$ (Figure 7.3h), GAMMs and GLMMs were qualitatively consistent for arrival mass and laying date. In all age-corrected and uncorrected cases, the proportion of variation explained was low (Table 4.1); minimum adequate GLMMs acquired using AIC retained no explanatory variables in either the age-corrected or the uncorrected case.

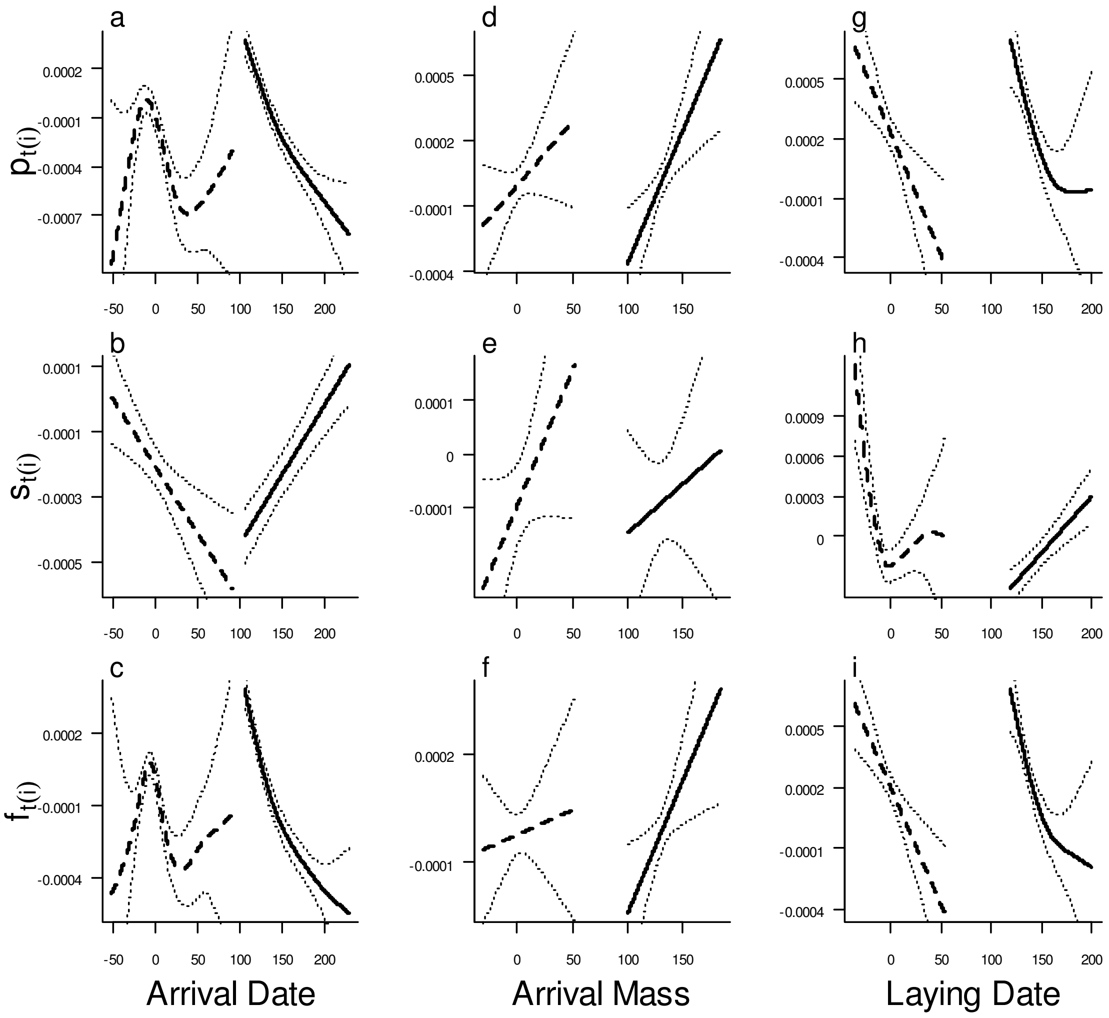

Figure 7.3. Generalized additive mixed-model selection gradients of arrival date (a–c), arrival mass (d–f), and laying date (g–i) against annual realized fitness ($p_{t(i)}$), and the contributions of survival ($S_{t(i)}$) and fecundity ($F_{t(i)}$) to it. For arrival and laying dates, day 1 is 1 January. Solid lines are uncorrected selection gradients, dashed lines are age-corrected; dotted lines are 95% confidence intervals. Note the different scales on the y-axes. Although some significant effects were detected, the minimum adequate model did not include the phenotypic trait in any case due to the large amount of unexplained variation (Table 4.1). As such, the precise shapes of these gradients have little value. All stages are pooled together in these figures.

7.5 DISCUSSION

This study investigated the effect of age on the estimation of selection in three Common Tern phenotypic traits. It was hypothesized that selection for earlier arrival date and laying date, as well as increased arrival mass, would be detected. Contrary to these hypotheses, minimum adequate models of selection pressure retained neither age-corrected nor uncorrected phenotypes, despite detection of significant effects due to low proportions of variation explained by the explanatory variables (Table 4.1). These phenotypes therefore had little biological relevance to annual realized fitness. Individual fitness was not associated with the phenotypic traits investigated, despite persistent individual differences. Short-term changes in phenotypic trait distributions were not driven by micro-evolutionary change. In spite of the lack of significant selection, age-corrected laying date increased significantly over the course of the study.

Natural selection acts on the distribution of phenotypes at any given point in time and can lead to rapid micro-evolutionary change (Hairston et al. 2005). Coulson et al. (2006b) developed a novel approach to estimate selection over short time periods and termed this quantity ‘‘individual contribution to population growth.’’ This quantity is the difference between observed population growth and population growth without the contribution of one individual. Population growth rate is dependent, in part, upon the age-structure of the population at a given point in time (Coulson et al. 2001), because individuals of different age have different phenotypes and fitness. Many phenotypes alter with age, including the three considered here (Figure 7.1). Had age not been corrected for, increased significance and proportion of explained variation between phenotypic trait values and fitness would have been reported in eight out

of nine comparisons (Figure 7.3, except 10.3e). In six of nine comparisons, the direction of selection would have been either opposite (Figures 10.3a–c, h) or significantly different from zero (Figure 7.3d, f). GAMMs and GLMMs produced similar results. The GAMM for selection on arrival date via pt(i) and Ft(i) found no significant directional selection, in contrast to the GLMM, but it did identify a nonlinear component (Table 4.1, Figure 7.3a, c). There is no guarantee that selection is strictly linear: GLMMs may overestimate selection in the earliest arrivals because the model is determined by the majority of data, whereas GAMMs are determined by the fitting methods and knot locations used (Wood 2006). Extreme values are therefore incorporated differently. These nonlinear gradients (Figure 7.3a, c) suggest that the precise arrival date is largely unimportant, provided that an individual does not arrive late, which facilitates mating between pair members (Gonzalez-Solis et al. 1999) or similar aged birds (Ludwigs and Becker 2005).

Persistent individual differences, defined as the proportion of variation explained by identity fitted as a random effect in GAMMs, were detected in all three phenotypes and are of biological relevance: a two-year old that arrives early and heavy relative to other two-year-olds, will arrive early and heavy relative to these individuals throughout its life. This consistency is one reason for the attractiveness of these phenotypes as quality measures (Sydeman and Eddy 1995, Arnold et al. 2004). However, reported relationships between laying date and fledgling production (deForest and Gaston 1996, Winkler et al. 2002, Arnold et al. 2004) may be biased if earlier breeders are older individuals, which, for the reasons outlined in the Introduction, have greater reproductive success (Curio 1983, Forslund and Pärt 1995). Young individuals, which lay later (Figure 7.1c), have more variable fledgling production (Ezard et al. 2006). Despite such persistent individual differences, the low proportion of variation explained by selection gradients suggests that these phenotypes are inadequate quality measures, they are not key fitness determinants, and any selection pressure that they are under is weak.

Given such negligible selection pressure, might the main target of selection be elsewhere? Although early conditions have lifetime fitness consequences (Cam et al. 2003, Ludwigs and Becker 2006), Common Terns are income breeders: energy for reproduction is dependent on acquired resources rather than on reserves. Birds in good condition can breed early and successfully (Wendeln 1997) and therewith generate apparent selection for early breeding (Price et al. 1988). Environmental covariance between phenotypes and fitness can also cause the strength of selection to be overestimated (Kruuk et al. 2003). For example, female Collared Flycatchers responded to warmer winters at the population level by laying more eggs earlier (Przybylo et al. 2000). Blue Tits responded to an experimental increase in food by laying and incubating earlier in the laying sequence (Nilsson and Svensson 1993). Wendeln and Becker (1999) found that breeding success was highly correlated with parental condition, defined as body mass between incubation and chick-rearing. Increased parental condition enables increased parental effort, which has been shown to be positively correlated with fledgling production (Wendeln and Becker 1999b, MacColl and Hatchwell 2003). The lack of significant selection on age-corrected arrival mass suggests that successful individuals improve their condition between arrival and hatching (Wendeln and Becker 1996). Is this period more influential in determining annual realized fitness for income breeders than the phenotypes analyzed?

Individual responses to environmental stochasticity may explain why so-called ‘‘good’’ phenotypes show inconsistent reproductive success: short-term, local conditions can impact clutch size significantly (Becker et al. 1985). Quality of food (Massias and Becker 1990, Wendeln et al. 1997) and meal frequency (Frank 1992, Lewis et al. 2006) are potential reasons for the observed change in age-corrected laying date: a reduced proportion of three-spined sticklebacks (*Gasterosteus aculeatus*) in the diet has been detected in recent years at the Banter See (P. H. Becker, unpublished data). The stickleback, and other fresh water prey, were pivotal in explaining why mainland breeding colonies around Wilhelmshaven commenced breeding some 14 days before the offshore Wadden See colony (Wendeln et al. 1997). Conditions during migration and at overwintering sites may also be critical (Norris et al. 2004): laying date is delayed in birds that arrive late or in poor condition. Without detailed data however, verification will prove difficult.

The amount of unexplained variation suggests that unreported measures are more influential and that any consequences of ‘‘optimal’’ phenotypic trait expression on individual fitness are indirect. The consequences of changes in phenotypic trait distributions on population processes (Hairston et al. 2005), and of population processes on phenotypic trait distributions (Saccheri and Hanski 2006), depend critically on the amount of variation explained by the relationship between phenotypic traits and fitness, not only on whether or not that relationship is significant. Although significant selection pressure was detected, the biological relevance of this pressure is low. The amount of unexplained variation restricts any consequences of arrival date, arrival mass, and laying date on population and evolutionary processes, especially in the short term. These results do, however, demonstrate the importance of correcting for age when identifying factors associated with changes in seabird phenology.

CHAPTER 8

DISCUSSION

8.1 THESIS OVERVIEW

The predominant theme of this thesis was how structure and stochasticity interact to affect population dynamics. Specifically, analyses addressed the following principal questions:

- Under what, if any, circumstances do less data-intensive deterministic methods provide an acceptable approximation of processes that operate in the real, i.e. stochastic, world?
- What insights are gained from more complex analysis that calculates descriptive quantities of population growth?
- Do individuals of similar state have similar performance?
- Under what circumstances do individual responses to unpredictable and predictable stochasticity alter individual performance, and consequently population growth?

In summary, the chief conclusions of the analyses were:

- In **chapter 2**, prospective and retrospective analyses were used to decompose the contribution of life-cycle components to mean and variance in population growth:
  - mean and variance of demographic rates influenced population dynamics in an inconstant manner across the life-cycle;
  - sex-differences were subtle but potentially important;
  - covariance between demographic rates explained high proportions of variation in population growth.
- In **chapter 3**, multiple perturbation measures assessed the consequences of mathematical scale on biological inference:
  - correlations between quantities with similar data requirements were frequently high, although the rank importance of demographic rates was not;
  - the incorporation of variation in demographic rates generated weaker correlations, especially when considering individual heterogeneity and a dynamic population structure.

- Analyses in **chapter 4** investigated how individual decisions following unpredictable predation led to population consequences:
  - predator attack covaried with increased rates of divorce and within-colony dispersal;
  - individuals, which dispersed within the colony, had reduced fledgling production in post-predation breeding seasons but those that divorced did not; this effect was as strong as typical determinants of individual quality.
- In **chapter 5**, a decomposition of long-run stochastic growth was compared to a decomposition of deterministic growth:
  - the results of both decompositions correlated strongly;
  - different aspects of long-run stochastic growth were not uniformly sensitive to the same demographic rates;
  - the association between demographic rates and long-run stochastic growth was inconstant between habitat states.
- These results were shown to be largely insensitive to changes in the number of habitat states, auto-correlation in the Markov chain and the explanatory power of the environmental driver on the population dynamics in **chapter 6**.
- The analyses in **chapter 7** investigated whether changes in distributions of arrival date, arrival mass and laying date were subject to selection and, if so, driven by differences in fecundity or survival:
  - in eight out of nine comparisons, the failure to correct for age generated deceptive estimates of selection;
  - in six out of nine comparisons, the direction of selection differed between age-corrected and uncorrected estimates;
  - individuals remained within the same part of the phenotype distribution throughout life;
  - age-corrected estimates of selection were weak and explained little variation in fitness, suggesting that these phenotypes were not under intense selection in this population.

8.2 PREVALENT THEMES, CAVEATS AND IMPLICATIONS FOR FUTURE WORK

The results of each set of analyses are discussed within each chapter; what follows here are general themes drawn across the thesis. Stochasticity has long been recognised by ecologists as playing an important role in population dynamics. Andrewartha and Birch (p. 26, 1954) partitioned the environment an animal is exposed to into four components: "(i) weather, (ii) food, (iii) other animals, and organisms causing disease, and (iv) a place to live". They noted that further subdivision may be required. The devil in demographic analysis appears to be in precisely such detail (Benton et al. 2006). The questions posed in this thesis aimed to assess how various aspects of an individual's environment influenced its performance and consequently population dynamics. Recent theoretical developments have provided a comprehensive suite of tools to probe aspects of the relationship between environment and population. This relationship has assumed increased importance as evidence mounts that demographic, ecological and evolutionary processes are linked (Hairston et al. 2005, Saccheri and Hanski 2006, Metcalf and Pavard 2007, Pelletier et al. 2007a) in an increasingly variable world (Boyce et al. 2006). Analyses focused on interactions between the first three components identified by Andrewartha and Birch (1954).

8.2.1 Consequences of Heterogeneity between Individuals

Individual heterogeneity was vast (chapter 7), although can be suppressed by group cohesion when large numbers of individuals respond in similar fashion to, for example, the threat of predation (chapter 4). One hypothesis for the negligible amount of explained variation in selection a gradient of arrival date, arrival mass and laying date is that these phenotypes are incorrect measures of individual quality, despite the high consistency of individual expression across breeding seasons (chapter 7). A more revealing quantity may be to consider changes in phenotype distribution within breeding seasons. Trajectories of condition may explain more variation in short-term realised fitness than a phenotypic trait measured at a given snapshot during an interval. Bighorn sheep (*Ovis canadensis*), which endured greater mass change between the start and end of a breeding season, produced more offspring in the subsequent season (Pelletier et al. 2007b). Short-term individual responses to the environment are likely to be critical in income breeders, such as common terns, and trajectories of condition over short time intervals might prove more successful in determining causes of individual heterogeneity.

The “biggest cause of heterogeneity between individuals occurs due to differences between them in their stage or age” (p. 1174, Benton et al. 2006). A failure to consider age can generate biased estimates of phenological change (chapter 7) and different age-classes made different contributions to mean population growth and variation around it (chapters 2 and 3). Environmental stochasticity experienced by the whole population impacts different age-classes in dissimilar ways (chapters 5 and 6). Inter-class differences due to population structure are vital aspects of population projection (Caswell 2001). When considered together, the results of chapters 2, 3, 5 and 6 suggest that a population’s ability to respond to environmental change depends in part upon its structure. This strengthens the argument for perturbation analysis to consider changes in population structure (Haridas and Tuljapurkar 2007), especially given the differential response of different age-classes to environmental stochasticity.

8.2.2 Consequences of Environmental Stochasticity

The high correlation between decompositions of deterministic and long-run stochastic growth (chapters 5 and 6) is arguably surprising given the large discrepancy between elasticities of mean population growth and elasticities of variation around it (chapters 2 and 3). Natural populations are subject to environmental stochasticity, which influences their dynamics in a complex fashion (Bjornstad and Grenfell 2001, Lande et al. 2003). Use of measures that assume a stable distribution of distributions (chapters 5 and 6) or based upon asymptotic assumptions (chapters 2 and 3) neglect this complexity. The decomposition of long-run stochastic growth, which assumes the former, ignores informative detail: habitat-stage elasticities showed marked variation in contributions to habitat-stage elasticity between habitat states (chapters 5 and 6). This implies that different stages of the life-cycle were differentially sensitive to environmental change. Analyses therefore should consider this non-uniform response.

A decomposition of long-run stochastic growth did not produce results and conclusions that were markedly different from those of a (much simpler) decomposition of deterministic (mean) growth. If this is the case in a system poorly described by the mean matrix and characterized by dramatic fluctuations in demographic rates in response to environmental stochasticity, then what use is it? Lande (2007) showed furthermore that, for a genotype or phenotype, long-run stochastic growth is not a valid measure of fitness in a fluctuating environment. In demographic and evolutionary applications, the answer is apparently “not much”. Changes in intensity of environmental variation can alter population fluctuations in cyclic populations (Reuman et al. 2006), which may weaken the predictive power of models that extrapolate from (relatively) short studies. There is no guarantee that data currently collected will simply be repeated for the next 100,000 years (e.g. Stige et al. 2007), as assumed by long-run stochastic growth.

Transient dynamics can differ markedly from long-term measures (Koons et al. 2005, Caswell 2007, Haridas and Tuljapurkar 2007, Townley et al. 2007). A novel approach might be to consider the variable world as sequentially connected transients. They can result from rapid and unpredictable environmental change, and have ecological and evolutionary consequences: evolutionary change in body and beak size in response to drought (Grant and Grant 2002) contributed more to population dynamics than ecological variables in Darwin’s finches (*Geospiza fortis* and *Geospiza scandens*, Hairston et al. 2005). Given the existence of environmental dependence of measures proportional to selection gradients (chapters 5 and 6) in addition to recent work emphasizing how selective pressures can influence population dynamics, and vice versa (Hairston et al. 2005, Saccheri and Hanski 2006), it seems necessary to incorporate interdependence between demographic and evolutionary processes in predictions of population abundance. The distribution of body size explained up to a fifth of variation in population growth of the Soay sheep population (Pelletier et al. 2007a), an amount which varied dramatically with environmental stochasticity.

8.3 CONCLUSIONS

The population is a fundamental force in ecology and evolution. This work adds weight to the argument that characteristics of individual performance in response to environmental variability are pivotal to increasing understanding of changes in population abundance. Demographic models based on long-term measures of population growth neglect the marked effects of short-term environmental stochasticity: long-run stochastic growth appears no different in its predictive power of population dynamics than analysis of the mean matrix for vertebrate populations. Individuals of different age have different characteristics and performance: if age is not incorporated, erroneous predictions of selective pressure and phonological change result. A failure to incorporate either structure or stochasticity neglects crucial aspects in population regulation, and therefore ecological and evolutionary change.

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APPENDIX 1

THE ACCURACY OF THE BANTER SEE AUTOMATIC REMOTE DETECTION SYSTEM

A1.1 INTRODUCTION

Linear mixed-effect modelling (Diggle et al. 2002) and capture-mark-recapture (Lebreton et al. 1992) are examples of methods that are recommended without consideration of analysis carried out as well as the repeatability and quality of data collected. Use of "black box" technologies can however generate bias: the fewer parameters that are estimated, the fewer parameters can be incorrectly estimated. For results to remain acceptable, it is crucial to note, any decision not to employ powerful analytical tools needs to be justified adequately.

The Banter See remote, automatic detection system minimizes anthropogenic interference in the breeding colony of common terns (*Sterna hirundo*). The system generates a vast amount of data. In 2003, for example, a total of 4,737,352 individual identification codes from 653 marked individuals were registered, of which 324 were identified as breeders. The number of registrations per individual was very high, with a median of 2,365 and range from 1 to 193,778. Two-year old subadults, i.e. prospectors (Dittmann and Becker 2003), were registered on average 2020 times with median registration frequency of 228 and 12 birds registered on fewer than 5 occasions. Breeders were registered more often: median registration frequency was 2886 for 324 individuals, all of which were registered on more than 5 occasions. Before egg-laying, breeders were recorded, on average, at more than 12 different resting platforms (Ludwig and Becker 2006). Two-year old subadults were recorded frequented, on average, 24 platforms. Emigration (adults <1%, subadults < 3%, Becker, unpubl. data) and transponder loss or failure (2.2%, 20 of 927) rates were low based on data until the 2003 cohort to account for returning individuals at ages older than 2. The high redundancy of multiple readings per individual is the basis of the reliability of the transponder system, but is it sufficiently accurate given the theoretical developments now readily available and implementable?

This appendix examines the accuracy of the Banter See remote, automatic detection system with regard to the oft-used capture-mark-recapture framework (CMR, Lebreton et al. 1992). It shows that recapture rates using the system are high and that survival estimates of adult birds do not differ significantly from 95% confidence intervals estimated using a capture-mark-recapture framework.

A1.2 METHODS

A1.2.1 Study Population

All data were collected at the Banter See common tern colony (53°27'N, 08°07'E) within the harbour area of Wilhelmshaven on the German North Sea coast. This mono-specific colony is the subject of a long-term population study (Becker et al. 2001). The colony site consists of six rectangular concrete islands of equal size. Each island is 0.9m from the neighbouring one, measures 10.7*4.6 metres, is surrounded by a 60cm wall. Walls are equipped with 44 elevated platforms for terns to land and rest on. Breeding territories are considered to be homogeneous.


Figure 1. Island E of the Banter See colony with an antenna on one of the 44 elevated platforms (background) and a "nest antenna" temporarily placed around nest 581 (as indicated by the marker next to the nest in the foreground). The occupants of nest 581 in 2005, when the photograph (Thomas Ezard) was taken, were an individual of unknown origin and Deliah (ID code: 6043568).

Common Terns have been ringed since 1980 in Wilhelmshaven and 1984 at the study site (ringing centre "Vogelwarte Helgoland"). All fledglings have been ringed and marked with transponders (TROVAN ID 100, TROVAN, Cologne, Germany) since 1992; 101 breeders were caught whilst incubating and tagged between 1992 and 1995. Each elevated platform has an antenna, which can read the 10 digit alphanumeric code of each individual at a distance not greater than 11cm. Only individuals with know years if birth were included in the analysis. Full methodological of the antennae system are available in Becker and Wendeln (1997).

A1.2.2 Capture-Mark-Recapture (CMR) Analysis

The model structure was based upon a Cormack-Jolly-Seber model (Φ_t; p_t), where both survival (Φ) and recapture (p) are time-dependent due to environmental stochasticity (Lebreton et al. 1992) and the inconstant number of antennae at the colony site due to the temporal availability of finance. Only live recaptures were considered. As common terns spend variable amounts of time before return to their natal colony site (Dittmann and Becker 2003), the hypothesis of age-dependent recapture was also tested. Program MARK (http://www.warnercnr.colostate.edu/~gwhite/mark/mark.htm, White and Burnham 1999) was used for analysis.

All models were constructed using parameter index matrices. Various model structures were tested to obtain the minimum adequate model, which was selected according to the Akaike's information criterion (AIC), which provides a compromise between explained deviance and number of parameters (Burnham and Anderson 2002). Models within 4 AIC values – the lower bound of Burnham and Anderson's (2002) recommendation – are considered equivalent; among equivalent models, the one with fewest parameters is preferred as the minimum adequate. If the number of the parameters was identical, the minimum adequate model had the lowest AIC.

All birds with known birth year were used. The first capture occasion was when the transponder was injected and subsequent recaptures at annual intervals. Capture-recapture histories were available for 2652 individuals, of which 1938 were only captured once. As the earliest bird of known age was born in 1980, this is the first year of capture; 1981 to 2006 were the years of potential recapture for this individual, although note that the automatic system was only operational from 1993. The oldest recorded individual reached 21 years of age. As such, the maximum number of age-classes is 21 and maximum number of recapture occasions 25.

A1.3 RESULTS AND CONCLUSION

Model	**AICc**	**ΔAICc**	**Num. Par**	**Deviance**
$\Phi_{2-21}p_{93,96,98,02}$	3512.7	0	21	991.2
$\Phi_{2,3,(4,5),>6}\ p_{93,(9698),02}$	**3514.6**	**1.9**	**8**	**1019.3**
$\Phi_{2,3,4,5,>6}\ p_{93,96,98,02}$	3516.3	3.6	10	1017.0
$\Phi_{2,3,>4}\ p_{93,96,98,02}$	3517.9	5.2	7	1024.7
$\Phi_{2-14,>14}\ p_{93,96,98,02}$	3521.8	9.1	14	1014.4
$\Phi_{age}\ p_{time}$	3536.4	23.7	30	996.6
$\Phi_{2,3,>4},\ p_{93,(9698),02}$	3539.0	26.3	6	1047.8
$\Phi_{2,3,>4}\ p_{annual}$	3540.5	27.8	17	1027.1
$\Phi_{2,3,4,5,6,>6}\ p_{93,02}$	3608.0	95.3	10	1108.8
$\Phi_{age}\ p_{93}$	3608.3	95.6	19	1090.8
$\Phi_{2,3,4,5,>6}\ p_{92}$	3608.4	95.7	7	1115.1
$\Phi_{2,>2}\ p_{92}$	3612.8	100.1	3	1127.6
Constant	3612.8	100.1	3	1127.6

Table 1. The minimum adequate and other principal models as used to estimate capture-mark-recapture estimates for the Banter See common tern population. There were a maximum of 21 age-classes and 25 recapture occasions (the first bird was ringed in 1980) for data through to birds that returned in 2006. A total of 2652 capture histories were used, of which 1938 were captured only as fledglings. Φ relates to survival age-classes, with 2-14 indicating each year from 2 to 14 inclusive considered individually, p to recapture year-classes. Values split by commas are distinct; those within brackets are grouped together. > implies all classes above this point for Φ. Values for p are the lower bound of the year grouping (excluding the class 1980-1992, which has a recapture rate of essentially 0 for all models) and runs until either the year before the lower bound of the next class or 2006 as appropriate.

Table 1 shows the AIC values of the minimum adequate and other principal models; a full model (one parameter for each year and age combination) was not fitted as there is little way of justifying and identifying all parameters (White and Burnham 1999). The model that minimized the residual deviance featured 21 age-classes, but sample size for individuals older than 14 years is very small. When these classes were pooled together to attempt to reduce the bias caused by these sample sizes, the AIC of the model increased.

Parameter	Estimate	S.E.	95% CI	Observed
$\Phi_{0-1,1-2}$	0.743	0.011	(0.721,0.764)	
Φ_{2-3}	0.931	0.013	(0.901,0.952)	0.832
Φ_{3-4}	0.883	0.018	(0.843,0.913)	0.831
Φ_{4-6}	0.937	0.015	(0.903,0.964)	0.867
$\Phi_{>6}$	0.880	0.014	(0.851,0.904)	0.852
$P_{<1993}$	0	0	(0,0)	
$P_{96-97,98-01}$	0.873	0.013	(0.844,0.896)	
$P_{>02}$	0.953	0.007	(0.937,0.966)	

Table 2. Capture-mark-recapture (CMR) estimates, associated 95% confidence intervals and recorded estimates at the Banter See for the age-classes of the minimum adequate model (see Table 1). Some cells are shaded as these are not estimable using the automatic detection system. Recorded values that are outwith the confidence intervals of the CMR estimates are shown in **bold**. Since individuals do not return to the breeding colony for at least 18 months after fledging, there is no way of comparing the CMR estimate at this stage. SE refers to standard error of the estimate and CI confidence interval.

The minimum adequate model retained 6 age-classes for survival and 4 age-classes for recapture. Recapture rates increased with increasing antennae number: since 1996 recapture rates have been at least 87% according to a model that groups 1996-1997 with 1998-2001 as advocated by the minimum adequate model (Figure 1; Table 2). Survival estimates based on observations from the colony site were within 95% confidence intervals of capture-mark-recapture estimates for individuals of at least 5 years of age (Figure 1; Table 2).

Mean survival rates of individuals at the Banter See were within the 95% confidence intervals from capture-mark-recapture estimates from age 5 (Figure 2), although the model that splits recapture rates into four year-classes (since 1992) for individuals older than 3 finds no significant differences between observed survival and CMR estimated survival (Table 2). A hypothesis for the under-estimate of the observed Banter See survival for young age-classes is that local survival likely under-estimates actual survival (Martin et al. 1995). It should be noted however that not all individuals return to the colony site until they are at least two years of age (Becker et al. 2001). If modelling uses return and recruitment rates rather than survival at young ages (Ezard et al. 2006), then the bias observed in younger age-classes is at worst minimised and at best nullified.

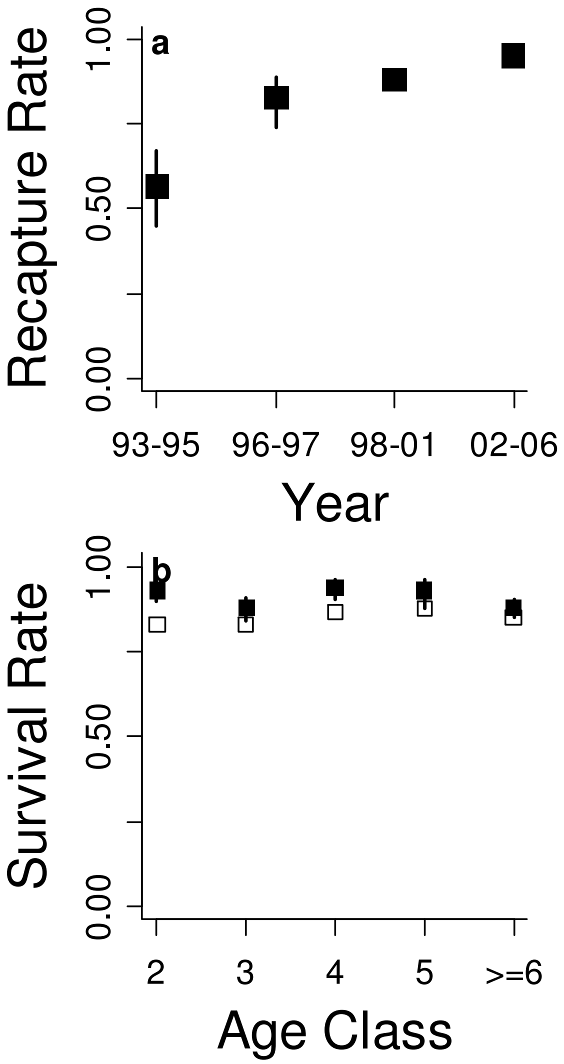


Figure 2. (a) recapture rates with associated 95% confidence intervals and (b) survival estimates from a capture-mark-recapture framework with associated 95% confidence intervals (solid symbols and lines) and recorded estimates (open symbols) at the Banter See. For clarity, the groupings used in the minimum adequate model (see Table 1) have been left distinct in this figure. Age-classes are given in Table 2.

The assumption that analyses are not overtly biased by the failure to use capture-mark-recapture estimates appears to be valid. Data over future seasons may further reconcile differences between CMR estimates and rates calculated using the automatic, remote detection system.

APPENDIX 2

FURTHER DETAILS ON THE POPULATION MODEL AND MARKOV CHAIN

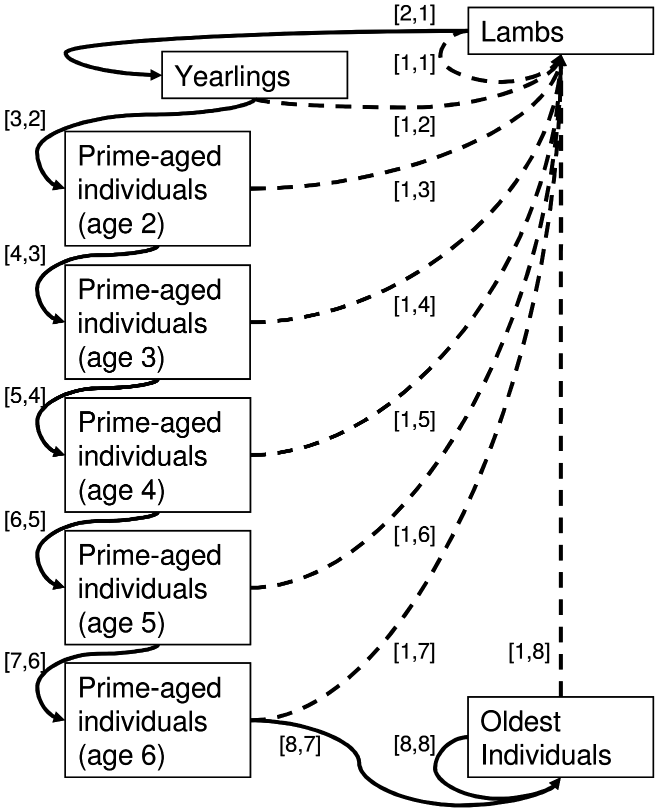
Further detail on how the transition matrices **A**(t) and habitat transition matrix **H** were constructed. Details relate specifically to chapter 5, but are also relevant for the analyses in chapter 6.

A2.1 MATRIX PROJECTION MODEL

Four age-classes have been identified as the most parsimonious age-structure for female Soay sheep (Catchpole *et al.* 2000): lambs (*L*), yearlings (*Y*), prime-aged (*P*, 2-6 years old) and older (*O*, >6 years old). A post-breeding Leslie matrix model (Caswell 2001) **A** was constructed with 8 age-classes where sub-diagonal elements are survival rates (*s*, August to August) and top row elements are fecundity rates (*f*, lambs, which survive to the August in year t+1, born from individuals that survive from August in year t until the birth pulse in year t+1):

$$\mathbf{A} = \begin{vmatrix} fL & fY & fP & fP & fP & fP & fP & fO \\ sL & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP & sO \end{vmatrix}$$

The corresponding life-cycle graph (with matrix elements given as [row, column] next to each age-age transition) is overleaf (Figure A2.1):



A2.2 ENVIRONMENTAL STOCHASTICITY

Tree regression generates discrete classes of the three explanatory variables (Venables and Ripley 1999). In an additive model containing sward height, NAO and adult: lamb ratio, NAO was consistently subdominant except for a small change in *fP*, which has previously been shown to be invariant to environmental change (Coulson *et al.* 2001). Results indicated that sward height should be split at approximately 3.5 (range: 2.02 to 5.24) and that adult: lamb ratio should be split at approximately 3 (range 1.52 to 3.32). Two classes were adopted for sward height and adult: lamb ratio, thus producing four habitat states when combined. No years were classified as low sward and low adult: lamb ratio, which left three habitat states (Fig. 2a) to construct the Markov Chain. The habitat transition matrix **H** was therefore of size 3*3:

$$\mathbf{H} = \begin{vmatrix} 0.2 & 0 & 0.75 \\ 0.4 & 0 & 0.25 \\ 0.4 & 1 & 0 \end{vmatrix}$$

For example, five years were in habitat state 1 (denoted by squares in Fig. 1). The subsequent habitat state is 1 in 1992, 2 in 1994, 3 in 1998, 2 in 2003 and 3 in 2004. The state at time t is the column number and the state at time t+1 is the row number. For example, the transition probability from state one to state two is 0.4 (cell [1,2] in **H**).

The auto-correlation in the Markov chain can be determined from its subdominant eigenvalue (Tuljapurkar 1990), which can explain potentially as much variation as differences between the states themselves (Tuljapurkar and Haridas 2006). In this instance, auto-correlation was relatively low (-0.4 + 0.3i, absolute value 0.5), certainly more so than in Tuljapurkar et al.'s (2003) and Tuljapurkar & Haridas' (2006) example, where in the least correlated state it is >0.9.

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Population sex ratio shift from fledging to recruitment: consequences for demography in a philopatric seabird

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In many dimorphic bird species, offspring sex ratio is skewed towards the production of the smaller sex. Offspring sex ratio can be biased in monomorphic birds however, and the demographic consequences of such bias are unknown. Sex-specific mortality and dispersal are fundamental mechanisms of sex ratio adjustment at the population level, but evidence for adjustments is weak and feedback into population dynamics poorly understood. Here, we link sex ratio at fledging with sex-specific subadult return and recruitment at the Banter See common tern *Sterna hirundo* colony. Using molecular sexing methods and a remote detection system, we permanently tracked individuals from four complete cohorts ($n = 1171$ fledglings) across these life-history stages at their natal colony site, which permitted a structured analysis of sex ratio across multiple seasons. Sex ratio shifted significantly from significant daughter dominance at fledging to higher proportions of natal males among recruits; return and recruitment rates of sons were significantly higher than daughters ($p \leq 0.002$). No significant between-year differences were detected. 47.4% of natal male recruits were paired with a non-natal female, but only 37.0% of natal female recruits had a non-natal partner. Elasticity analysis suggested that natal males have a greater influence on natal population growth rate than natal females. Sex biased dispersal is the most probable reason for these results indicating higher emigration to and immigration from other colonies in females, the less territorial and less philopatric sex. This pattern may be related to different gender roles in parental duties and with respect to competition for local resources.

Selection should maintain sex allocation at equality by favoring shifts in the opposite direction to any population bias (Fisher 1930). However despite the recent increase in knowledge on this topic (Clutton-Brock et al. 2002), the evidence of adaptive sex ratio adjustment in response to operational adult sex ratio in a population is weak and any feedback into population dynamics remains poorly understood (Cockburn et al. 2002, Le Galliard et al. 2005, Durell 2006). Besides sex-specific mortality the fundamental mechanism of sex ratio adjustment at the population level is sex-specific dispersal, which measures the rate of change in the location of individuals relative to their location at birth (Boyd 2002).

Dispersal is a key component of population dynamics and life history in vertebrates (Greenwood 1980, Efford 1998, Smith and Green 2006) and responds adaptively to a wide range of social and demographic cues (Le Galliard et al. 2005, 2006). Sex-biased dispersal is common among animals across diverse taxa. In mammals, male biased dispersal is typical (Clark 1978, Dobson 1982, see also Efford 1998 for the brush tail possum *Trichosurus vulpecula*), whereas in the majority of bird species, natal dispersal (defined as dispersal between the sites of birth and first breeding) is skewed towards females and males show higher natal philopatry (reviewed by Greenwood 1980, Clarke et al. 1997, Newton 2003). Seabirds provide large amounts of evidence for this pattern: Manx shearwater *Puffinus puffinus* (Brooke 1978), short-tailed shearwater *P. tenuirostris* (Bradley and Wooller 1991), Cory's shearwater *Calonectris diomedea* (Rabouam et al. 1998), kittiwake *Rissa tridactyla* (Coulson and Nève de Mévergnies 1992), western gull *Larus occidentalis* (Spear et al. 1998). On the other hand, male-biased dispersal was detected in brown jays *Cyanocorax morio* (Williams and Rabenold 2005) and no sex bias was found in the dispersal of greater flamingos *Phoenicopterus ruber roseus* (Barbraud et al. 2003). Estimating dispersal is difficult, and especially so in birds, because of their high mobility. Capture-recapture data is often used (Lebreton et al. 2003, Cam et al. 2004), although sex-specific information is frequently lacking (but see Nichols et al. 2004).

Offspring sex ratio and dispersal are argued to be mutually dependent, so that sex ratio has been proposed to be biased in favor of the dispersing sex (Efford 1998, Dale 2001, Le Galliard et al. 2005). Furthermore, offspring sex ratio is skewed towards the production of the smaller sex in many dimorphic species (Kalmbach et al. 2001, Benito and González-Solís 2007). Offspring sex ratio can however be female biased even in birds with negligible sexual size dimorphism such as starlings *Sturnus vulgaris* (Bradbury et al. 1997) or terns *Sterna* sp. (Fletcher and Hamer 2004, González-Solís et al. 2005). The reasons of primary (at hatching) and secondary (at fledging) sex ratio bias, as defined by Mayr (1939), are often studied and discussed (reviewed by Dhondt and Hochachka 2001, Cockburn et al. 2002), but rarely investigated for the whole population across several years. Exceptions are recent studies of Weimerskirch et al. (2005) on wandering albatrosses *Diomedea exulans* and of Durell (2006) on Eurasian oystercatchers *Haematopus ostralegus*. In these studies, male biased primary and secondary sex ratio was nullified by a higher mortality of subadult males, which balanced the sex ratio at recruitment. To our knowledge nothing is known about gender differences in dispersal of terns (Clarke et al. 1997).

In this investigation, we were able to link secondary offspring sex ratio with sex-specific natal return and recruitment (first breeding attempt) of an entire seabird colony over multiple years. We studied a colony of common terns *Sterna hirundo*, a small philopatric monogamous seabird and long-distance migrant (Becker and Ludwigs 2004). Common terns show limited sexual size dimorphism: adult males are about 1 to 6% larger than females in bill and head measurements and are also slightly heavier (Becker and Ludwigs 2004). Sons fledge 3% heavier than daughters (Becker and Wink 2003). We used molecular methods to sex four complete cohorts from the colony "Banter See" and tracked their individual history at the natal colony site by remote, automatic detection of their return and recruitment. This approach permitted a structured analysis of sex ratio across multiple seasons, which is necessary to obtain an understanding of the demographic consequences of sex ratio changes at different life-history stages (Cockburn et al. 2002).

In this paper, we investigated variation in the sex ratio of four cohorts along the transition from fledging to recruitment and focused on the following questions: (1) is daughter dominance at fledging (González-Solís et al. 2005) consistent across years? (2) Does sex ratio change with transition to recruitment? (3) Do return and recruitment rates differ between male and female fledglings? (4) If sex ratio is unbalanced in recruitment rates to the natal colony, gender-specific frequency of pairings with natal individuals should be expected, and the sexes should contribute differently to growth rate of the natal population.

Methods

Study site and definitions

The Banter See common tern colony is the subject of a long-term individual-based population study (Becker et al. 2001) and increased, on average, by 15% per year from 1992 to 2006. Since 1998, the colony size increased from 250 to 470 pairs and all fledglings have been sexed using body feathers and standard PCR methods (Becker and Wink 2003). Chicks were marked with metal rings (ringing centre "Helgoland") and passive transponders (ID 100, TROVAN, 2 × 11 mm), providing a permanent form of individual identification at their natal colony (for details see Becker and Wendeln 1997). The fledglings leave the site on average when 26 days old (Becker and Wink 2003). The fate of all chicks is known by checks performed throughout the breeding season until the last fledgling had left the colony (Middleton and Prigoda 2001). Of the common terns, 99% return to their natal colony for the first time when aged 2 or 3 to prospect the colony (Dittmann and Becker 2003) before recruiting when 3 or 4 (mean recruitment age of males 3.6 years, females 3.2 years). Only 11% of individuals recruit when ≥ 5 years old (Ludwigs and Becker 2002).

During each season, all marked individuals present at the colony site were recorded remotely and automatically by an antenna system installed at 44 resting platforms around the colony site and during incubation by portable nest antennae (Becker and Wendeln 1997, Becker et al. 2001, Dittmann and Becker 2003). Antennae at resting platforms have been inconstant in number, increasing over the course of the study (from 12 in 1993 to over 30 in 1998 and 44 since 2002).

The transponder-based detection system is very effective. In 2003 for example, a total of 4 737 352 individual codes from 653 marked common terns were registered. Of these 653 324 were identified as breeders at the nest. The number of registrations per individual is very high (median = 2365; range 1–193 778). Two-year old subadults (prospectors) were registered on average 2020 times (median of 228 individuals, 12 birds were registered <5 times), but breeders were registered more often (median = 2886, 324 individuals, all registered more than 5 times). Before egg-laying, breeders were recorded, on average, at more than 12 different resting platforms (Ludwig and Becker 2006). Two-year old subadults were recorded, on average, at 24 platforms. Among 53 birds which returned to the colony at age two and recruited at age four, 98% were also registered in their second year of prospecting when they were three years old (Ludwigs and Becker 2002). Emigration rates to adjacent colony sites were low (adults $<1\%$, subadults $<3\%$, unpubl. data), as were transponder loss or failure-rates (2.2%, 20 of 927 returned subadults from the cohorts 1995-2003). The high redundancy of readings per individual is the basis of the reliability of the transponder system. A capture-mark-recapture analysis (White and Burnham 1999) estimated a recapture probability of 0.881 (95% CI 0.851, 0.906) between 1998 and 2001 and 0.953 (0.937, 0.966) since 2002 (Ezard and Becker unpubl.). Survival estimates from marked individuals of 5 years and older at the Banter See were not beyond 95% confidence intervals of capture-mark-recapture survival estimates (Ezard and Becker unpubl.). As such, population modeling (see below) is performed without use of mark-recapture techniques.

The methods enable the analysis of exact sex-specific return rates of the investigated cohorts at the individual level, as well as of sex ratios at the following life-history stages: fledglings, subadults and recruits. "Subadult" is here defined as a pre-breeding individual that has returned to its natal colony site, i.e. a prospecting bird in the year(s) before recruitment. We used the cohorts 1998–2001 for the evaluation of return and recruitment rates (n = 1171 fledglings), and registration data from 2000 until 2006. Ring recoveries reported between 1992 and 2007 from birds emigrating from "Banter See" and recorded as breeders or during the breeding season at colony sites >25 km distant, or immigrating to "Banter See" and hatched at colony sites >25 km away are presented as supplementary information. In order to analyse pairings of natal recruits, we looked at the pairing patterns of all recruits, which started to breed between 1998 and 2006 (n = 520). All recruit-pairs were grouped into two categories under consideration of sex: pairs consisting of a recruit paired with a natal mate, and pairs consisting of a recruit and a non-transponder marked bird, which was assumed to be an immigrant.

Population modeling

To obtain estimates of sex-specific contributions to asymptotic population growth rate, a perturbation analysis was conducted on a two-sex post-breeding Leslie transition matrix (Caswell 2001). If vital rates differ between the sexes and if both parents are responsible for the rearing of offspring, models based on only one of the sexes may produce biased results and two-sex models are required (p. 570, Caswell 2001). Some simplifying assumptions were made. Although subadults can return at different ages and prospect for multiple years, in the model subadults prospect the colony for one year and recruit the season after as the majority does (Ludwigs and Becker 2002, Dittmann and Becker 2003). Although different age-classes contribute differently to population growth rate and its variation (Ezard et al. 2006), all experienced breeders are here considered to be of uniform quality. Where one member of a breeding pair was unknown, it was assumed the unknown partner was of the opposite sex. An additional individual was then added to the number of the opposite sex in a particular year for calculation of sex-specific fledgling rate only. Each bird in a pair was assumed to be responsible for half of each fledged chick so that the pair is dually responsible for their offspring. This ensured all fledglings appeared only once in the analysis and that all breeding pairs consist of a male and female bird. However, that local return rate is assumed to be local survival rate makes it likely to underestimate true survival due to emigration (Martin et al. 1995).

According to these assumptions, the two-sex matrix based on mean demographic rates is:

$$\mathbf{A} = \begin{array}{c} \begin{array}{cc} \text{------- Male -------} & \text{------- Female -------} \end{array} \\ \begin{bmatrix} 0 & 0 & 0.125 & 0.327 & 0 & 0 & 0.108 & 0.352 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.492 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.740 & 0.908 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.069 & 0.447 & 0 & 0 & 0.069 & 0.379 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.383 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.668 & 0.903 \end{bmatrix} \end{array}$$

Figure 1 shows the associated life-cycle graph and gives codes for each matrix element. Local subadult survival and recruitment rates across the four cohorts were taken from Table 2; fledgling rates and adult survival were estimated from all marked individuals in the population in the years when each cohort recruited. As an illustration, consider an individual born in 1998. It returned, according to the model, in 2000, recruited in 2001, was an experienced breeder in 2002 and remained in this class until its death. Adult survival and fledgling rates for the 1998 cohort is therefore based on all marked individuals in 2002.

A was used to calculate elasticities of asymptotic population growth rate (λ) for each demographic rate independently. Elasticities of mean population growth $\partial \ln\lambda / \partial \ln a_{ij}$ are the proportional change in λ resulting from a proportional change in a demographic rate (Caswell 2001). Cells [2, 1] and [6, 5] contain 1 as subadult return rate ([3, 2] and [7, 6] respectively) comprises survival over the first two years of life (common terns do not return to their colony site after fledging during their first year of life). Average fledgling rate per experienced pair is the sum of cells [1, 4], [1, 8], [5, 4] and [5, 8]. The elasticities of these cell groups were summed to obtain a single elasticity per demographic rate (Caswell 2001). All matrix calculations were performed using R ver. 2.3.1 (R Development Core Team).

Statistics

Binomial tests were used to test the sex ratio, chi^2 statistics for annual variation, sex-specific pairing patterns, return- and recruitment rates. All tests were performed with SPSS 11.0, are two-tailed and the level of significance is $p \leq 0.05$ and of marginal significance if >0.05 but <0.1. A binomial GLM was also fitted with males coded as 'successes' and females as 'failures' to analyze changes in their proportion at the Banter See. This proportion was regressed against year, life-history stage and their interaction. Year was fitted as a categorical and life-history stage as a categorical and continuous explanatory variables in different models. If categories were not significantly different from each other, they were collapsed into fewer groups (p. 534 in Crawley 2002). The minimum adequate model was obtained in a reverse stepwise procedure (p. 530 in Crawley 2002) using the Akaike's information criterion, which provides a compromise between explained deviance and number of parameters (Burnham and Anderson 1998). As controlling for overdispersion did not significantly change any conclusions, results are presented with the deviance parameter set to 1 and the complementary log-log link function was used as this minimized deviance (p. 564 in Crawley 2002).

Results

Sex ratio shift

Daughters dominated the four cohorts of fledglings which successfully left the colony site (Table 1, significant in 1999 and in total; on average 8.8% more daughters than sons fledged). This female dominance ceased when individuals returned (49% females on average): in three of four cohorts a higher proportion of males was detected (ns, Table 1). The recruits of all cohorts were predominantly males, on average 57% ($p = 0.082$, Table 1). Consequently, sex ratio

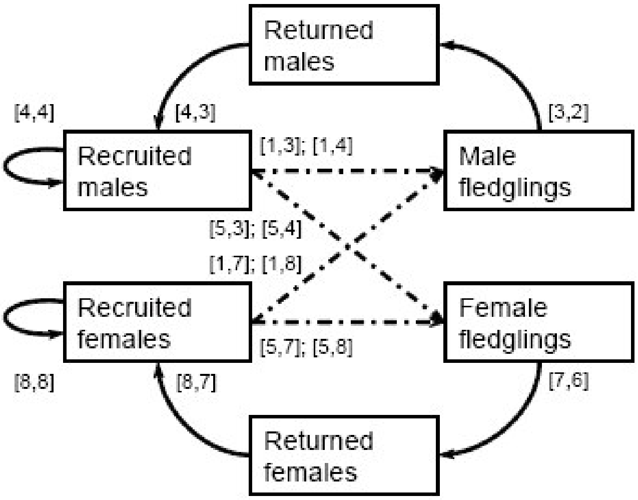

Fig. 1. Life-cycle graph of the two-sex matrix model used to analyse the growth of the common tern breeding colony "Banter See". Numbers in square brackets refer to cells of the two-sex matrix ([row, column]).

shifted from significant daughter dominance in fledglings to a marginally significant higher proportion of natal males among recruits (Table 1).

The binomial GLM found a significant relationship between life-history stage and proportion of males and females at the Banter See. The model which treated stage as a three category variable (AIC = 74.9) performed no better than a two category variable with fledglings vs return and recruitment (AIC = 74.3), but the most parsimonious model treated stage as a continuous variable (AIC = 72.9; Fig. 2). According to this model, life-history stage caused a significant increase in the proportion of males at the colony ($\beta = 0.137$, SE = 0.042, p = 0.001) and explained 65.3% of the residual deviance.

No significant between-year-differences in sex ratio were evident when inter-annual variability within the status groups was tested (cf. Table 1: fledglings, $chi^2 = 1.675$, DF = 3, p = 0.643; returned individuals, $chi^2 = 2.884$, DF = 3, p = 0.410; recruits, $chi^2 = 0.932$, DF = 3, p = 0.818).

Table 1. Status and sex ratio of common terns, fledged at Banter See 1998–2001. The proportion of males is presented (number of individuals in brackets; significant differences are given bold).

Cohort	Proportion of males		
	Fledged	Returned	Recruited
1998	0.47 (106)	0.59 (46)	0.57 (37)
1999	**0.43 (371)****	0.46 (163)	0.51 (117)
2000	0.46 (194)	0.51 (78)	0.57 (56)
2001	0.47 (500)	0.52 (229)	0.57 (129)
Total	**0.46 (1171)****	0.51 (516)	0.57 (339)$^{1)}$

** p < 0.01; $^{1)}$p = 0.082; binomial test.

Sex specific return and recruitment rates

The return rates of sons ranged between 44.4 and 54.0% (average 49.1%; Table 2) and of daughters between 33.9 and 41.5% (average 39.9%; Table 2). In the 1998 and 2001 cohorts as well as all years combined, the higher return probability of males was significant (Table 2). Overall male return rate was 10.8% higher (p < 0.002).

Recruitment rates of sons ranged between 31.1 and 42.0% and of daughters between 21.1 and 28.6% (Table 2). In the 1999 and 2001 cohorts and in the total, recruitment rate was significantly higher for sons than daughters (Table 2). Overall male recruitment rate was 10.8% higher (p < 0.001).

Between return and recruitment, the average loss of males was 14.3% and of females 15.9% (Table 2). In the 1999 cohort and for all years, significantly more returned males than returned females recruited (1999: 80.0% males, n = 75, 64.8% females, n = 88, $chi^2 = 4.635$, p = 0.031; total: male recruits 71.0%, n = 262, female recruits 60.2%, n = 254, $chi^2 = 6.621$, p = 0.01).

All 11 common terns hatched and ringed at Banter See and recovered as breeders or probable breeders elsewhere were females, 10 breeding at the Dutch part of the Dollart (about 80 km west of Banter See), one on Amrum island (Germany, 125 km away); six of them had emigrated after prospecting the natal colony whereas five never had returned to the home colony. Among the five sexed immigrants to Banter See colony ringed as chicks at other sites, two females were registered as experienced breeders, two other females and one male as two- or three-year old first time breeders. These immigrants came from German, Dutch or Belgian breeding sites (Minsener Oog 28 km, Delfzijl (Dollart) 79 km, Zeebrügge 412 km).

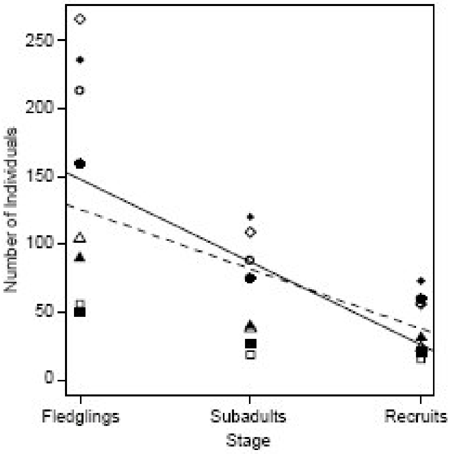

Fig. 2. Changes in numbers of males (solid symbols) and females (open symbols) for the four cohorts (squares: 1998; circles: 1999; triangles: 2000; diamonds: 2001) with trend lines (males: dashed; females: solid). The most parsimonious model according to the Akaike's information criterion fitted the life-history stage as a continuous explanatory variable against the proportions of males and females in a binomial generalized linear model. It found a significant change in the proportion of natal males and natal females at the Banter See colony from fledging to recruitment via return and explained 65.3% of the variance.

Pairings of natal recruits

The proportion of native mates for recruit females ranged from 52.8% to 85.7% between 1998 and 2006. The proportion of native mates for males ranged from 40.6% to 63.6% simultaneously. During these seasons the proportion of unknown mates of male recruits was significantly higher than that of females (males: 47.4%, n = 293; females: 37.0%, n = 227; $chi^2 = 5.687$, DF = 1, p = 0.017). 62.3% of these mates of unknown origin (n = 223) were females and only 37.7% males.

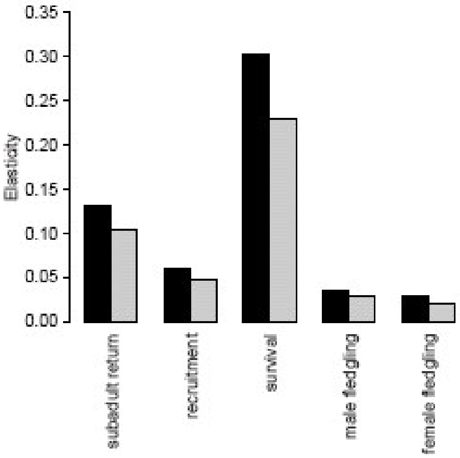

Fig. 3. Elasticities of λ from matrix **A**. Elasticities of male demographic rates have a greater effect on λ than their female equivalents. Black bars are male; grey bars female. Elasticities of subadult return and fledgling rate are pooled (see Methods 'Population modeling').

Population matrix models

The matrix analysis produced similar growth rates to those observed for the whole colony. Colony growth since 1998 has, on average, been 11.1% per year using number of nests (marked and unmarked birds) or 9.7% using number of marked breeders; λ was 9.3% according to the two-sex matrix. Male adult survival was the most influential on λ, and male rates are consistently more influential on λ than their female equivalents in the two-sex matrix **A** (Fig. 3).

Discussion

The number of fledglings was female biased across the four cohorts studied at the population level. At recruitment, however, the opposite was true and natal recruits were consistently male-biased (Table 1) as in returned Nazca boobies *Sula granti* (Maness et al. 2007). In other bird species, offspring sex ratios fluctuated between different years and environmental conditions (Komdeur et al. 1997, Torres and Drummond 1999), temporally (Cooch et al. 1997, Millon and Bretagnolle 2005) or over large spatial scales (Byholm et al. 2002, Millon and Bretagnolle 2005). Such variation is typical for vertebrate populations and a problem for sex ratio investigations (Cockburn et al. 2002). The non-significant inter-annual variation in the return and recruitment proportions among the four cohorts suggests that the patterns

Table 2. Proportion of male and female common tern fledglings returning and/or recruiting (cohorts 1998–2001) to the Banter See colony until 2006 (chi^2-test; significant inter-sex differences are given in bold).

Cohort	Fledglings		Returned %			Recruited %		
	♂	♀	♂	♀	p	♂	♀	p
1998	50	56	54.0	33.9	**0.037**	42.0	28.6	0.148
1999	159	212	47.2	41.5	0.277	37.7	26.9	**0.026**
2000	90	104	44.4	36.5	0.263	35.6	23.1	0.056
2001	235	265	51.1	41.1	**0.016**	31.1	21.1	**0.011**
Total	531	640	49.1	39.9	**0.002**	34.8	24.0	**<0.001**

Table 2. Proportion of male and female common tern fledglings returning and/or recruiting (cohorts 1998–2001) to the Banter See colony until 2006 (chi^2-test; significant inter-sex differences are given in bold).

Cohort	Fledglings		Returned %			Recruited %		
	♂	♀	♂	♀	p	♂	♀	p
1998	50	56	**54.0**	**33.9**	**0.037**	42.0	28.6	0.148
1999	159	212	47.2	41.5	0.277	**37.7**	**26.9**	**0.026**
2000	90	104	44.4	36.5	0.263	35.6	23.1	0.056
2001	235	265	**51.1**	**41.1**	**0.016**	**31.1**	**21.1**	**0.011**
Total	531	640	**49.1**	**39.9**	**0.002**	**34.8**	**24.0**	**<0.001**

n = 293; females: 37.0%, n = 227; chi^2 = 5.687, DF = 1, p = 0.017). 62.3% of these mates of unknown origin (n = 223) were females and only 37.7% males.

Population matrix models

The matrix analysis produced similar growth rates to those observed for the whole colony. Colony growth since 1998 has, on average, been 11.1% per year using number of nests (marked and unmarked birds) or 9.7% using number of marked breeders; λ was 9.3% according to the two-sex matrix. Male adult survival was the most influential on λ, and male rates are consistently more influential on λ than their female equivalents in the two-sex matrix **A** (Fig. 3).

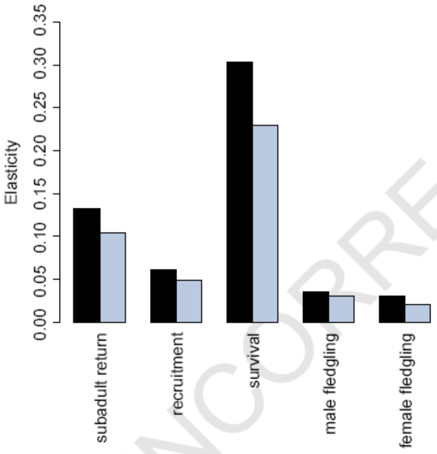

Fig. 3. Elasticities of λ from matrix **A**. Elasticities of male demographic rates have a greater effect on λ than their female equivalents. Black bars are male; grey bars female. Elasticities of subadult return and fledgling rate are pooled (see Methods 'Population modeling').

Discussion

The number of fledglings was female biased across the four cohorts studied at the population level. At recruitment, however, the opposite was true and natal recruits were consistently male-biased (Table 1) as in returned Nazca boobies *Sula granti* (Maness et al. 2007). In other bird species, offspring sex ratios fluctuated between different years and environmental conditions (Komdeur et al. 1997, Torres and Drummond 1999), temporally (Cooch et al. 1997, Millon and Bretagnolle 2005) or over large spatial scales (Byholm et al. 2002, Millon and Bretagnolle 2005). Such variation is typical for vertebrate populations and a problem for sex ratio investigations (Cockburn et al. 2002). The non-significant inter-annual variation in the return and recruitment proportions among the four cohorts suggests that the patterns observed for this population and period of time are consistent.

Female-biased fledging sex ratio at the population level in the common tern was at least partly caused by a higher nestling mortality of male chicks (González-Solís et al. 2005). Given that common terns are only slightly dimorphic in size, higher nestling mortality of males suggests that reasons other than size are involved in the sensitivity of sons to adverse conditions (Fletcher and Hamer 2004). One reason is sibling competition within the brood, which influences growth and survival and may have long-lasting fitness consequences in common terns (Becker and Wink 2003) and other species (Torres and Drummond 1999, Velando et al. 2002, Uller et al. 2004, Kim and Monaghan 2006).

The sex ratio bias at fledging seemed to be independent from mean colony reproductive success as it was evident in favorable (1.8 fledglings per pair in 1999 and 2001) and moderate seasons (0.6 and 0.8 fledglings per pair in 1998 and 2000 respectively). However, nestling mortality of males was heterogeneous not only between years but also between brood sizes, probably resulting from an impaired capacity of two-chick brood parents to rear sons (González-Solís et al. 2005). Several studies have shown that brood sex observed for this population and period of time are consistent.

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The female biased secondary sex ratio found in the common tern contrasted with the male biased return and recruitment to the natal colony. Although the sex ratio shift could be caused by differential survival, the lack of evidence of sex-specific survival for common terns immediately after fledging (Schauroth and Becker 2007) or as adults (Nisbet and Cam 2002; recruits: Ludwigs and Becker 2007) suggests that dispersal is the dominant force (Fig. 4). This assumption is supported by the female bias in sex-known immigrants and emigrants. Among the natal recruits' mates originating from other colonies nearly two-thirds were females. Correspondingly, among the ring recoveries available, the great majority of emigrants from and immigrants into the Banter See colony were females. Male common terns were the more philopatric gender to the natal colony, which is a general pattern for the majority of bird species (Greenwood 1980, Clarke et al. 1997). Lower female birth site fidelity is particularly known in Lariiformes (Coulson and Nève de Mévergnies 1992, Spear et al. 1998). Although most animals disperse when young and before they start breeding (Greenwood and Harvey 1982, Wolff 1993, Reed et al. 1999, Newton 2003), Coulson and Nève de Mévergnies (1992) asked the question: do emigrants return to the natal colony and then emigrate, or do most never return to their place of birth? Our data indicate that some females may start breeding at a non-natal site without return to the natal colony at any time, whereas other females may disperse between prospecting at the natal site and recruitment elsewhere, as found in common guillemots *Uria aalge* (Crespin et al. 2006).

In general, the less territorial sex is more likely to disperse in birds. Greenwood (1980) and Greenwood and Harvey (1982) suggested that female biased dispersal in birds is linked to three factors: (1) defence of territories by males prior to mating; (2) subsequent female choice among males and their territories; and (3) monogamous cooperation in rearing young. The findings presented here conform to these relationships: prospecting and recruiting male common terns seem to be more attracted by natal sites and invest more in defence of a future nest territory than females (Ludwig and Becker 2006). Although both parents care for the clutch and chicks, the male assumes the major role as food supplier by feeding the mate and, predominantly, the chicks (Becker and Ludwigs 2004). This could exert further selection pressures on philopatry: male common terns might benefit more from colony site fidelity through their acquaintance with local resources, especially food availability (Becker and Ludwigs 2004), local predators and/or social neighbours in the colony (Danchin et al. 2004). Information and its use is an important factor in evolutionary ecology (Danchin et al. 2004, Dall et al. 2005) and might not purely be the basis of high male philopatry but also of coloniality in general (Brown and Brown 2001). As such, a pre-disposition in males for higher developed spatial cognition and memory might not only aid foraging but also locating the natal colony site and philopatry to it in this long-distant migrant.

In contrast, for females it might be more important to find a male with a nest territory, and the resource of available males at any colony site might be a more important cue for their prospecting and recruitment decision than philopatry (Dittmann et al. 2005, Ludwig and Becker 2006). The prediction that competition will be most pronounced and prolonged among the more philopatric sex (reviewed by Cockburn et al. 2002), is supported by the finding that female common terns recruit when younger than males and therefore have older mates (Ludwigs and Becker 2005). Female common terns from a small colony were more likely to favour a foreign colony for prospecting than males and their average attendance at the natal colony was less (Dittmann et al. 2005). These results indicate lower bonds of subadult female common terns to their natal colonies. Hence it follows that mixing of gene pools as adaptation to avoid inbreeding depression, kin competition or risk due to fluctuating environments (Keller and Waller 2002) may be guaranteed predominantly by female common terns, whereas higher male birth site fidelity may function to stabilize the natal colony and maintain adaptations to the specific conditions at each colony site. The different roles male and female common terns play in the natal population and the strong relationships of this to coloniality could be one important selective driver of the observed sex ratio bias and shift. The 'local resource competition' hypothesis (Clark 1978, Greenwood 1980, Cockburn et al. 2002) implies that males interact and compete for the resources available to the colony, whereas the return from parental investment in females is not devalued by an increase in competition for local resources.

Males had consistently higher return and recruitment rates than females, which resulted in 11% more male natal recruits present at the home colony (Fig. 4). According to the perturbation analysis, male rates were more influential on natal population growth rate than their female equivalents (Fig. 3). As recruits paired predominantly with other

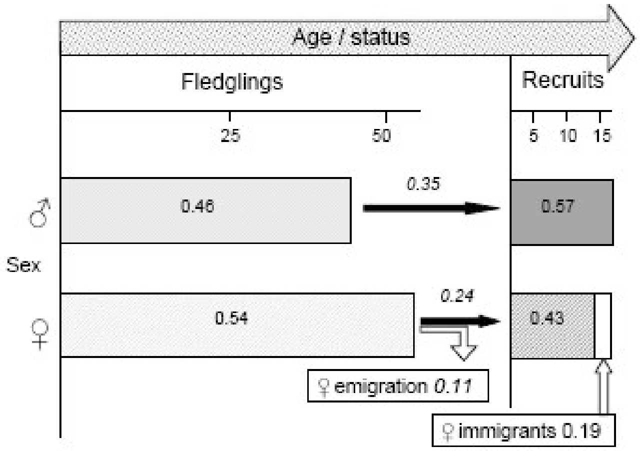

Fig. 4. Averages of sex ratio bias in fledglings and natal recruits of common terns (proportions), of recruitment rates (italics, bold), of estimated female emigration rates (italics) and proportion of immigrants among the female recruits. The calculation is shown for 100 fledglings. More females emigrate than are needed immigrate in order to compensate for the deficit of partners of natal male recruits.

recruits (Ludwigs and Becker 2005), the surplus of natal males paired as first time breeders was presumably compensated by immigration of young females (Fig. 4). Indeed, 10.4% more natal male recruits than natal female recruits were mated with an unmarked immigrant partner. The number of females available for pairing is, to a significant extent, driven by immigration, which affects the number of prospective mates for natal males that breed. If the results reported here are a general phenomenon, and if there is no higher mortality in female than male subadults, the surplus of female fledglings might be expected to immigrate into non-natal colonies with the consequence of a general female bias among prospecting and recruiting adults. This corresponds with the observation that in tern and gull colonies (Lariiformes) adult sex ratio appears to be regularly female-skewed (Donald 2007). On the other hand, a reduction in the number of immigrating females would increase competition between philopatric males as the probability of attracting a mate would be lower.

A complex set of environmental and social factors and sex influence immigration and emigration rates. In monogamous species, such as the common tern, the more influential part of natal population development may be the more philopatric gender. Consequently, gender bias in secondary sex ratio, subadult dispersal and recruitment to the natal colony are factors that should be acknowledged and considered in population modeling: males – and particularly natal males – matter (Rankin and Kokko 2007). Our results are another clear example that female-focused demography is only one side of the coin: more attention should be devoted to the frequently ignored male gender, especially if both sexes provide parental care.

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Prospectors' colony attendance is sex-specific and increases future recruitment chances in a seabird

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Abstract

In most long-lived vertebrates, including seabirds, young non-breeders often attend potential breeding sites. In seabird colonies, this prospecting behaviour has nearly never been studied with respect to potential sex-specific benefits, and its fitness consequences are largely unknown. We compared attendance patterns of sexed common tern prospectors at six subcolonies with future breeding status and nesting site choice. We also tested for potential effects of population density. Birds that arrived earlier at the colony were recorded more often along the season. This arrival effect was stronger in males, which generally spent more time at the colony. Birds prospecting for two consecutive years attended the colony more intensively in the second year. A high colony attendance enhanced recruitment probability in both sexes, but only in females, it was linked with a higher probability to return. Attendance at a preferred subcolony increased during the season. For first breeding, individuals favoured the subcolony where they had prospected most intensively in the previous season. In males, this subcolony fidelity was stronger and increased simultaneously to breeding pair density. We conclude that prospecting is a process of integration into the community of breeders, and that benefits are higher for males, the more territorial sex in this species.

Keywords: Prospecting behaviour; Density-dependence; Coloniality; Life history; Sex; *Sterna hirundo*

1. Introduction

Many long-lived birds and mammals reproduce for the first time at higher ages than at physiological onset of sexual maturity (Petzsch, 1969; Hector et al., 1986; Bradley and Wooller, 1991; Danchin et al., 1991; Del Hoyo et al., 1992; Weilgar et al., 1996; Patton et al., 2001; Parnell, 2002). Among birds, seabirds are known for their longevity with the largest species attaining near anthropogenic life expectation (Bradley and Wooller, 1991; Del Hoyo et al., 1992; Weimerskirch, 1992; Nisbet et al., 2002). In most, if not all, studied seabird species, young – but presumably sexually mature – individuals attend colonies of conspecifics without breeding during one or several seasons as so-called prospectors (Lockley, 1942; Warham, 1958; Harrington, 1974; Serventy and Curry, 1984; Klomp and Furness, 1990; Danchin et al., 1991; Boulinier et al., 1996; Schjørring et al., 1999; Crawford et al., 2002; Dittmann and Becker, 2003). It has been assumed that they are prevented from breeding by strong intraspecific competition for breeding sites (e.g. Wooller and Coulson, 1977; Duncan, 1978; Coulson, 1991; Klomp and Furness, 1992), by a lack of skills, information, or partner (Curio, 1982; Weimerskirch, 1992; Ludwigs and Becker, 2002; Dittmann and Becker, 2003). On the other hand, a phase of non-breeding might offer the chance to select a high quality breeding site, to profit from private and public information and thus to enhance the total lifetime reproduction success (Boulinier and Danchin, 1997; Danchin et al., 1998; Schjørring et al., 1999; Doligez et al., 2002).

In most species, young birds arrive later at potential breeding grounds than experienced breeders (e.g. Pickering, 1989; Porter, 1990; Halley et al., 1995; Stewart et al., 2002). Arrival date is an important ultimate determinant of whether a young bird will breed for the first time in a given season or remain a prospector (Ludwigs and Becker, 2002). However, it is questionable which proximate mechanisms underlie the obvious value of early arrival dates in this context. We may expect that a prospector uses attendance to become familiar with a site selected for possible future breeding (Halley et al., 1995; Dittmann et al.,

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2005), provided that site quality in the prospecting season predicts that in the following season (Boulinier and Danchin, 1997). A certain minimum of site attendance may therefore be necessary before recruitment is possible. A relationship between site attendance patterns during prospecting and a bird's fate in a following season has rarely been documented (but see Halley et al., 1995; Schjørring et al., 1999; Cam et al., 2002) and in most cases, the postulated effects of prospecting on first reproduction are difficult to separate from those of age, sex, year or site. In addition, attendance patterns may strongly depend on the spatial scale of the observation (Doerr and Doerr, 2004; Parejo et al., 2006). Recording prospectors at two colonies, which are several kilometers from each other, Dittmann et al. (2005) report a relationship between proportional registration days and future breeding probability at one of the colonies.

For species breeding in social groups such as colonies, a higher individual familiarity with future breeding neighbours might facilitate a first breeding attempt by reduced aggression (Großkopf, 1970; Burger et al., 1979; Myers, 1983; Tolske, 2004), particularly under conditions of high density when competition for breeding sites is enhanced (Butler and Janes-Butler, 1982; Hötker, 2000). Site familiarity and, thus, site fidelity, should be more important for the more territorial sex which, in most seabirds, is the male (Greenwood, 1980).

In this study of a common tern (*Sterna hirundo*) colony on the German Wadden Sea coast, attendance patterns of transponder-marked prospectors of known age and sex were automatically recorded at six subcolonies throughout eight consecutive breeding seasons on a small spatial and temporal scale. We related attendance patterns to individual fate and, in case of recruitment, nest-site choice. In a variety of aspects, we give insight into a life stage, which is difficult to study in long-lived animals and connect individual to population ecology.

We tested the following predictions that can be made given previous studies on prospecting:

- Early arrival date and higher age will positively co-vary with colony attendance;
- High colony attendance of prospectors will increase recruitment probability in the following season.
- Throughout the prospecting phase, birds will spend an increasing amount of time at one selected site.
- Birds will breed for the first time at the previously favoured site, especially under high-density conditions.
- The above relationships will be stronger in males, i.e., the more territorial sex.

2. Materials and methods

This study was part of an ongoing long-term study conducted since 1992 in a colony of common terns in the harbour area of Wilhelmshaven, Lower Saxony, Germany. We collected the data used in this study between 1997 and 2005. The colony site, called 'Banter See' (53°27′N, 08°07′E), consists of a row of six artificial concrete islands, numbered with A–F (Becker and Wendeln, 1997). Each island measures 11 × 5 m and is surrounded by a low wall (60 cm high), equipped with in total 44 elevated places for the terns to land and rest on (resting platforms, Becker and Wendeln, 1997). The distance between the islands is about 1 m. Despite the small distances between the islands, we considered them as functional subcolonies because the walls surrounding the islands served as effective sight barriers for birds sitting on the ground and because birds could not come into contact with conspecifics from neighbouring islands without flying. Tolske (2004) suggests that, for breeders' spatial use of the site, the visibility of the own nest – which is fundamentally influenced by these walls – is of importance, and therefore also for the probability of interactions with other individuals. During so-called panic flights, evasive flights typical for terns when groups of birds fly up synchronously without any obvious reason, often only individuals from single subcolonies leave the place, indicating a certain social bond between members from one island (pers. obs.). So the islands formed parts of a colony which were clearly separable from each other, both spatially and concerning the behaviour of individuals. These criteria of subcolony definition are in accordance to those in other studies (e. g. Halley et al., 1995; Danchin et al., 1998; Schjørring et al., 1999). In this study, the term 'subcolony' was operating on a scale of meters, whereas the nearest other colony was in a distance of several kilometers, thus forming a clearly separated social unit (Dittmann et al., 2005). Over the study years, the colony 'Banter See' grew from 180 to 530 breeding pairs. Due to the limited size of the site, the increase in pairs directly reflects an increase in breeding density which is, however, still far beyond the theoretical carrying capacity for the site, compared to other studies (Loose, 1998).

Before fledging, we marked all chicks with steel rings and with subcutaneously injected passive transponders (Becker and Wendeln, 1997). These transponders send an individual alphanumeric code when activated by special antennas placed on the resting platforms around the colony with a recording interval of 10 s. The system allows life-long identification of birds without re-trapping at the natal colony. We distributed all antennas (1993–94: 12; 1995–96: 22; 1997–98: 30; 1999–2001: 35; since 2002: 44) equally among the platforms and, until 2001, we changed their position regularly in intervals of 2–3 days in order to record the presence of marked birds with equal probability at all subcolonies. Birds' registration continued throughout the breeding season from mid April until late August. We checked the identity of all transponder marked breeders by placing an antenna around each nest of the colony. With this method, we were able to distinguish reliably between breeders and non-breeders.

The majority of surviving young terns return for the first time to the natal colony in their third calendar year and start breeding there one or two years later (Ludwigs and Becker, 2002; Dittmann and Becker, 2003). We therefore defined prospectors as 2–3 year-old native individuals from which no breeding attempt was known so far. We defined first-time breeders as recruits. We considered the date when a bird was recorded for the first time in a given season as its arrival date in that season.

From 1997 onwards, we sampled a few live body feathers from all chicks of about 18 days old for sexing the birds with standard molecular methods (Becker and Wink, 2002). In addition, we sexed birds by observing copulating pairs of which, at least one partner was marked with a transponder or with a ring.

To measure prospector attendance at the colony, we defined each of the 24 full hours of a day with at least one registration of an individual at the colony as one 'attendance hour at the colony' (AHC). In this sense, a bird could theoretically reach a maximum of 24 AHC per day. We calculated colony attendance (CA) of a bird in a given season as follows:

$$\mathrm{CA}_x = \sum_{d=1}^{a} \mathrm{AHC}_x$$

where AHC = attendance hour at the colony, x = individual bird considered, d = day of the season when the bird visited the colony, a = number of days that the bird visited the colony

We fitted generalized linear mixed models (GLMM) by penalized quasi-likelihood in the R environment, version 2.3.1 (R Development Core Team 2006, Vienna, Austria), using the 'MASS' package, version 7.2–27. To test for effects of study year, arrival date, age and sex on colony attendance, we fitted a GLMM with Gamma error structure and an inverse-link function to account for the non-normal error distribution of the data. We entered the individual as a random factor because some birds were observed prospecting in more than one year. To select the minimum adequate model, we employed a backward stepwise procedure from the full model and removed non-significant terms sequentially and tested model fit by the squared correlation between observed and fitted values. Significant year effects were detected by fitting year as a factor: CA was significantly higher in 2001 and significantly lower in 1998 and 2000. To simplify the model, we pooled the other years and used them as a reference group to 2001, as well as (also pooled) 1998 and 2000.

To measure the attendance of prospectors at the six different subcolonies, we defined the parameter 'attendance hour at a subcolony' (AHS) as each of the 24 full hours of a day with at least one registration of an individual prospector at a subcolony. We calculated subcolony attendance (SA) for each bird and subcolony as follows:

$$\mathrm{SA} = \sum_{d=1}^{a} \mathrm{AHS}$$

where AHS = attendance hour at the subcolony, d = day of the season when the bird visited the subcolony, a = number of days that the bird visited the colony

We defined the subcolony with the highest SA value per individual and season as the favoured subcolony. For some individuals that reached equal SA values on two or more subcolonies, we defined the subcolony with the highest number of single transponder registrations as the favoured subcolony. Despite this criterion, four birds were still registered equally on two subcolonies and we therefore omitted them from the analysis of subcolony preference. To test if prospectors establish themselves on their favoured subcolony throughout the season, we calculated the proportional subcolony attendance during each of seven consecutive periods of 10 days following the birds' arrival as follows:

$$\mathrm{SA}_{s_p} = \frac{\sum_{d=1}^{10} \mathrm{AHS}_{f_p}}{\sum_{s=1}^{6} \sum_{d=1}^{10} \mathrm{AHS}_{s_p}} * 100$$

where AHS = attendance hour at a subcolony, f = subcolony with highest value of SA in season (=favoured subcolony), s = subcolony considered, d = day of the 10-day-period when the bird visited the subcolony, p = number of the 10-day-period considered

To test for changes in attendance at the favoured subcolony throughout the season, we fitted a GLMM with binomial error distribution with logit link function. Sex was treated as a factor and individual as a random effect.

To test the roles of prospecting intensity and sex for the bird's status in the following season, we distinguished the status groups 'non-returner', 'second-time prospector' and 'recruit'. Into the group of second-time prospectors, we also included 4-year-old birds. We performed a multinomial logistic regression with status as the dependent variable. We used the 'intermediate' status group (second-time prospector) as a reference group. In the results, we present the B-values ± standard error.

If not stated otherwise above, we performed the statistics with SPSS for Windows, Release 12.0.2G, 2004, SPSS Inc., Chicago, IL, U.S.A. (level of significance $p = 0.05$). We give only p-values for two-tailed tests of significance.

3. Results

3.1. Does colony attendance increase with earlier arrival date and with age?

In both sexes, earlier arrival was associated with a higher number of colony attendance hours. Males reached a higher number of colony attendance hours than females (Table 1, Fig. 1), although the increase was consistent for both sexes. Colony attendance was higher in 2001 and lower in the years 1998 and 2000 compared to the other years. Age had no significant effects on the number of colony attendance hours, and we therefore omitted age as a factor from the model. However, in additional analyses using only data from individuals prospecting for two consecutive years (when 2–3 year-old), both males and females attended the colony more intensively in the second season (males: mean CA ± SD = 118.19 ± 135.54 versus 258.06 ± 231.56, Wilcoxon-Test: $n = 154$, $Z = -7.43$,

Table 1

Colony attendance (CA) of common tern prospectors is dependent on sex, arrival (Julian) date and year. (GLMM with Gamma error structure and an inverse link function; individual is fitted as a random effect)

Independent variable	Parameter estimate ± S.E	df	t	p
Intercept	−0.0175 ± 0.0018	667	−9.862	<0.001
Female sex	0.0037 ± 0.0006	667	6.566	<0.001
Arrival date	0.00015 ± 0.00001	243	12.220	<0.001
Years 1998, 2000	0.0032 ± 0.0012	243	2.754	0.006
Year 2001	−0.0022 ± 0.0005	243	−4.151	<0.001

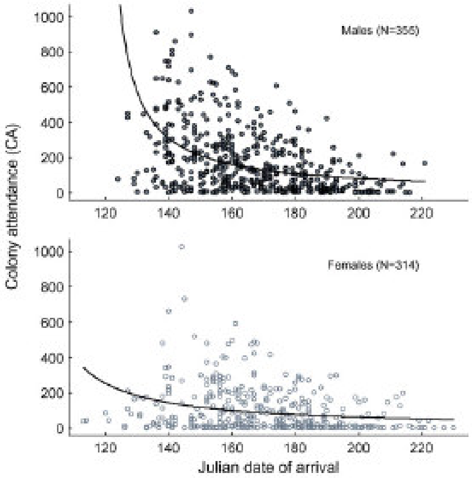

Fig. 1. Influence of arrival date and sex on colony attendance (CA) of common tern prospectors. ● Males; ○ Females.; cf. Table 1).

$p < 0.001$; females: mean CA ± SD = 73.32 ± 100.94 versus 122.52 ± 172.53, Wilcoxon-Test: $n = 92$, $Z = -3.12$, $p = 0.002$).

3.2. Colony attendance and future status

High colony attendance was associated with a higher probability to breed for the first time in the following season instead of prospecting for a second time. The effect was weaker in males than in females (Multinomial logistic regression, $n = 759$: Intercept: $B = -0.37 \pm 0.16$, Wald = 4.95, df = 1, $p = 0.026$; CA: $B = 0.006 \pm 0.001$, Wald = 25.94, df = 1, $p < 0.001$; male sex: $B = 0.01 \pm 0.21$, Wald = 0.003, df = 1, $p = 0.95$; male sex*CA: $B = -0.003 \pm 0.001$, Wald = 6.36, df = 1, $p = 0.012$; Fig. 2).

Females with a high colony attendance were less likely not to return than to prospect for a second time; this relationship was not found in males (Multinomial logistic regression, $N = 499$: Intercept: $B = 0.21 \pm 0.17$, Wald = 1.45, df = 1, $p = 0.23$; male sex: $B = -1.52 \pm 0.26$, Wald = 33.79, df = 1, $p < 0.001$; CA: $B = -0.013$, S.E = 0.003, Wald = 18.72, df = 1, $p < 0.001$; male sex*CA: $B = 0.013$, S.E = 0.003, Wald = 18.56, df = 1, $p = 0.001$; Fig. 2).

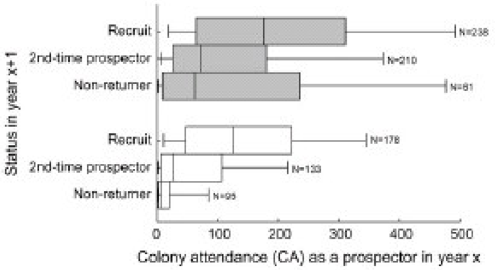

Fig. 2. Colony attendance (CA) of prospectors and status in the following season. ■ Males; □: Females. The boxes include 50% of the values; horizontal lines indicate the median; whisker caps indicate the 5th and 95th percentiles.

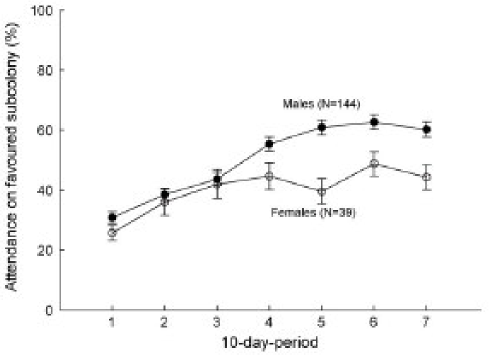

Fig. 3. Mean individual attendance (SA) ± S.E of male and female prospectors at the favoured subcolony during seven consecutive periods of 10 days each throughout the season. ● Males; ○ Females.

3.3. Increased individual attendance at one subcolony during the season

In both male and female prospectors, individual attendance on the favoured subcolony increased significantly throughout seven consecutive periods of each 10 days (GLMM: effect of period: $F_{6,183} = 22.73$, $p < 0.001$). The increase was more pronounced in males than in females (GLMM: effect of period*effect of sex: $F_{6,183} = 3.31$, $p < 0.003$; Fig. 3). From the fourth period onwards, males attended the favoured subcolony more intensively than females (Fig. 3).

3.4. Favoured subcolony during prospecting and subcolony of recruitment

In both male and female 2–3 year-old prospectors, we found a significant correlation between their favoured subcolony and the subcolony where they bred for the first time in the following year (Nonparametric correlations: males: $r_S = 0.603$, $n = 238$, $p < 0.001$; females: $r_S = 0.348$, $n = 177$, $p < 0.001$; Fig. 4). However, fidelity towards the previously favoured subcolony was significantly stronger in male than in female recruits (Crosstabulations, $\chi^2_1 = 8.66$, $n = 415$, $p = 0.003$).

3.5. Subcolony fidelity during colony growth

For male, but not female prospectors, the proportion of individuals that would breed on the favoured subcolony in the following season increased with growing breeding pair density (Logistic regression: males: $n = 238$, $B = 0.003$, S.E = 0.001, Wald = 3.94, df = 1, $p = 0.047$; females: $n = 177$, $B = 0.001$, S.E = 0.002, Wald = 0.61, df = 1, $p = 0.44$; Fig. 5).

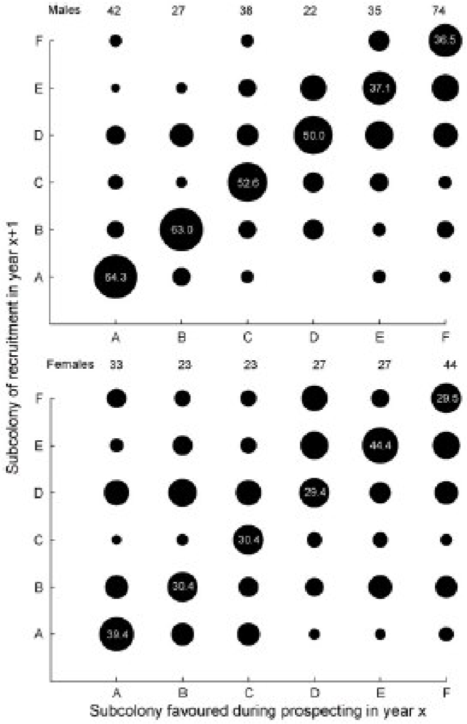

Fig. 4. Comparison of the subcolony favoured during prospecting and the subcolony of subsequent recruitment in male (top) and female (bottom) common terns. Bubbles in one column represent 100% of recruits that had favoured the subcolony given below during prospecting. Values above the bubble columns give the sample sizes, values within bubbles give the percentages of birds recruiting on the subcolony favoured during previous prospecting.

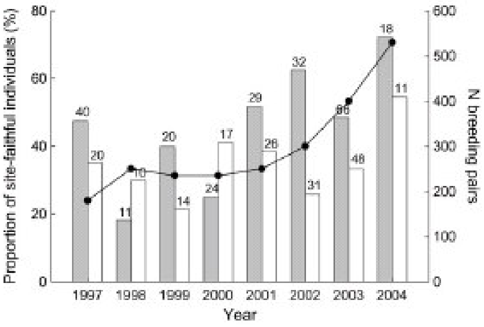

Fig. 5. Proportion of individuals recruiting on the subcolony favoured in the previous season with number of breeding pairs. ■ Males; □: females. ●: number of breeding pairs. Numbers above the bars give the sample sizes.

4. Discussion

In accordance with some of the few other studies documenting prospector attendance patterns (e. g. Pickering, 1989; Halley et al., 1995; Bradley et al., 1999; Reed et al., 1999) we found that earlier arrival date within the season was linked with a higher colony attendance of prospectors. This confirms the assumption that the chance for more intensive prospecting is one advantage of arriving early (Dittmann and Becker, 2003). Results also indicate that late arriving birds did not depart correspondingly late in order to attend the colony site when breeders have already left. This suggests that presence of older colony members plays an important role for prospectors, e.g., as individual protection (Tella et al., 2001), a source of information (Danchin et al., 1998; Doligez et al., 2002; Pärt and Doligez, 2004; Serrano et al., 2004) or as counterparts in social interactions (Erwin, 1978; Burger et al., 1979; Cadiou et al., 1994). Some differences in prospector colony attendance observed here between years were probably caused by variation in food availability. The particularly high colony attendance of prospectors in 2001 coincided with a very high breeding success of the colony whereas in 1998 and 2000, when prospector attendance was lowest, breeding success was rather poor (Becker, 1998; personal observations). On the German Wadden Sea coast, breeding success of common tern colonies is mainly determined by food availability (Becker and Finck, 1985), and annual fluctuations of the latter affect all the colonies in a similar way (Becker, 1998). As food availability influences the time budget for foraging and, in turn, for colony attendance in breeders (Norberg, 1977; Frank and Becker, 1992), it is very likely that it does so also in prospectors.

In many seabirds including the common tern, males are assumed to be more engaged in gaining access to and defending future nest territories (Glutz von Blotzheim and Bauer, 1982; Weimerskirch, 1992). If this is already of significance for prospectors, an intensive prospecting activity should be more important for males than for females. Male common tern prospectors arrive earlier (Dittmann and Becker, 2003) and are consequently recorded during a higher number of days than females (Dittmann et al., 2005). In this study, by measuring a time parameter of smaller scale (CA), we could confirm that male terns in fact spend more time at the colony than females.

In individuals prospecting for two consecutive years (here at ages of 2 and 3 years), colony attendance increased with age, a finding which is consistent with those of Pickering (1989) and Halley et al. (1995). But when adding colony attendance data of all 2 and 3-year-old birds prospecting only for one season, we did not find any age effect. This indicates that only birds attending the colony rather rarely in their first prospecting season – e. g. mediated by a late arrival date – are forced to prospect for a second time in order to reach a certain level of colony experience.

If prospecting birds prepare themselves for a first breeding attempt (Cadiou et al., 1994; Halley et al., 1995; Boulinier and Danchin, 1997; Schjørring et al., 1999), we should expect differences in future behaviour dependent on prospecting intensity. Our results show that colony attendance is indeed linked with the bird's status in the next year: In female, but not male prospectors, individuals visiting the colony rarely were less likely to return in the following season. To explain this sex-specific difference, it has to be kept in mind that non-returners were more frequent in females than in males, and in this group, we were unable to distinguish between individuals that died and those that emigrated to another colony. Due to lower philopatry (Dittmann et al., 2005) but no higher mortality in female common terns (Nisbet and Cam, 2002) we assume that, in female prospectors, low attendance at the observed colony reflected indirectly a higher attendance at foreign colonies prior to emigration there for first breeding in the following season (Dittmann et al., 2005) – without return to the home colony. Higher female emigration rates are a general finding in most seabirds except ducks (overview Greenwood, 1980).

In contrast, for both sexes, a high prospecting activity enhanced the probability of a first breeding attempt in the following season instead of prospecting for a second time. Correspondingly, some other authors report that prospectors which are seen more often at a colony (Halley et al., 1995; Schjørring et al., 1999) or which show even squatting behaviour at foreign nests (Cam et al., 2002) are also more likely to breed there in the following year. Here, the effect of colony attendance for the likelihood of subsequent recruitment was stronger in females than in males, indicating that the mechanisms increasing recruitment probability may differ between sexes.

Dittmann et al. (2005) describe a strong decrease in individual prospector flights between two common tern colonies from the first to the second half of a bird's attendance time. They suggest the occurrence of a site choice after collecting information (Zack and Stutchbury, 1992; Boulinier and Danchin, 1997; Reed et al., 1999; Doerr and Doerr, 2005), leading to increased attendance at the finally chosen site. Indeed, on the lower-scaled level of subcolonies observed here, prospectors spent a continuously increasing proportion of time at one certain subcolony which could be a future nesting site (Warham, 1958; Halley et al., 1995; Schjørring et al., 1999). Indeed, in recruits of both sexes, we found a significant positive correlation between the subcolony of recruitment and the subcolony favoured during previous prospecting. Male recruits were significantly more faithful towards the previously favoured subcolony than females and the degree of faithfulness did increase with the strong increase in density of breeding pairs in the colony throughout the study years. We assume that prospecting is, as well as a phase of collecting information, a process of social integration into a colony through enhanced presence within the community of future breeding neighbours (Großkopf, 1970; Reed and Dobson, 1993; Serrano et al., 2003). Tolske (2004) reports regular aggressive encounters between common tern prospectors and of prospectors with established breeders with prospectors being superior in most cases. Prospectors that arrived early are less frequently chased per time unit than late arrivals, suggesting a social establishment of prospectors with time by means of individual recognition. An individual recognition, which is only possible from year to year if the majority of breeding neighbours remain the same from one season to the next, implies longevity and strong fidelity towards the nesting territory, two characteristics for many seabird species including the common tern (Del Hoyo et al., 1992; González-Solís et al., 1999; St Clair et al., 1999). Males, as the more territorial sex, may gain higher benefits from an already well-known social environment at recruitment than females (Reed and Dobson, 1993; Van der Jeugd, 2001; Serrano et al., 2003). This is in line with a higher average age of recruitment, but not of first arrival in males (Dittmann and Becker, 2003; Ludwigs and Becker, 2002) – which may be mediated by a longer phase of integration of males into the colony. The importance of personal familiarity with future breeding neighbours may increase with their density because the latter can increase competition and favour the development of individual mitigating strategies (Ens et al., 1995). This view is also supported by the complementary case of drastically reduced ages of first-time breeders in colonies where density of established breeding neighbours has been heavily reduced by man (Duncan, 1978; Coulson, 1991), suggesting a loss of need for a long prospecting phase and emphasising the role of prospectors as potential 'population buffers' (Klomp and Furness, 1992). In addition, the higher fidelity of males towards a territory in a high-density environment observed here also could indicate that such territories are of greater value which might act as a motor of coloniality in general.

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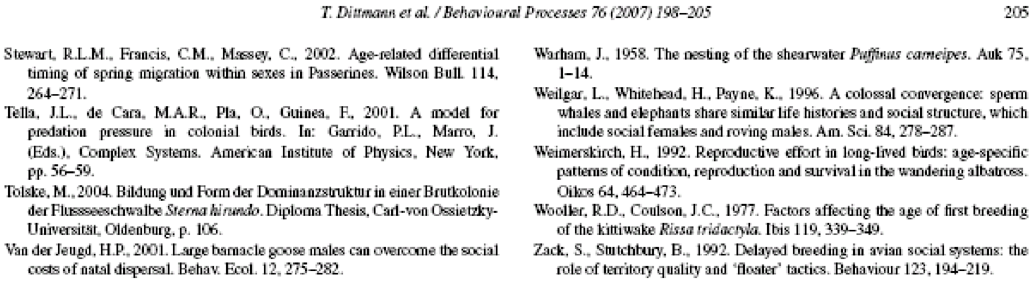

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