



# Static and dynamic expression of life history traits in the northern fulmar *Fulmarus glacialis*

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Understanding the static and dynamic expression of life history traits is a prerequisite for the development of a causal theory of the evolution of aging and of life histories. We analyzed the statics and dynamics of reproduction and survival in a wild population of the northern fulmar, *Fulmarus glacialis* (Procellariidae). Survival rate is most influenced by year as compared to age and cohort. When temporal variation is ignored, survival rate increases slowly with age and then declines more rapidly at late ages. Survival rate contingent upon reproductive ‘stratum’ (producing an egg, hatching an egg, fledging a hatchling) also exhibits this pattern. Survival and reproduction have a positive static association in that survival rate increases as the apparent energy allocated to reproduction increases (as indexed by stratum). There is a broad distribution of realized lifetime reproductive success, which could be due to ‘fixed’ heterogeneity, with some individuals always having low survival and reproduction and others always having high survival and reproduction, or be due to ‘dynamic’ heterogeneity, with all individuals having the same expected reproductive and survival rates. Analysis of stochastic stratum dynamics indicates that individuals do not remain long in any given stratum and suggest that the variation among individuals with respect to lifetime reproductive success is due to dynamic heterogeneity. The probability of producing an egg increases with age for both sexes, whereas the probability of producing a fledgling initially declines with age and then increases. These results underscore the necessity of understanding the static and dynamic expression of demographic traits when making a causal claim about their evolution.

Important claims for (Hamilton 1966) and against (Hayflick 2000) the occurrence of senescence of reproduction and survival in natural populations were predictions as to what “must” occur, as opposed to being claims based on a broad foundation of data. We now know that reproduction and survival decline with age in some taxa, are constant with age in other taxa, and increase with age in still others (Curio 1983, Ezard et al. 2007, Limmer and Becker 2009, Vieyra et al. 2009). These results challenge us anew to understand the biology of aging at the empirical and theoretical levels (Finch and Austad 2001, Vaupel et al. 2004, Baudisch 2008). Central to this endeavor are long-term studies of individual lives (Cam and Monnat 2000, Nussey et al. 2008). Such studies license more than the traditional (and important) static ‘snapshot’ assessment of differences among individuals; what they license is an analysis of the dynamics of expression of traits by individuals. The development of a causal theory of aging requires an understanding of the statics and of the dynamics of demographic traits; this is the approach of Featherman and Petersen (1986), who wrote (p. 342) that a “focus on labile process or on the dynamics of reversible change avoids the undesirable conflation of aging with either progressive or regressive states exclusively”. This focus underlies our prior empirical and conceptual work (Orzack et al.

unpubl., Li and Schmiedek 2002, Tuljapurkar et al. 2009, Steiner et al. 2010).

Our overall goal is to understand the ecological and evolutionary basis of expression of reproduction and survival in natural populations, without a preconception about what ‘must’ occur. Here, we analyze individual data from a long-term study of the northern fulmar, *Fulmarus glacialis*, at a colony on Eynhallow, in the Orkney Islands, Scotland. Our analysis consists of three facets. The first is the investigation of the influences of age, cohort and year on survival. The second is the investigation of the statics and dynamics of reproduction and survival and of their relationship. The third is the investigation of the influence of age on reproduction.

## Material and methods

### Study population

The study of the Eynhallow population was started in 1951 by Robert Carrick and George M. Dunnet. An overview of the study can be found in Dunnet (1991) and Ollason and Dunnet (1988) (see also Michel et al. 2003, Grosbois and Thompson 2005, Lewis et al. 2009). The 382 males and

415 females in our analysis were recorded as reproducing on Eynhallow between 1958 and 1995.

Reproductive investment differs between the sexes in obvious ways (the female lays the egg) and also in more subtle ways (e.g. males spend more time on the nest, Macdonald 1977, Ollason and Dunnet 1978, 1988) but the involvement of both sexes prior to egg laying through fledging allowed us to assign a reproductive outcome to each individual. A pair can remain mated for many years (Lewis et al. 2009), although individuals can change mates; this dependence between the female data and male data led us to analyze them separately.

### Survival rates

We used capture–mark–recapture methods to estimate survival rate (Lebreton et al. 1992) because no deaths were recorded. We assessed the influence of age, cohort and year on survival rate. Age was defined relative to first reproduction since few individuals were of known absolute age (Ollason and Dunnet 1978 reported that the average age at first reproduction was 8.4 for males and 10.3 for females; both estimates have standard errors of less than one year). The age-independent survival rate was defined as the proportion of individuals alive at time  $t$  that were alive at time  $t + 1$ . The age-dependent survival rate for age  $i$  ( $i \geq 1$ ) was defined as the proportion of age  $i$  individuals that were alive at age  $i + 1$ . There were separate estimates for ages 1 to 24 and an aggregate estimate for individuals 25 years and older (since few individuals survived past age 25).

In our first analysis of the relationship between reproduction and survival, we assessed the influence on survival rate of fixed and dynamical reproductive covariates (Moyes et al. 2006). The former were the ages at which the first hatchling and the first fledgling were produced. The latter were the cumulative numbers of hatchlings and fledglings at a given age.

In our second analysis of the relationship between reproduction and survival, we used the approach of Nichols et al. (1994) to assess the influence on age-dependent survival rate of the following reproductive ‘strata’: ‘egg’ – laying an egg (that did not hatch), ‘hatch’ – laying and hatching an egg (that did not fledge), and ‘fledge’ – laying, hatching and fledging an egg. Estimates of stratum-specific resighting probabilities and stratum-specific transition probabilities were age-independent; no qualitative conclusions were affected by this assumption since the age-dependence of resighting probabilities and of transition probabilities was weak.

All models of the relationship between reproduction and survival were time-invariant. The logit link was used for all model fitting. Analyses were done using the program MARK (Cooch and White 2010). Further details are available upon request.

### Reproduction

We used mixed-effect analyses to assess the age-dependence of egg production and of fledging production (Pinheiro and Bates 2004). The expectation of the response variable was the logit of the probability of reproduction in a given year.

The predictor was a constant, linear or quadratic function of age. Individuals were treated as random effects influencing all of the terms in a given model. We used the R routine `lme4` available at <http://cran.r-project.org/>. In these analyses, all eggs contributed to egg outcomes (in contrast to the stratum analyses, in which the egg and fledge strata were defined exclusively of one another).

### Model selection

Comparisons between models were based upon the Akaike information criterion (AIC); in most analyses, it was corrected for sample size and for overdispersion (QAICc). The estimate of overdispersion was calculated via logistic regression for the most general model under consideration (Cooch and White 2010); in our covariate analyses of survival rate, dispersion was estimated from an otherwise identical model that lacked the covariate. We interpreted a difference of 2 or more units between AIC or QAICc values to indicate that two models differed in support (Burnham and Anderson 2002). A negative difference supports the first model and a positive difference supports the second model.

## Results

### The dynamics of survival rates

We assessed the influence of age, cohort and year on survival rate (Table 1). For females, the QAICc difference of  $-31$  between model 1, which has an age-independent survival rate, and model 2, which has age-dependent survival rates, suggests that survival rate is better viewed as age-independent. For males, the QAICc difference of  $-14$  supports the same conclusion. We next compared model 1 with model 3, which has cohort-dependent survival rates. Their QAICc difference is 14 for females and 113 for males, which suggests that there is more support for cohort variation than for an age-independent model.

Finally, we next compared model 2 and 3 with model 4, which has year-dependent survival rates. The resulting QAICc differences were positive for both sexes, which suggests that annual variation of survival rates is greater than variation due to age and cohort. Linear and quadratic models fit to the time series of annual survival rates have more support than does model 4; these parametric models have approximately equal support (Orzack et al. unpubl.). The linear model predicts a declining trend of survival rates; the first estimated annual survival rates are 0.96 (females) and 0.97 (males) and the last estimated annual survival rate for both sexes is 0.88. This decline was also found by Grosbois and Thompson (2005).

The analyses in Table 1 suggest that survival rate is best viewed as mainly influenced by external environmental variation rather than by age or cohort. This underscores the need to understand the larger context in which a species’ demography is expressed. An investigator might reasonably stop at this point after concluding that age is an unimportant influence on survival rates of this species.

However, in keeping with the focus of many demographers, we now examine the influence of age on survival rates.

Table 1. Models describing the influence of age, cohort, and year on the survival rate.

Model no.	Model for female survival rate and resighting probability	QAICc	Delta QAICc	QAICc weight	No. of parameters	Deviance
4	Year-dependent	5984.45	0.00	1.00	69	4080.25
3	Cohort-dependent	6073.95	89.50	0.00	72	4163.37
1	Age-independent	6088.36	103.91	0.00	2	4322.37
2	Age-dependent	6119.07	134.62	0.00	49	4256.97

QAICc values based on an estimate of overdispersion from model 3 = 1.06.

Model no.	Model for male survival rate and resighting probability	QAICc	Delta QAICc	QAICc weight	No. of parameters	Deviance
4	Year-dependent	6036.63	0.00	1.00	68	4216.41
3	Cohort-dependent	6067.00	30.36	0.00	70	4242.54
1	Age-independent	6179.92	143.28	0.00	2	4495.63
2	Age-dependent	6193.23	156.60	0.00	47	4417.07

QAICc values based on an estimate of overdispersion from model 3 = 1.06.

Our intent is to illustrate a point about the dimensionality of standard demographic analyses and not to endorse the dismissal of environmental variation as an important influence on the demography of natural populations.

### The age-dependence of survival rates

Survival rates for ages 1 – 25 are shown in Fig. 1A for females and in Fig. 1B for males. A parametric model with quadratic age-dependency on the logit scale has more support than a linear model (the QAICc difference is –4 for females and –10 for males). For both sexes, this suggests that survival rates increase slowly until mid-life and then decline at older ages; note that the estimate for ‘age’ 25 encompasses all older ages (the presence of an estimated decline at the end of life is not dependent upon this amalgamation). These results agree and disagree with previous analyses. Dunnet and Ollason (1978) claimed that survival rate declined with age (although the trend was fitted by eye), but later analysis (Buckland 1982) apparently caused Dunnet (1991) to rescind this claim. Neither of these claims distinguished between females and males.

A typical assessment about survival rates like those in Fig. 1 is that they decline in an ‘overall’ sense. This view usually underwrites a claim that the decline is caused by unavoidable physiological senescence. We discuss below why the observed pattern is not sufficient by itself to support this claim (see also Vaupel and Yashin 1985, Blarer et al. 1995).

### The influence of fixed and dynamical reproductive covariates on survival rates

We assessed the influence of reproduction up to and including a given age on the ‘aggregate’ survival rate (= the survival rate for all individuals of that age and older). In all but two cases (as noted in Table 2), a model with such a survival rate has much more support than does an age-dependent model.

As shown in Table 2, the aggregate survival rate based on the covariate ‘age of first hatchling’ (AFH) or ‘age of first fledgling’ (AFF) is always greater than the survival rate without the covariate. For example, for the 314 females who

produced their first hatchling by age two, the estimated survival rate was 0.93 with AFH and 0.90 without AFH. Similarly, for the 241 females who had produced their first fledgling by age two, the estimated survival rate predicted was 0.93 with AFF and 0.90 without AFF. In addition, the estimated survival rate decreases as individuals who reproduced earlier are excluded (e.g. compare the survival rate for, say, AFH = 2 and AFH = 12). Although the various AFH and AFF categories are not independent (e.g. all individuals with  $AFH \leq 2$  have  $AFH \leq 12$ ), we conclude that early energy allocation to the first offspring is associated with increased survival.

The analyses of dynamical covariates are shown in Table 3. For females, cumulative hatchling production has a negative influence on aggregate survival rate (age = 2 and 4), no influence (age = 12 and 16), or a positive influence (age = 8 and 20); all influences are slight. For example, for age = 2, females with one hatchling had an estimated subsequent survival rate of 0.93, whereas females with two hatchlings had an estimated survival rate of 0.92. Few individuals produce more than four hatchlings or fledglings.

For males, cumulative hatchling production has a slight positive influence on the survival rate for all values of age. For example, for age = 2, a male with one hatchling had an estimated survival rate of 0.93, whereas a male with two hatchlings had an estimated survival rate of 0.94.

The results for cumulative fledgling production are similar. There are slight mixed trends for females as fledgling number increases and slight positive trends for males.

These results support the claim that the relationship between reproduction and survival differs between females and males. Among females, the negative trends are for individuals who reproduce early (age = 2 and 4). Perhaps the creation of the egg is a special burden for young females. Older females appear to not be affected by this task, as indicated by the flat or increasing trends for larger values of age. We view these as tentative inferences, given the slight magnitude of the changes and the uncertainty of the estimates (not shown).

The physiological implications of the fixed and dynamical covariate analyses are partially complementary. The fixed analysis implies that reproduction and survival are positively

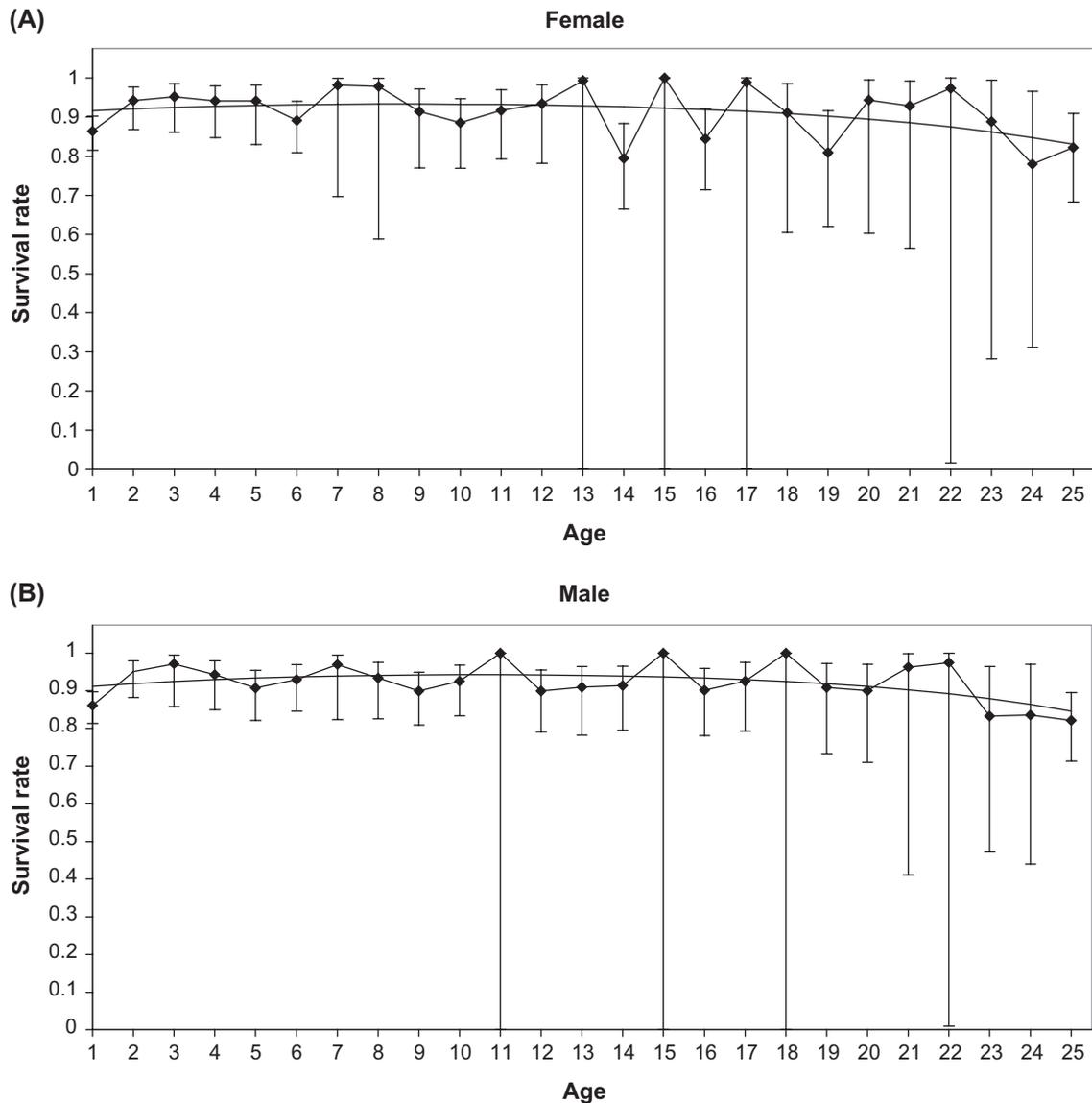


Figure 1. Age-specific survival rates for females (A) and males (B). Estimates from model 2 in Table 1 are shown with 95% confidence intervals. Parametric estimates derived from a quadratic model are shown as a smooth curve.

associated in both sexes. The dynamical analysis implies the same for males and for older (but not younger) females.

### The multi-stratum analysis of reproduction and survival

We assessed whether the age-dependency of survival rates depends on the reproductive stratum. One motivation was previous work on the mute swan (Orzack et al. unpubl.) in which there was no ‘senescent’ decline of survival rate for the reproductive stratum with the most energetic cost even though there was a ‘senescent’ decline for the non-stratified survival rate. To this extent, it would be a mistake to regard the latter decline as being caused by unavoidable physiological decline. The absence of decline for the stratum with the high reproductive cost suggests that the expression of survival is not subject to a tradeoff, at least within a given year; instead, it appears that better reproduction and survival reinforce one another within a given year (Discussion).

The need to distinguish between demographic pattern and process is in keeping with our goal of focusing on ‘labile process’ so as to avoid conflating ‘aging with either progressive or regressive states exclusively’.

We first fit model 1 (Table 4), which has non-stratified age-dependent survival rates (it also has transition probabilities between strata). As expected, the survival rate estimates associated with model 1 are close to those in Fig. 1. A quadratic model also best fits the trend of age-specific survival rates (not shown).

Model 2, 3, 4 and 5 contain stratified age-specific survival rate estimates. Model 2 contains separate estimates for each stratum, while model 3, 4 and 5 contain estimates for combinations of strata. Model 3, which has estimates for the egg stratum and for the combined hatch and fledge strata, has the most support. This may indicate that producing an egg is qualitatively different (for either sex) than hatching the egg or fledging the hatchling. None of these stratified models has more support than non-stratified model 1.

Table 2. Models describing the influence of the covariates age of first hatchling (AFH) and age of first fledgling (AFF) on the aggregate survival rate for all ages greater than AFH or AFF. All models have age-dependent resighting probabilities. Range denotes the span of ages with survival rates potentially influenced by the covariate. All estimates are based upon a model in which the survival rate estimate is age-independent except where \* denotes an average over age-specific survival rates (because the model with most support has age-dependent survival rates).

AFH	Range	Female survival rate			Male survival rate		
		With covariate	Without covariate	n	With covariate	Without covariate	n
2	2 – 25	0.93	0.90	314	0.93	0.91	277
4	4 – 25	0.92	0.90	337	0.93	0.91	299
8	8 – 25	0.91	0.90	354	0.92	0.91	316
12	12 – 25	0.90	0.88	358	0.91*	0.90	321

AFF	Range	Female survival rate			Male survival rate		
		With covariate	Without covariate	n	With covariate	Without covariate	n
2	2 – 25	0.93	0.896	241	0.93	0.91	219
4	4 – 25	0.92	0.890	274	0.93	0.91	251
8	8 – 25	0.91	0.897	307	0.93	0.91	284
12	12 – 25	0.90	0.878	314	0.90*	0.90	289

The interaction between reproduction and survival is more clearly understood by the use of parametric models, which also have more support than models without a function describing survival rate (Table 4). We fit linear and quadratic models on the logit scale; only the quadratic models are shown, as each had more support than did the associated linear model.

For females and for males, model 9, which contains the egg stratum and a combined hatch and fledge stratum, has the most support. Survival rates for the egg stratum increase with age and then eventually decline; this is especially evident for males (Fig. 2, 3). The evolutionary implications of the stratum-specific patterns are addressed in the Discussion.

### Stochastic stratum dynamics

The transition probabilities between reproductive strata as described by a first-order Markov process are shown in Table 5. These estimates were generated by model 9 in Table 4; all models in Table 4 produced similar estimates.

The temporal autocorrelation,  $\rho$ , associated with the transition matrix measures the asymptotic tendency for individuals to remain in any given stratum. For females, the estimate of  $\rho$  is 0.225; for males, the estimate is 0.250. The coefficient defined by Dobrushin (1956) provides a non-asymptotic estimate of this tendency (Seneta 1979); the estimated coefficient is 0.245 for females and 0.261 for males. These estimates do not account for mortality; estimates of  $\rho$  that do so are 0.229 for females and 0.260 for males (see Matthews 1970 for the method of calculation).

The half-life of stratum residence time can be estimated as  $-1/\ln|\rho|$ . Using the mortality-adjusted values of  $\rho$ , the estimated half-life is 0.68 year for females and 0.74 year for males. This is much shorter than the average relative age of the last (observed) reproduction, which is approximately

Table 3. The estimated aggregate survival rate after a given age as a function of the amount of cumulative hatchling or fledgling production up to and including the given age. For a given age, the integer number of hatchlings or fledglings closest to the observed average number is marked by an italicized survival rate.

		Females: no. of hatchlings					
		1	2	3	4	5	6
Age	2	0.93	0.92				
	4	0.93	0.92	0.92	0.91		
	8	0.91	0.91	0.91	0.91	0.92	0.92
	12	0.90	0.90	0.90	0.90	0.90	0.90
	16	0.89	0.89	0.89	0.89	0.89	0.89
	20	0.87	0.87	0.87	0.87	0.88	0.88

		Males: no. of hatchlings					
		1	2	3	4	5	6
Age	2	0.93	0.94				
	4	0.91	0.93	0.94	0.95		
	8	0.92	0.92	0.92	0.93	0.93	0.93
	12	0.91	0.91	0.91	0.91	0.92	0.92
	16	0.89	0.89	0.89	0.90	0.90	0.90
	20	0.86	0.87	0.87	0.87	0.87	0.87

		Females: no. of fledglings					
		1	2	3	4	5	6
Age	2	0.93	0.92				
	4	0.93	0.92	0.92	0.91		
	8	0.90	0.91	0.91	0.91	0.92	0.92
	12	0.89	0.90	0.90	0.90	0.90	0.90
	16	0.89	0.89	0.89	0.89	0.89	0.89
	20	0.86	0.87	0.87	0.88	0.88	0.88

		Males: no. of fledglings					
		1	2	3	4	5	6
Age	2	0.93	0.94				
	4	0.91	0.93	0.94	0.95		
	8	0.92	0.92	0.92	0.93	0.93	0.93
	12	0.91	0.91	0.91	0.92	0.92	0.92
	16	0.89	0.90	0.90	0.90	0.90	0.90
	20	0.87	0.87	0.87	0.87	0.88	0.88

10 years for both sexes; this is an underestimate because there are many right-censored individuals late in the time series. This lack of fidelity influences lifetime reproductive success (LRS). There are two explanations for the observed heterogeneity of LRS among individuals. It could be ‘dynamic’ heterogeneity, as generated by the stochastic stratum dynamics described above; it could also be ‘fixed’ heterogeneity arising from innate or acquired quality or frailty differences (Tuljapurkar et al. 2009). Of course, dynamic and fixed heterogeneity could both be present.

We used Monte Carlo simulation to assess whether dynamic heterogeneity is a sufficient explanation of the observed distribution of LRS. Our two measures of LRS were the total number of hatchlings and the total number of fledglings.

In order to generate a simulated distribution of LRS based on the assumption that there is no fixed heterogeneity among individuals, we first created a set of individual life

Table 4. Models describing the relationship between survival rates and reproductive strata. E denotes egg, H denotes hatch, and F denotes fledge.

Females						
Model no.	Model for survival rate	QAICc	Delta QAICc	QAICc weight	No. of parameters	Deviance
9	Quad (Strata: E ≠ H = F)	9375.89	0.00	0.56	13	8168.15
6	Quad (No Strata: E = H = F)	9378.19	2.29	0.18	10	8176.50
7	Quad (Strata: E ≠ H ≠ F)	9379.52	3.63	0.09	16	8165.70
10	Quad (Strata: E = F ≠ H)	9379.79	3.89	0.08	13	8172.04
8	Quad (Strata: E = H ≠ F)	9381.00	5.11	0.04	13	8173.25
1	No Strata: E = H = F	9389.61	13.72	0.00	30	8147.22
3	Strata: E = H ≠ F	9409.28	33.39	0.00	49	8127.56
4	Strata: E ≠ H = F	9410.23	34.33	0.00	48	8130.60
5	Strata: E = F ≠ H	9413.45	37.56	0.00	48	8133.82
2	Strata: E ≠ H ≠ F	9420.32	44.42	0.00	62	8111.32

QAICc values based on an estimate of overdispersion from model 2 = 1.07.

#### Males

Model no.	Model for survival rate	QAICc	Delta QAICc	QAICc weight	No. of parameters	Deviance
9	Quad (Strata: E ≠ H = F)	9075.12	0.00	0.85	13	8008.57
7	Quad (Strata: E ≠ H ≠ F)	9078.68	3.56	0.14	16	8006.05
8	Quad (Strata: E = H ≠ F)	9088.26	13.14	0.01	13	8021.71
10	Quad (Strata: E = F ≠ H)	9093.65	18.53	0.00	13	8027.10
6	Quad (No Strata: E = H = F)	9094.04	18.92	0.00	10	8033.55
1	No Strata: E = H = F	9104.70	29.57	0.00	28	8007.62
4	Strata: E ≠ H = F	9115.94	40.82	0.00	51	7971.32
5	Strata: E = F ≠ H	9120.23	45.11	0.00	43	7992.25
3	Strata: E ≠ H ≠ F	9130.86	55.74	0.00	48	7992.50
2	Strata: E ≠ H ≠ F	9135.75	60.62	0.00	61	7970.17

QAICc values based on an estimate of overdispersion from model 2 = 1.09.

history trajectories. Each had an age of last reproduction that matched an observed (apparent) age of last reproduction in the data set (sampling without replacement). This ensemble of trajectories formed a synthetic cohort of size 415 for females and of size 382 for males.

Any given life history trajectory *i* was assigned a reproductive history (stratum sequence) by sampling with replacement from among 3000 stratum sequences generated by the transition matrix shown in Table 5. The proportion of each stratum sequence in the sampled-by-replacement distribution was its associated probability of surviving to the age of last reproduction for trajectory *i*. This probability was generated by the multiplication of the one-year survival rates associated with the stratum sequence. The survival rates and the transition probabilities were derived from Model 9 in Table 4.

We created 50 synthetic cohorts in this way so as to estimate the mean and variance of the distribution of LRS generated by dynamic heterogeneity.

Figure 4 and 5 show the observed distribution of LRS and the average distribution of LRS for the 50 synthetic cohorts. For females, the Kolmogorov–Smirnov (KS) test of stochastic similarity indicates that the observed and predicted distributions are not significantly different ( $\alpha = 0.05$ ) (fledglings: test statistic = 0.2632,  $p = 0.5262$ ; hatchlings: test statistic = 0.3333,  $p = 0.193$ ). One-sided KS tests to assess whether the observed distribution is stochastically less than the predicted distribution (implying that some females have fixed high quality) or stochastically greater (implying

that some females have fixed low quality) are not significant (not shown). For males, the KS test indicates that the observed and predicted distributions are not significantly different (fledgling: test statistic = 0.25,  $p = 0.4413$ ; hatchlings: test statistic = 0.2133,  $p = 0.633$ ). One-sided KS tests do not support a claim that there is an excess of low or high quality males (not shown). These results support the claim that the observed distribution of LRS for each sex is determined by dynamic heterogeneity (see Tuljapurkar et al. 2009 for similar results for other species). The apparent absence of fixed heterogeneity is consistent with the action of strong purifying natural to create a local trait optimum (Orzack and Sober 1994a, 1994b).

### The age-dependency of reproduction

We used AIC for model selection here because the estimates of the scaled deviance for both traits were close to 1.0.

There was most support for a linear influence of age on the logit of the probability of egg production (for females the AIC difference for this model as compared to the quadratic model was  $-7$ ; for males the AIC difference was  $-8$ ). As shown in Fig. 6, the estimated probability of egg production increases with age. The increasing discrepancy between male and female estimates as age increases suggests that males benefit more from age than do females.

There was most support for a quadratic influence of age on the logit of the probability of fledgling production (for

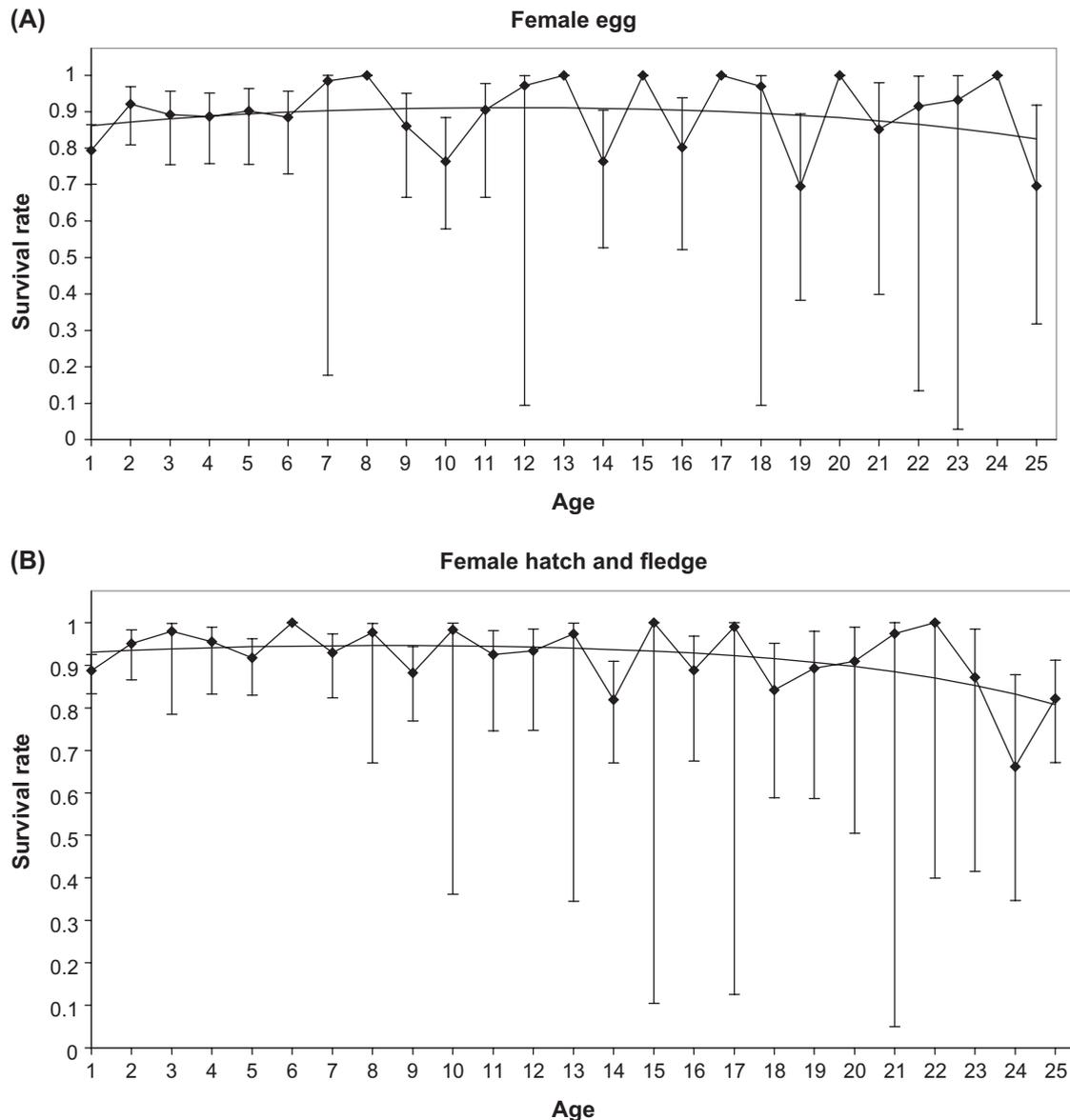


Figure 2. Age-specific survival rates for female egg stratum (A) and combined hatch and fledge strata (B). Estimates from model 4 in Table 4. 95% confidence intervals are shown. Parametric estimates from model 9 in Table 4 are shown as a smooth curve.

females the AIC difference for this model as compared to the linear model was  $-21$ ; for males the AIC difference was  $-8$ ). As shown in Fig. 6, the probability of fledging success declines but eventually increases (Dunnet and Ollason 1978 noted that breeding success was positively associated with age).

## Discussion

The study of the influence of environmental variation on the demography of natural populations has until recently been very limited as compared to the study of the influence of age. Reasons for this neglect include the beliefs that stochastic analyses are 'difficult', that deterministic analyses provide a 'mean field approximation' of reality, and that any analysis must omit something. None of these is compelling enough to sustain the lack of attention to environmental variation and more and more recent work includes analyses

of environmental variation (Lande et al. 2003, Tavecchia et al. 2005, Oro et al. 2010, van de Pol et al. 2010). Our finding that environmental variation exerts a stronger influence on survival than does age (or cohort) is a reminder of the need for broader analyses. It is telling to think that a biologist might examine Table 1 and wonder why age gets so much attention.

The goal of our examination of the interaction between reproduction and survival is to properly understand the causal basis of changes of age-specific survival rates. Traditionally, declining late-age survival rates like those in Fig. 1 are viewed as being caused by unavoidable physiological senescence resulting from the ever-increasing accumulation of deleterious mutations and/or the increasing expression of the negative effects of pleiotropy.

Our analysis provides several reasons as to why such a conclusion can be misleading. First, estimates of survival rate increase until mid-life. This is most evident for the egg stratum

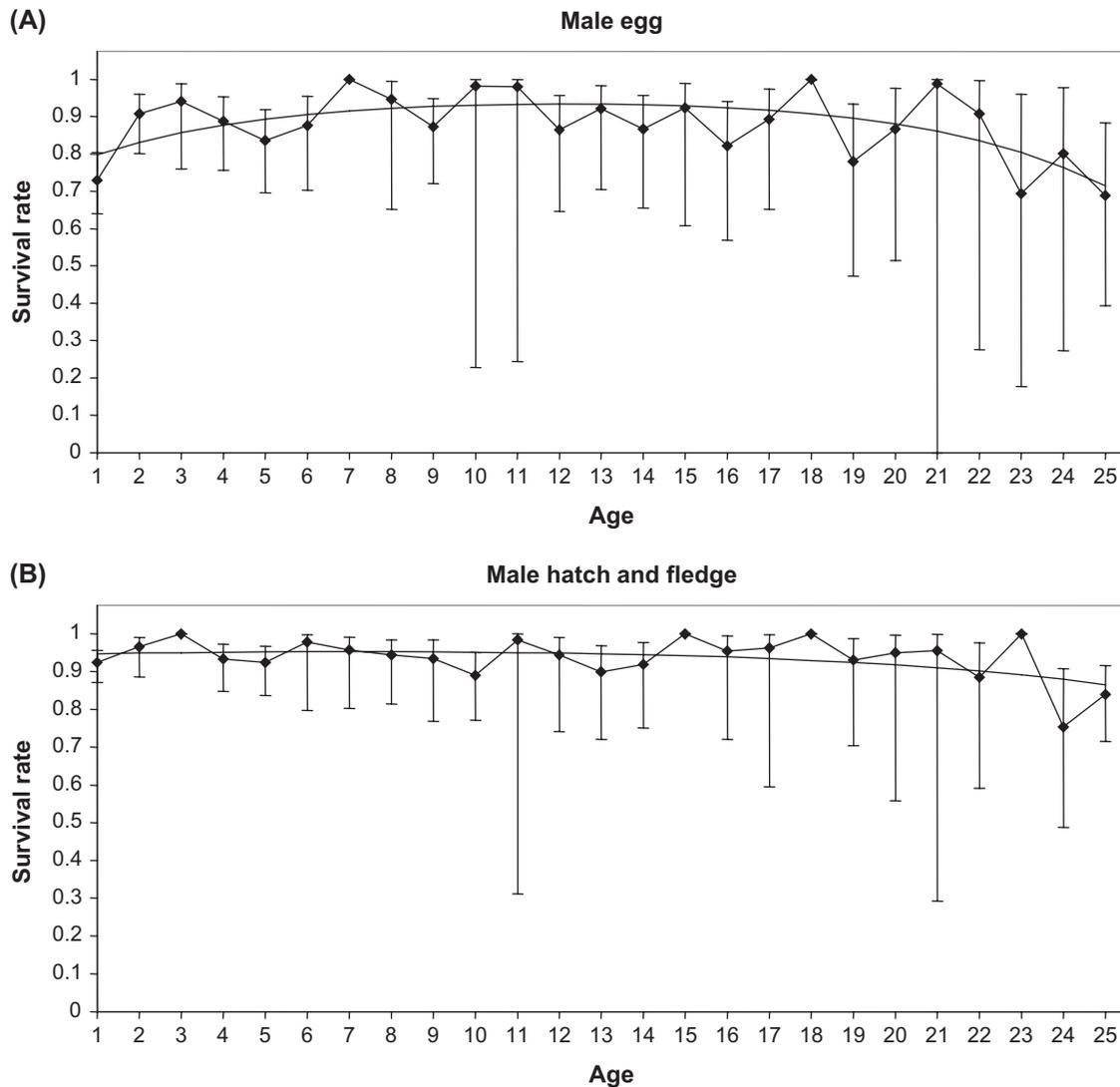


Figure 3. Age-specific survival rates for male egg stratum (A) and combined hatch and fledge strata (B). Estimates from model 4 in Table 4. 95% confidence intervals are shown. Parametric estimates from model 9 in Table 4 are shown as a smooth curve.

for males; this illustrates the importance of understanding the organismal context in which survival rates are expressed (Orzack et al. unpubl.). This increase conflicts with Hamilton's (1966) prediction that survival rates after the start of reproduction should decline. Our analysis of the age-dependency of survival rates does not account for heterogeneity of

Table 5. Markovian transition matrices associated with multistratum models of survival and reproduction. Element  $i, j$  is the estimated age-independent probability of transition from state  $i$  to  $j$  as generated by model 9 in Table 4.

Females	Egg	Hatch	Fledge
Egg	0.265	0.479	0.256
Hatch	0.189	0.615	0.196
Fledge	0.222	0.37	0.408
Males	Egg	Hatch	Fledge
Egg	0.284	0.435	0.281
Hatch	0.205	0.585	0.210
Fledge	0.224	0.324	0.452

recapture rates. Such heterogeneity has the potential to generate age-dependent survival rates, despite the fact that the underlying survival rates are age-independent. Carothers (1979) and Buckland (1982) present opposite conclusions about the influence of such heterogeneity on survival data from this population. We regard Carothers' conclusion that heterogeneity of recapture rates has little influence as more credible. However, we note that if Buckland is correct that an age-independent survival rate underlies the age-dependent trends shown in Fig. 1–3, it only strengthens the need for skepticism about the generality of Hamilton's prediction.

Second, reproductive ability appears to increase with age (although non-monotonically in the case of fledgling production, Fig. 6). This increase could be at the expense of late-age survival (Nussey et al. 2008, p. 397). Such a tradeoff would imply that survival rates for the egg stratum (less energy investment) would be higher than those for the hatch and fledge strata (more energy investment). However, the egg stratum generally has lower survival rates than does the combined hatch and fledge stratum. This suggests that a tradeoff is not present.

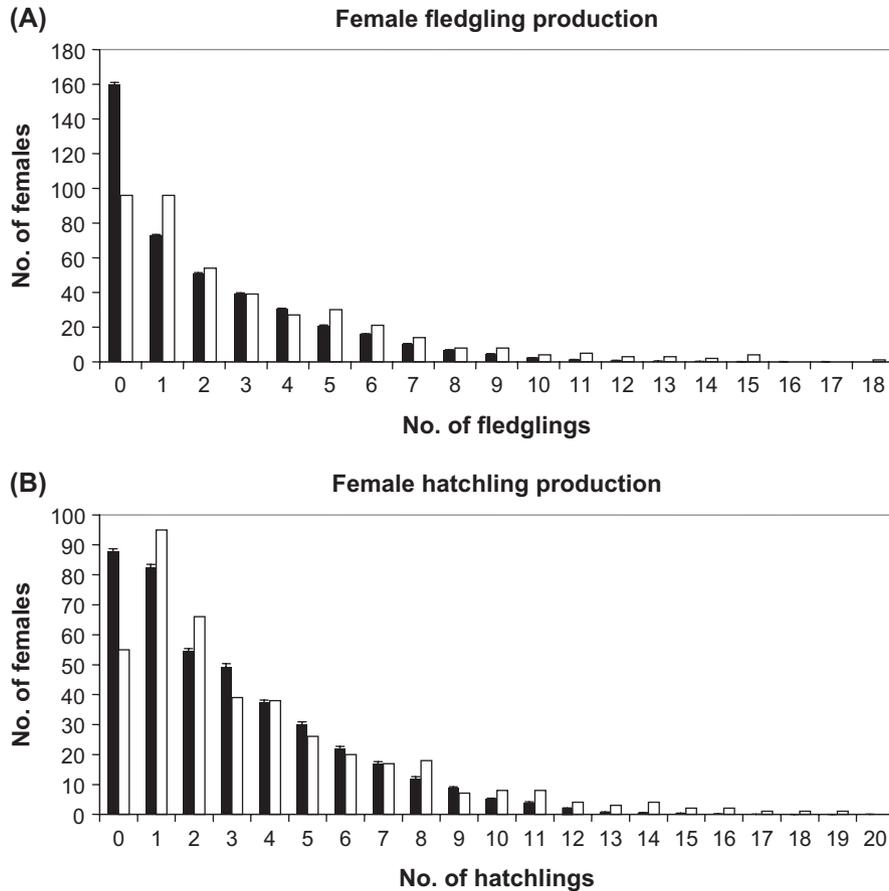


Figure 4. Observed (white) and expected (black) distributions of lifetime reproductive success for females. A) Fledgling production. B) Hatchling production. Each expected number of females is the average value derived from fifty synthetic cohorts ( $\pm$  SE).

More generally, there is no reason to privilege reproduction as being immune from the influence of deleterious mutations, which “should” influence the entire body (Hamilton 1966). If reproduction does not show senescence, one should conclude at minimum that the assumptions of Hamilton’s theory are not met. There are other possible conclusions. One is that the conceptual approach in Hamilton (1966) is flawed; perhaps it is incorrect to view the evolution of age-specific reproductive rates as being governed only by natural selection. Another possible conclusion is that natural selection governs these rates but that it causes reproduction to increase towards the end of life so that energy is not wasted (Cichon 2001, Rebke et al. 2010). Ideally, analyses of age-dependent reproductive rates and whether they confirm the evolutionary theory of senescence should test these competing explanations (Weladji et al. 2010) or at least make a priori decision as to whether senescence of reproduction is expected. All too often, a possible contradiction to the theory of senescence is explained away as being due to bias and/or poor data quality. If this continues to happen, the evolutionary theory of senescence would lose true explanatory power.

Third, it is one thing to believe that energy allocated to a bodily structure associated with reproduction is energy not allocated to survival. This is the static idealization underlying claims about the ‘necessity’ of negative association. However, even when there is fixed energy allocation to reproductive structures, one can still view the energy allocated to current

reproduction and survival as dynamic, that is, as dependent upon current physiology as determined by energy intake just during, say, the current breeding season. Such an allocation can transcend any simple dichotomy between germ and soma. Energy allocated to, say, the immune system may benefit survival and reproduction because it improves, say, foraging ability. To this extent, there is no immutable negative association between reproduction and survival; they could be positively associated. For the fulmar, one imagines that at the start of each breeding season, individuals are more or less equal in terms of their potential reproductive outcome for that year. In the ensuing months, differences arise in regard to foraging success. Poor foraging results in low survival and low ability to fledge offspring and good foragers have high survival and high ability to fledge offspring. These different outcomes tend not to carry over to the next breeding season, as indicated by our estimates of the half-life of stratum residence time, which are very short as compared to the average span of reproduction.

The scenario by which reproduction and survival may jointly increase or decrease is not based upon a deep model of organismal physiology. But it is plausible, at least as much or more so than a model of physiology in which the energy allocation to reproduction and to survival is a one-time event. At minimum, this model suggests that the relationship between reproduction, survival and age is not a ‘unitary’ phenomenon; this matches the findings of Palacios et al. (2007) and

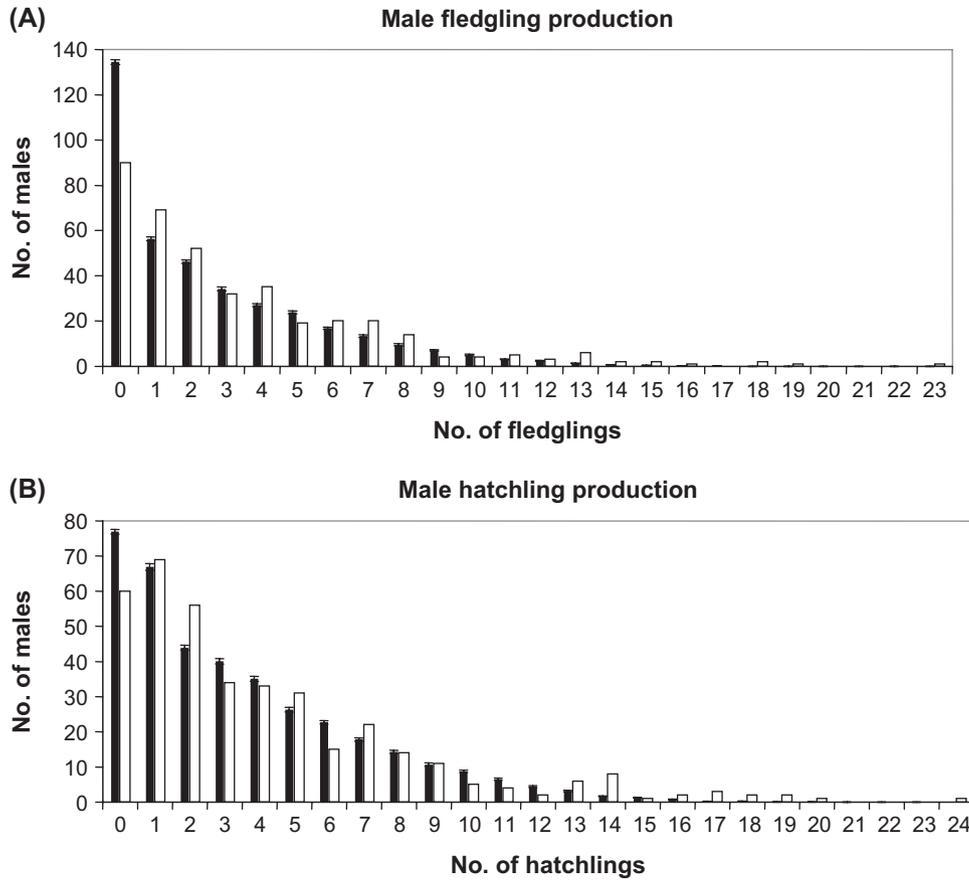


Figure 5. Observed (white) and expected (black) of lifetime reproductive success for males. (A) Fledgling production. (B) Hatchling production. Each expected number of males is the average value derived from fifty synthetic cohorts ( $\pm$  SE).

Vleck et al. (2007), which illustrate that the expression of aging differs among traits and among environments.

Van Noordwijk and De Jong (1986) showed that a positive static association between reproduction and survival can occur if there is more between-individual variation of energy acquisition than there is variation of energy allocation to

reproduction, despite the assumption that there is a negative association for each individual. Conversely, an overall negative association can occur if there is little variation of acquisition relative to allocation.

Van Noordwijk and De Jong's explanation may apply here but we lack evidence either way. We are skeptical that it

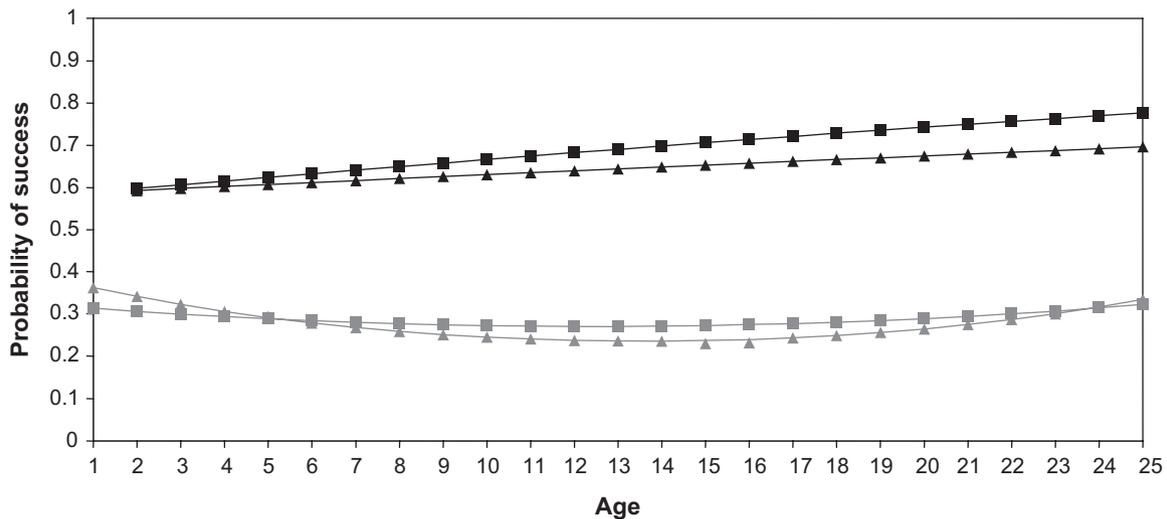


Figure 6. Estimates of age-specific probabilities of egg production (black) and fledgling production (gray). Female estimates are denoted by triangles and male estimates are denoted by squares. There is no age 1 estimate for egg production because each life history record commences with this event.

does apply but understand that it would be more compelling if we had experimental data relating to the relative variability of energy acquisition and of allocation. Of course, almost all claims that an observed positive association between reproduction and survival masks underlying negative associations also lack such data. Judicious search for such associations should not stop; we also need investigations of whether a negative association at the population level masks positive associations at the individual level.

Our dynamical approach is more phenomenological. We view any association between reproduction and survival as plausibly reflecting the true physiology of individuals, instead of as something that has necessarily supervened over a negative association. It is essential to understand the dynamical expression of any given observed association between reproduction and survival by, for example, measuring the half-life of the association. The power of this approach is evident, as our analyses of stratum dynamics suggest that the association between high reproduction and high survival is labile. To this extent, at minimum, we can contrast two views of the trait, one in which the static trait association causes an apparent departure from evolutionary equilibrium and another in which the dynamics of the trait association are consistent with equilibrium.

The essential difference between the classical view of the association between reproduction and survival and our view comes down to the conception of the environment. In the former view, a negative association is assumed to always exist and it acts to drive the evolution of a balance between reproduction and survival. Environmental variation may play a role in explanation, but as in Van Noordwijk and De Jong's analysis, it acts only to obscure a fundamental underlying negative association, which does not qualitatively change. To this extent, this view has at its core a static conception of the environment.

Our view is that understanding the realized dynamics of the association between reproduction and survival is the key to evolutionary understanding. This is true for positive or negative associations, but especially so in the former instance, given that a positive association is advantageous. Here, environmental variation does not obscure a more fundamental static association; instead, individual associations, whatever they may be, and their temporal dynamics are fundamental in a joint sense. To this extent, this view has at its core a dynamic conception of the environment.

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