

Individual heterogeneity and senescence in Silvereyes on Heron Island

JONAS KNAPE,^{1,5} NICLAS JONZÉN,¹ MARTIN SKÖLD,² JIRO KIKKAWA,³ AND HAMISH MCCALLUM⁴

¹Department of Biology, Lund University, Sweden

²Department of Statistics, Örebro University, Sweden

³School of Integrative Biology, University of Queensland, Brisbane, Australia

⁴Nathan Campus, Griffith School of Environment, Australia

Abstract. Individual heterogeneity and correlations between life history traits play a fundamental role in life history evolution and population dynamics. Unobserved individual heterogeneity in survival can be a nuisance for estimation of age effects at the individual level by causing bias due to mortality selection. We jointly analyze survival and breeding output from successful breeding attempts in an island population of Silvereyes (*Zosterops lateralis chlorocephalus*) by fitting models that incorporate age effects and individual heterogeneity via random effects. The number of offspring produced increased with age of parents in their first years of life but then eventually declined with age. A similar pattern was found for the probability of successful breeding. Annual survival declined with age even when individual heterogeneity was not accounted for. The rate of senescence in survival, however, depends on the variance of individual heterogeneity and vice versa; hence, both cannot be simultaneously estimated with precision. Model selection supported individual heterogeneity in breeding performance, but we found no correlation between individual heterogeneity in survival and breeding performance. We argue that individual random effects, unless unambiguously identified, should be treated as statistical nuisance or taken as a starting point in a search for mechanisms rather than given direct biological interpretation.

Key words: breeding; individual heterogeneity; parameter identifiability; senescence; Silvereye; survival; *Zosterops lateralis chlorocephalus*.

INTRODUCTION

Closed populations are driven by the processes of survival and reproduction. Individual variation with respect to these traits is of interest in a range of fields including evolutionary ecology, population dynamics, and demography. Recent studies have found that individuals who perform well with respect to one vital rate often perform well with respect to other vital rates (Cam et al. 2002, McCleery et al. 2008). An interpretation is that the population has individuals of both high and low quality, the opposite of what one would expect if individual level trade-offs were dominant. Thus individual heterogeneity is of prime interest for exploring the potential for selective forces to operate. This view of individual heterogeneity is, for example, the basis of the heritability estimates that can be obtained from “animal models” (Kruuk 2004).

Individual heterogeneity also has consequences for population dynamics. Traditionally, population dynam-

ics have been analyzed by aggregating individuals into a relatively small number of classes, such as age or size. This aggregated approach assumes that the main characteristics of the population are captured by the classification and that all individuals within each class can be considered similar with respect to vital parameters. Over the last decade or so, there has been increasing recognition that general heterogeneity among individuals can be important, particularly for understanding the behavior of small populations because it can affect the demographic variance (Bjørnstad and Hansen 1994, Cam et al. 2002, Vindenes et al. 2008).

Categorizations such as age, size, sex, and so on can indeed be important and accurate estimates of their effect on life history traits and evolutionary processes are often of interest. For instance, there is a burgeoning literature on senescence in wild populations (Jones et al. 2008). Detecting senescence is difficult if there is individual variation in fitness because less fit individuals tend to die earlier than fitter individuals, obscuring potential changes in demographic parameters with age in the surviving individuals (Vaupel and Yashin 1985, Nussey et al. 2008). Similar effects can arise because of selective appearance of individuals (van de Pol and Verhulst 2006). When individual heterogeneity and age effects are simultaneously included in models these issues can render the models not identifiable. This is the

Manuscript received 26 January 2010; revised 5 October 2010; accepted 6 December 2010. Corresponding Editor: B. E. Kendall.

⁵ Present Address: Department of Environmental Science, Policy and Management 137 Mulford Hall, #3114, University of California, Berkeley, California 94720 USA.
E-mail: jknap@berkeley.edu

case with survival models including both full age structure and unconstrained individual heterogeneity (Zens and Peart 2003). Simply put, a non-identifiable model offers several competing explanations for the same data. If missed, issues with identifiability can lead to inference that is only weakly supported by the data and therefore require careful consideration.

Individual heterogeneity is thus a nuisance in estimation of life history parameters, but at the same time a quantity of major interest for understanding the action of natural selection and with consequences for population dynamics. However, as we will show, the well known issues with estimating vital rates in presence of individual heterogeneity directly transfer over to issues with estimating the individual heterogeneity itself and hence age dependent vital rates can be a nuisance in estimation of individual heterogeneity. This problem appears to not often be discussed in the rapidly growing literature that is often focused on the merits of different methods for model fitting (e.g., Gimenez and Choquet 2010), rather than the ecological interpretation of the results.

We here analyze data on individual survival and breeding events from a closed population of Silvereyes (*Zosterops lateralis chlorocephalus*), a passerine bird species breeding on Heron Island, Australia (Kikkawa 2003). By comparing models with different assumptions about aging and individual heterogeneity in survival and breeding performance we present support for both senescence and individual heterogeneity but find that the rate of senescence in survival cannot be determined without knowledge of the heterogeneity variance. We further show that different assumptions about how age affects survival may lead to different estimates of the variance in individual heterogeneity.

MATERIAL AND METHODS

The study population and data set

Heron Island (23°26' S, 151°57' E) is a wooded coral cay about 17 ha in area on the southern Great Barrier Reef, 70 km off the Australian coastline. Silvereyes are the only common resident passerine species (see Plate 1). Their population was monitored accurately from 1965 to 1993, with almost all birds individually color banded. In addition, nests and breeding activities were intensively monitored between 1979 and 1993, providing individually based information on clutch size and fledgling survival (McCallum et al. 2000, Clegg et al. 2008). We estimate survival based on data from a thorough pre-breeding census performed in September of each year. The breeding season of Heron Island Silvereyes extends from October through March and most adult mortality occurs in the non-breeding season. Details on field methods are given in, e.g., Kikkawa (1980) and Kikkawa and Wilson (1983).

Unlike many other long-term time series of vertebrate populations, this is a wild population that is essentially closed, with negligible emigration and immigration

(Kikkawa and Wilson 1983, Degnan 1993, McCallum et al. 2000). In this paper, we analyze data from the period in which detailed breeding information is available (1979–1993). Over that period, the total adult population (one year old and above) fluctuated between 342 individuals (1989) and 483 individuals (1982) (McCallum et al. 2000). Analysis of the time series of total population counts showed evidence of density dependence (McCallum et al. 2000), at least partially driven by a negative relationship between adult population size and survival through to first breeding. Cyclones caused reductions in population size. Between 1979 and 1993, they occurred in January and February 1980 and January 1992, causing slight increases in adult mortality but mainly impacting juvenile survival.

The recapture probability is very close to 1 in this data set: a Cormack-Jolly-Seber model (Lebreton et al. 1992) with constant resighting probability and time dependent survival yielded a resighting probability estimate of 0.984 (standard error 0.002). To simplify the analyses we assume that the state (dead or alive) of all birds is known in each year. About 5% of the birds were first captured at an age older than one year. If the age of those birds could not be determined from the record of their pair relations we assumed them to be 2 years old when first captured. Breeding attempts for which the identity of either parent was unknown were excluded from analysis.

Models

We take an approach similar in spirit to that of Cam et al. (2002) and model breeding and survival simultaneously. We compare models with different assumptions about aging and individual heterogeneity in survival and breeding output by a model selection approach. More specifically, we compare models allowing for senescence with models where age effects are constant for adult individuals and models including and excluding individual random effects. By individual heterogeneity we refer to individual random effects that are constant throughout the life of individuals.

Survival model.—Juvenile survival in silvereyes is substantially lower than adult survival (Robinson-Wolrath and Owens 2003) and the data on juvenile survival are less precise than the data on adult survival since initial marking of young birds was done at different ages. We therefore exclude all birds that did not survive to the time of the first pre-breeding census from the analysis and only consider birds that are one year or older. We use four main variants of survival models that differ in the type of age effect, constant or linear for adults, and in whether or not individual random effects are included. We define s_{it} to be 1 if individual i survives from the pre-breeding census in year t to the census in year $t + 1$ and 0 otherwise. The full conditional survival model is a logistic regression with random effects:

$$s_{it} \sim \text{Be}(\varphi[\mu + f_S(\text{age}_{it}) + d_S n_t + \alpha_i + \varepsilon_t]). \quad (1)$$

Here, Be denotes the Bernoulli distribution and φ^{-1} is the logistic link function. The fixed effects parameters are μ , the intercept on the logit scale; f_S , a function of the age of individual i at time t defined below; and d_S , which represents density dependence through regression on the standardized number of adults n_t alive at the census in year t . We compare two versions of the age effect, f_S . Both are defined relative to individuals of age 1 so that $f_S(1) = 0$. The first has one survival probability for individuals of age 1 and another survival probability common to all individuals of age 2 or older, thus f_S is zero for individuals of age 1 and a_{2+} for older individuals. The second model of age effects has free parameters for both of the two first age classes and a linear term for older age classes because we expect changes in survival rates to be greatest at low ages for which there are also more data. Thus for the second age function, f_S is zero for individuals of age 1, a_2 for individuals of age 2, and $a_3 + a_r \text{age}_i$ (where age_i is the age of individual i) for older individuals. Similar, piecewise linear, age effects have previously been used in analyses of survival (Loison et al. 1999). The random effects of the survival model are $\alpha_i \sim \mathcal{N}(0, \sigma_i^2)$, which are constant through the life of an individual and independent between individuals, and $\varepsilon_t \sim \mathcal{N}(0, \sigma_\varepsilon^2)$, which are year effects assumed to be independent between years. We do not model sex differences in survival since they have previously been shown not to be important in this population (Catterall et al. 1989).

Breeding model.—One can consider breeding of individual Silvereyes in a given year to consist of two different processes; first producing or not producing any young (henceforth referred to as breeding success), and second producing a particular number of fledged young, given successful breeding (henceforth referred to as breeding performance). We focus on the latter and model the total number of fledged young during a season for all pairs that produced at least one fledgling. Breeding performance is expected to be less variable and less sensitive to external disturbances (such as nest predation) than breeding success. Unsuccessful breeding is also partly confounded by mortality during the breeding season. Complementary models of breeding success are analyzed in Appendix B.

As for the survival models, we use model selection to differentiate between models with constant and linear age effects in adults and with and without individual random effects. Both the female and the male, however, are involved in breeding and both can potentially influence the breeding output. Since Silvereyes are monogamous (Robertson et al. 2001) and re-mate only after the death of the partner, any effects of male and female identity and of male and female age are likely to be difficult to separate. We therefore only include one of the sexes at a time in the breeding model.

We let b_{ijk} be the total number of fledged offspring from clutches between female j and male k in the breeding season starting in year t . Since we model successful breeding attempts, all the b_{ijk} are equal to or greater than 1. The number of fledglings in excess of 1 produced by such a breeding pair in a specific year is modeled through a Poisson distribution,

$$b_{ijk} - 1 \sim \text{Po}(\exp(\lambda_0 + f_B(\text{age}_{ij}) + d_B p_t + \beta_j + \eta_t)). \quad (2)$$

Only female influence is included in the above model; in the corresponding model where male influence on breeding is considered the index j is replaced by k on the right hand side. The fixed effects parameters are λ_0 , an intercept at the log scale; f_B , an age function of the same form as defined for survival but with parameter values c_2 , c_{2+} , c_3 , and c_r ; and d_B , density dependence in breeding performance through the standardized number of breeding pairs in the breeding seasons starting in year t , p_t . The individual random effects $\beta_j \sim \mathcal{N}(0, \tau_j^2)$ are constant through the life of the animal and independent between animals and $\eta_t \sim \mathcal{N}(0, \tau_\eta^2)$ are independent random year effects. To check that the individual random effects are not just a result of overdispersion relative to the Poisson distribution we also fitted a model where the individual random effects were replaced by a random effect for each breeding event. In this latter model we included linear female effects of adult age.

Links between the models of breeding performance and survival are made on the individual level by allowing the individual random effects for survival and breeding performance to be correlated with $\text{corr}(\alpha_{i(j)}, \beta_j) = \rho$ for all j . The function $i(j)$ is defined to pick out the correct survival random effect for, in this case, female j 's. The correlation is thus defined only for individuals having random effects in the breeding model. Individual random effects are sometimes, somewhat problematically, interpreted as latent "quality measures" (Wilson and Nussey 2010). Under such an interpretation, a negative correlation between individual random effects for two traits positively correlated to fitness would represent an individual level trade-off while a positive correlation would suggest that birds were of either low or high quality.

The model is set in a Bayesian framework and fixed effects parameters have normal priors with zero mean and variance 10^4 , the correlation parameters ρ have a uniform prior on the interval $(-1, 1)$ and the standard deviations of the random effects have folded t priors (Gelman 2006) with 10 degrees of freedom. All models are analyzed by Markov chain Monte Carlo (MCMC) methods using the program JAGS. Convergence is assessed by visual inspection of traceplots and by running four different chains with over-dispersed starting values and comparing the parameter estimates. Each starting value is drawn from a normal distribution centered at the posterior mean of an initial trial run but with a standard deviation 20 times larger than the

TABLE 1. DIC values, effective number of parameters (NP), and Bayesian *P* values for the models of breeding performance investigated.

Model	Age effects		Random effect breeding	Correlation	DIC	NP	<i>P</i>
	Breeding	Survival					
m1	f, l	l	f	-0.30 (-0.12, 0.70)	4821	141	0.17
m2	f, l	c	f	0.27 (-0.78, 1.00)	4821	142	0.18
m3	f, l		f		4822	143	0.17
m10	f, c	c	f	0.24 (-0.76, 1.00)	4824	145	0.17
m4	m, l	l	m	0.29 (-0.12, 0.67)	4830	125	0.12
m5	m, l	c	m	0.23 (-0.76, 1.00)	4830	127	0.12
m6	m, l		m		4831	127	0.12
m7	f, l		od		4832	217	0.37
m14	m, c	c	m	0.25 (-0.77, 1.00)	4839	131	0.12
m8	m, l				4865	17	0.00
m9	f, l				4867	17	0.01

Notes: The age effect on breeding may be a linear (l) or constant (c) effect of female (f) or male (m) age. For models where the individual random breeding effects are allowed to be correlated to the individual survival random effect, the type of age effect on survival is also shown. These are either linear (l) or constant (c). Except for year effects, which are included in all models, the breeding random effects are either individual female effects (f), individual male effects (m), or overdispersion (od). The columns for type of age effects, breeding random effect, and correlations provide a complete definition of each model.

standard deviation estimated from the trial. Sensitivity to priors is checked by fitting models under a prior of the random effects with ten times the standard deviation of the original folded *t* prior.

Model selection is based on the deviance information criterion (DIC, Spiegelhalter et al. 2002) which is a Bayesian alternative to AIC model selection. DIC values are easy to compute from MCMC samples of Bayesian hierarchical models since they avoid integrating the likelihood over the intermediate layers. Although breeding output and survival are not independent in the full model, we present DIC-values separately for these two parts.

Goodness of fit is assessed by Bayesian predictive *P* values, the posterior probability that a replicate data set has a worse fit than the observed data (Gelman et al. 2003). The Bayesian *P* values for the breeding performance and survival models are computed based on the deviance of the model at the Poisson and Bernoulli level, respectively. A low *P* value of the breeding model would for example indicate that the deviance of the data relative to the Poisson distribution is higher than expected and is a signature of a poor fit and overdispersion.

RESULTS

The data consist of 5351 survival events and 1576 successful breeding events involving 729 female breeders and 681 male breeders. The model selection and credible intervals show support for both senescence and individual random effects in breeding performance, especially in females (Table 1, Table A1 in Appendix A). The age pattern suggests that breeding performance increases from age 1 to age 2 and eventually decreases when birds get older (Fig. 1). The age pattern is robust across models with or without individual heterogeneity and is similar between models with male and female influence

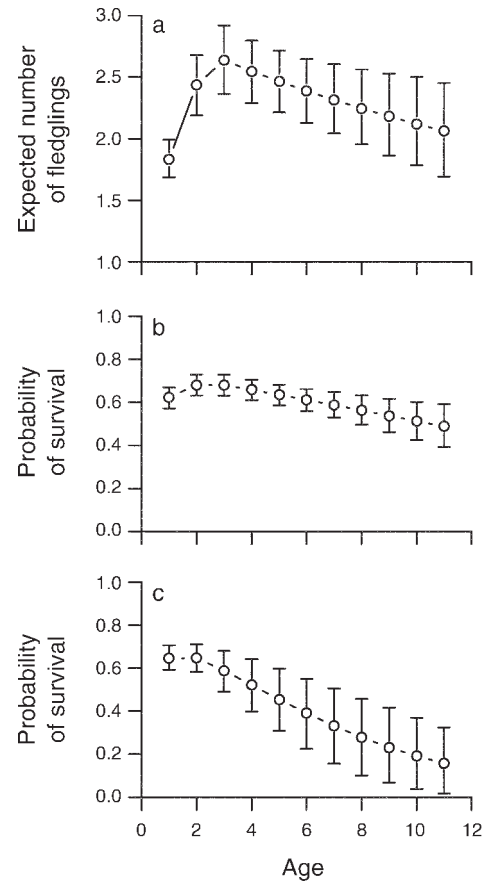


FIG. 1. (a) Posterior means and 95% credible intervals of the expected number of fledglings from successful breeding attempts and (b, c) probability of survival as a function of age. In panel (c), but not in panel (b), there is individual heterogeneity in survival. Estimates are computed with all random effects and effects of standardized covariates set to zero. The models used are: (a) model m2 defined in Table 1, (b) model m11 defined in Table 2, and (c) model m4 defined in Table 2.



PLATE 1. Allopreening Heron Island Silvereyes. Illustration credit: Jiro Kikkawa.

on breeding performance (compare posterior means of c_2 , c_3 , and c_r in Table A1). The latter similarity suggests that there may be some degree of confounding between male and female influences on breeding performance.

Female random effects are preferred over male random effects by the model selection criteria and are also preferred over the overdispersion model. The male random effects models have DIC values similar to the model with overdispersion (Table 1). The P values also show that overdispersion or individual random effects are needed to obtain an adequate fit of the Poisson distribution to the data (note the low P values for models m8 and m9). An additional model of breeding performance allowing for individual heterogeneity in the rate of senescence has a lower DIC value than the other models but otherwise gives nearly identical parameter estimates (Appendix B: Table B2).

Models including both heterogeneity and the possibility of senescence in survival all have much lower DIC values than the other models (Table 2). The DIC values for these models are, in contrast to DIC values for other models, sensitive to priors suggesting that DIC is not reliable in these cases. The corresponding variance component for survival has a high posterior mean ($\sigma_1 = 0.98$) and wide credible intervals (a 95% highest posterior density [HPD] interval of (0.49, 1.49); Table A2). In these models the precision of the estimates of senescence effects for survival was also low compared to models without individual heterogeneity (Fig. 1). This

indicates that there might be problems with identifiability of the individual variance component and the age effects in survival. This is further supported by the high effective number of parameters in the models with both heterogeneity and senescence parameters. It also means that the rate of senescence can not be estimated with precision since the rate of senescence increases with the variance of the individual heterogeneity (the posterior correlation between a_r and σ_1^2 in model m1 is -0.87). However, even the models without individual heterogeneity indicate senescence (Fig. 1, Table A2) and we therefore conclude that there is senescence also in survival.

The correlation between individual random effects for breeding performance and survival does not have any major effects on model selection. The posterior mean of the correlation is around 0.3 for most models but confidence intervals are wide, encompassing zero, and vary between models.

Both survival and breeding performance are influenced by a year effect but not by density dependence (Fig. A1, Table A2, Table A3).

Parameter estimates are essentially unchanged under the alternative priors on the random effects (Table A2 and A3). A model with unconstrained age effects also showed that the piecewise linear functions of age are consistent with the data (Appendix B: Fig. B1).

The age pattern for breeding success is similar to that for breeding performance with a marked increase from

TABLE 2. DIC values, effective number of parameters (NP), and Bayesian *P* values for the investigated models of survival.

Model	Age effects		Random effects		Correlation	DIC	NP	<i>P</i>
	Survival	Breeding	Survival	Breeding				
m4	l	m, l	yes	m	0.29 (−0.12, 0.67)	6628	546	0.45
m1	l	f, l	yes	f	0.30 (−0.12, 0.70)	6632	540	0.45
m11	l		no			6879	16	0.43
m12	c		no			6893	14	0.46
m5	c	m, l	yes	m	0.23 (−0.78, 1.00)	6894	31	0.45
m10	c	f, c	yes	f	0.24 (−0.76, 1.00)	6894	30	0.45
m13	c		yes			6894	30	0.45
m2	c	f, l	yes	f	0.27 (−0.78, 1.00)	6894	32	0.45
m14	c	m, c	yes	m	0.25 (−0.77, 1.00)	6894	31	0.46

Notes: The age effect on survival may be linear (l) or constant (c). If the individual random breeding effects are allowed to be correlated to the individual survival random effect, the type of age and random effect on breeding is also shown. The age effects are either linear (l) or constant (c) effects of female (f) or male (m) adult age. The breeding random effects are either individual female effects (f) or individual male effects (m).

age 1 to age 2 and a decline at older ages (Fig. B2). The variance of individual heterogeneity is high (Table B2), but we note that since breeding success is binary we cannot compare individual heterogeneity to overdispersion since the latter is not identifiable (this also applies to survival).

DISCUSSION

Interpreting individual heterogeneity random effects

The large difference in survival individual heterogeneity variance between the two age functions under study shows that heterogeneity estimates can be highly sensitive to model specification. Mortality selection is a direct effect of survival heterogeneity and is therefore difficult to separate from age dependent changes in survival (Hoem 1990). Any biological conclusions drawn about unobserved individual heterogeneity from survival data will therefore be uncertain and depend on the details of the model specification.

For breeding heterogeneity the situation is less clear. Since heterogeneity in breeding performance is not intrinsically linked to survival there is no automatic mortality selection. On the other hand, if individual survival or appearance heterogeneity is correlated with breeding heterogeneity, confounding between age effects and heterogeneity may again arise and could either mask or amplify age effects at the population level, depending on the sign of the correlation. The precise roles of such heterogeneities in the forming of age patterns are currently not well understood (Yashin et al. 2008). Here, model selection shows no support for a correlation between individual breeding performance and survival heterogeneity and both age effects and heterogeneity in breeding performance appear to be well estimated. There is some support for a positive correlation between individual breeding performance and breeding success (Appendix B), but estimates are imprecise. Exploratory model fits showed that correlations between individual breeding success and survival could not be reliably estimated, presumably because such correlation esti-

mates were driven by individuals that died at age 1 and never bred successfully and due to confounding between unsuccessful breeding attempts and breeding season mortality.

The specification of age structure can thus be crucial to estimates of individual heterogeneities just as heterogeneity can be crucial to estimates of age effects. Interpreting individual heterogeneity variance components is further complicated by the fact that random effects may pick up heterogeneity arising from other factors that were not included in the model and can be sensitive to outliers (e.g., Knappe et al. 2008). The very different conclusions about individual heterogeneity reached from two studies of the same data on Mute Swans (*Cygnus olor*; McCleery et al. 2008, Steiner et al. 2010) and two studies on Kittiwakes (*Rissa tridactyla*; Cam et al. 2002, Tuljapurkar et al. 2009) are illustrative of the model dependence of estimates and interpretations. It is therefore questionable to what extent the individual heterogeneity variance components could be interpreted biologically. Based on the results reported here we suggest that individual heterogeneity variance components are mainly treated as a statistical nuisance to improve the robustness in estimates of fixed effects, or possibly taken as a starting point in the search for explanatory covariates (see next section).

Implications for Silvereye life history traits

The extensive long-term data set for Silvereyes at Heron Island has been a rich source of information about population dynamics (Brook and Kikkawa 1998, McCallum et al. 2000) and evolution (Clegg et al. 2008). This study has elucidated potential roles of adult age and individual heterogeneity on both survival and fecundity as suggested in an earlier study (Kikkawa 2004). Individual heterogeneity in this population has been demonstrated for agonistic behavior (Kikkawa 1980), competitive abilities (Robinson-Wolrath and Owens 2003) and associated feeding habits (Scott et al. 2003), all presumably related to survival and reproduc-

tion. For example, Clegg et al. (2008) showed that culmen length has a nonlinear effect on adult survival in this population, although they did not look at the effect of adult age on survival. Thus there indeed is individual heterogeneity in survival, but these data are not available for all individuals and therefore not included in our study. If our heterogeneity estimates relate to quality differences among individuals, the relatively weak correlations between individual heterogeneity in breeding performance and survival suggest that the factors causing heterogeneity in survival may be different to those causing heterogeneity in breeding performance. On the other hand (still given that statistical heterogeneity represents quality differences), the positive correlation between individual breeding performance and breeding success could suggest that individuals that often breed successfully also tend to produce more fledglings when breeding. If in addition the quality differences are heritable, they could be a basis for microevolution in the population.

Our analysis is the first that has looked at the effects of adult age on fecundity and survival in this particular population. Similar to a recent study on Common Terns (*Sterna hirundo*; Rebke et al. 2010) we found a triangular shape in fecundity over age. Fecundity with respect to both breeding performance and breeding success increased from age 1 to age 2 and decreased at old ages, and we further found evidence of senescence in survival. Classical theory of evolution of senescence suggests that senescence should start around the age of first breeding, due to mortality causing reduction in selective pressure (decreased selection against deleterious mutations or antagonistic pleiotropy) after that age (Hamilton 1966). The senescence in breeding performance found here is fairly consistent with this hypothesis, but senescence is not evident until a few years after first breeding. Most silvereyes breed for the first time at an age of one or two years and while the exact onset of senescence is difficult to determine, peak breeding performance occurs around age 3–4 as shown by the models with unconstrained age effects (Figs. B1, B2). Using model c1 (Appendix B) and model m1, the resultant rate of decline in fecundity due to decline both in the number of fledglings and in the probability of breeding is approximately 0.11 fledglings per year between age 3 and 11.

In one of relatively few previous studies accounting for individual heterogeneity in wild animals, Bouwhuis et al. (2009) investigated age effects in breeding performance of Great Tits (*Parus major*), a species of roughly the same size and longevity as Silvereyes but with a different breeding biology (e.g., fewer clutches with larger clutch size). Peak reproduction occurred around age 3 and reproductive performance increased from age 1 to age 2. Although the measure of breeding performance differ between the studies in that Bouwhuis et al. (2009) included some but not all zero breeding outputs, the similarity in peak age of reproductive

performance between Silvereyes and Great Tits is at least coherent with the idea that senescence is largely determined by size and longevity (Jones et al. 2008).

For survival, the rate of senescence is uncertain (Fig. 1) and we see no way of estimating its onset while accounting for individual heterogeneity. In contrast to a few other studies (e.g., Cam et al. 2002), senescence in survival was detected even when individual heterogeneity was not accounted for. We conclude that individual heterogeneity in this population is not strong enough to mask senescence in survival and that the reproductive pattern as a function of age has a triangular shape.

ACKNOWLEDGMENTS

We are grateful to Tim Coulson, Torbjørn Ergon, and James Russell for valuable comments and suggestions that helped improve the manuscript. Jonas Knape and Niclas Jonzén were financially supported by the Swedish Research Council. The field data were collected jointly with Carla Catterall on Heron Island under the permits from Environment Australia and Queensland Parks and Wildlife Service, and the project was supported by the Australian Research Council and the University of Queensland.

LITERATURE CITED

- Bjørnstad, O. N., and T. F. Hansen. 1994. Individual variation and population dynamics. *Oikos* 69:167–171.
- Bouwhuis, S., B. C. Sheldon, S. Verhulst, and A. Charmantier. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proceedings of the Royal Society B* 276:2769–77.
- Brook, B. W., and J. Kikkawa. 1998. Examining threats faced by island birds: a population viability analysis on the Capricorn silvereye using long-term data. *Journal of Applied Ecology* 35:491–503.
- Cam, E., W. A. Link, E. G. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual covariation in life history traits: seeing the trees despite the forest. *American Naturalist* 159:96–105.
- Catterall, C. P., J. Kikkawa, and C. Gray. 1989. Inter-related age-dependent patterns of ecology and behaviour in a population of silvereyes (Aves: Zosteropidae). *Journal of Animal Ecology* 58:557–570.
- Clegg, S. M., F. D. Frentiu, J. Kikkawa, G. Tavecchia, and I. P. F. Owens. 2008. 4000 years of phenotypic change in an island bird: heterogeneity of selection over three microevolutionary timescales. *Evolution* 62:2393–2410.
- Degnan, S. M. 1993. Genetic variability and population differentiation inferred from DNA fingerprinting in silvereyes (Aves: Zosteropidae). *Evolution* 47:1105–1117.
- Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Analysis* 1:515–533.
- Gelman, A., J. B. Carlin, H. S. Stern, and D. R. Rubin. 2003. *Bayesian data analysis*. Chapman and Hall, London, UK.
- Gimenez, O., and R. Choquet. 2010. Individual heterogeneity in studies on marked animals using numerical integration: capture–recapture mixed models. *Ecology* 91:951–957.
- Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology* 12:12–45.
- Hoem, J. M. 1990. Identifiability in hazard models with unobserved heterogeneity: the compatibility of two apparently contradictory results. *Theoretical Population Biology* 37:124–128.
- Jones, O. R., et al. 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecology Letters* 11:664–673.

- Kikkawa, J. 1980. Winter survival in relation to dominance classes among silvereyes *Zosterops lateralis chlorocephala* of Heron Island, Great Barrier Reef. *Ibis* 122:437–446.
- Kikkawa, J. 2003. The Capricorn white-eye *Zosterops chlorocephalus*. *Sunbird* 33:64–76.
- Kikkawa, J. 2004. The eye of the white-eye: mechanisms of behaviour, ecology and evolution. [In Japanese.] Kaiyusha, Tokyo, Japan.
- Kikkawa, J., and J. M. Wilson. 1983. Breeding and dominance among the Heron Island silvereyes *Zosterops lateralis chlorocephala*. *Emu* 83:181–198.
- Knape, J., M. Sköld, N. Jonzén, M. Åkesson, S. Bensch, B. Hansson, and D. Hasselquist. 2008. An analysis of hatching success in the great reed warbler *Acrocephalus arundinaceus*. *Oikos* 117:430–438.
- Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the “animal model.” *Philosophical Transactions of the Royal Society B* 359:873–890.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Loison, A., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and J.-M. Jullien. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80:2539–2554.
- McCallum, H., J. Kikkawa, and C. Catterall. 2000. Density dependence in an island population of silvereyes. *Ecology Letters* 3:95–100.
- McCleery, R., C. Perrins, B. Sheldon, and A. Charmantier. 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. *Proceedings of the Royal Society London B* 275:963–970.
- Nussey, D. H., T. Coulson, M. Festa-Bianchet, and J.-M. Gaillard. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology* 22:393–406.
- Rebke, M., T. Coulson, P. H. Becker, and J. W. Vaupel. 2010. Reproductive improvement and senescence in a long-lived bird. *Proceedings of the National Academy of Sciences USA* 107:7841–7846.
- Robertson, B. C., S. M. Degnan, J. Kikkawa, and C. C. Moritz. 2001. Genetic monogamy in the absence of paternity guards in the Capricorn silvereye, *Zosterops lateralis chlorocephalus*, on Heron Island. *Behavioural Ecology* 12:666–673.
- Robinson-Wolrath, S. I., and I. P. F. Owens. 2003. Large size in an island-dwelling bird: intraspecific competition and the dominance hypothesis. *Journal of Evolutionary Biology* 16:1106–1114.
- Scott, S. N., S. M. Clegg, S. P. Blomberg, J. Kikkawa, and I. P. F. Owens. 2003. Morphological shifts in island-dwelling birds: the roles of generalist foraging and niche expansion. *Evolution* 57:2147–2156.
- Spiegelhalter, D. J., N. G. Best, and B. G. Carlin. and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society B* 64:583–639.
- Steiner, U. K., S. Tuljapurkar, and S. H. Orzack. 2010. Dynamic heterogeneity and life history variability in the kittiwake. *Journal of Animal Ecology* 79:436–444.
- Tuljapurkar, S., U. K. Steiner, and S. H. Orzack. 2009. Dynamic heterogeneity in life histories. *Ecology Letters* 12:93–106.
- van de Pol, M., and S. Verhulst. 2006. Age-dependent traits: a new statistical model to separate within- and between-individual random effects. *American Naturalist* 167:766–773.
- Vaupel, J. W., and A. I. Yashin. 1985. Heterogeneity's ruses: some surprising effects of selection on population dynamics. *American Statistician* 39:176–185.
- Vindenes, Y., S. Engen, and B.-E. Saether. 2008. Individual heterogeneity in vital parameters and demographic stochasticity. *American Naturalist* 171:455–467.
- Wilson, A. J., and D. H. Nussey. 2010. What is individual quality? An evolutionary perspective. *Trends in Ecology and Evolution* 25:207–214.
- Yashin, A. I., K. G. Arbeev, I. Akushevich, A. Kulminski, L. Akushevich, and S. V. Ukraintseva. 2008. Model of hidden heterogeneity in longitudinal data. *Theoretical Population Biology* 73:1–10.
- Zens, M. S., and D. R. Peart. 2003. Dealing with death data: individual hazards, mortality and bias. *Trends in Ecology and Evolution* 18:366–373.

APPENDIX A

Parameter estimates and figure of environmental variation (*Ecological Archives* E092-069-A1).

APPENDIX B

Additional models fitted to test model assumptions (*Ecological Archives* E092-069-A2).