

Reproductive improvement and senescence in a long-lived bird

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Heterogeneity within a population is a pervasive challenge for studies of individual life-histories. Population-level patterns in age-specific reproductive success can be broken down into relative contributions from selective disappearance, selective appearance of individuals into the study population, and average change in performance for survivors (average ontogenetic development). In this article, we provide an exact decomposition. We apply our formula to data on the reproductive performance of a well characterized population of common terns (*Sterna hirundo*). We show that improvements with age over most of adult life and senescence at old ages are primarily due to a genuine change in the mean among surviving individuals rather than selective disappearance or selective appearance of individuals. Average ontogenetic development accounts for approximately 87% of the overall age-specific population change.

common tern (*Sterna hirundo*) | age-specific reproduction | aging | heterogeneity | exact decomposition approach

In the study of life-histories it is important to capture the performance of individuals and changes in that performance over age. Changes in performance are often reported as changes in population averages, but individual heterogeneity can produce dynamics at the observed population level that are very different from dynamics at the individual level (1–3).

“Population level” refers to the observed averaged information over all individuals present at a given age regardless of whether they survive to the next age step. What we define as population change is the change observed directly in the aggregate field data and not the change in a hypothetical population of all individuals that were present at a given starting age x . “Individual level” refers to the change over age for each surviving individual averaged over all these survivors. We call this term “average ontogenetic development.”

The interpretation of population-level patterns can be problematic because of “within-generation phenotypic selection” (4). This is a change in the composition of the population if selective mortality removes frail (of lower quality) individuals at an earlier age than those individuals that are less frail (of higher quality) (1, 2), or if individuals that enter the population (here breeding population) as adults later than others through delayed recruitment or immigration (5) have a different performance than the resident population. We use the phrase “selective disappearance” to denote change in the mean of a phenotypic trait due to mortality and “selective appearance” to denote change due to new appearance of individuals. The term “compositional change” is used to refer to the combination of both selective appearance and disappearance. We develop a method to exactly decompose population change in an age-specific phenotypic trait with repeated measures into the components: average ontogenetic development, selective disappearance, and selective appearance.

An Approach to Decomposing Population Change. If there is no selective appearance, then population change P over age can be exactly additively decomposed into average ontogenetic development for the surviving individuals s plus compositional change due to selective disappearance d :

$$P = s + d, \quad [1]$$

where

$$P = V_{x+k} - V_x \quad [2]$$

is the difference between the averages of a trait of all individuals at one age (V_x) and the next age (V_{x+k}) with k being the age interval,

$$s = v_{x+k} - v_x \quad [3]$$

gives the respective difference for the individuals that survive from age x to $x + k$ at one age (v_x) and the next age (v_{x+k}), and

$$d = v_x - V_x \quad [4]$$

is the difference between the two means at the first age x (see *Example* and Fig. 1 for a specific case). The expected change due to selective disappearance is zero if the population is homogeneous. Eq. 1 holds because the survivors at the second age $x + k$ constitute the entire population at that age if no individuals enter the study at age $x + k$, so $V_{x+k} = v_{x+k}$ and

$$s + d = (v_{x+k} - v_x) + (v_x - V_x) \quad [5]$$

$$= v_{x+k} - V_x \quad [6]$$

$$= V_{x+k} - V_x \quad [7]$$

$$= P. \quad [8]$$

For the method to provide an exact description of change, all living individuals need to be measured in each year. The selective disappearance term can be reformulated into

$$d = (1 - f)(v_x - v_x^-), \quad [9]$$

where f gives the fraction surviving and v_x^- is the average of a characteristic for the individuals at age x that do not survive to age $x + k$.

Eq. 1 can be extended to account for new individuals entering the study at the second age $x + k$ (see *Supporting Equation* in *SI Methods* and Fig. S1 for the extension with selective appearance).

Our approach builds on previous decompositions of change, namely the Price equation and related decompositions (6–8). These equations express the term that captures selective dis-

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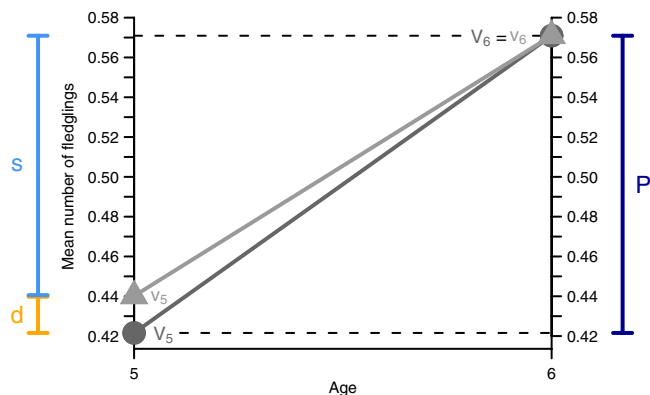


Fig. 1. Graphical representation of the decomposition of aggregate change at the population level into average ontogenetic development and change due to selective disappearance. P is the aggregate change in the mean number of fledglings produced from one age to the next—in this specific case we use data between age 5 and age 6, s is the average ontogenetic development, and d denotes the change due to selective disappearance. V_5 and V_6 are the averages of the number of fledglings at age 5 and 6, respectively, and v_5 and v_6 are the corresponding averages for the survivors.

appearance in the form of a covariance (6–8). We instead use a difference between the average trait of selected individuals (here survivors) and the mean of the entire population (9, 10). The method we propose is simpler, more intuitive in our context, and decomposes the change into parts with clear biological interpretation. The approach cannot estimate the latent frailty itself; it rather captures the effects of different processes leading to the aggregate observed population change in the mean of a phenotypic trait over an age step. We do not intend to separate out the total effects over the entire lifetime, we rather present an approach to decompose the population change at each age. Our approach describes the observed change retrospectively, following the same use of the Price equation recently developed by Coulson and Tuljapurkar (8) and Ozgul et al. (11). The formula is not intended to project forward in time—it is a way of decomposing observed change.

Application. In this article, we apply this approach to the problem of interpreting longitudinal data on age-specific reproductive performance for a long-lived bird species, the common tern (*Sterna hirundo*). It is widely believed that reproductive performance for birds and mammals increases at the earliest reproductive ages, reaches a plateau at intermediate ages, and often begins to decline at older ages (5, 12–48). Only a few studies, however, have tried to correct for compositional change within the population (5, 22, 24, 25, 27, 33–35, 42, 45, 46). Different authors have speculated about the importance of selective disappearance and individual changes, but they have not been able to quantify the contributions (15, 18, 25, 27, 28, 31, 33, 35, 42, 45, 47–50). Such quantification can be carried out using the approach that we are proposing here.

We use our approach to decompose population change of individually marked common terns of known age between age 3 and 21 years into contributing factors. Data on reproduction were collected from a long-term study between 1992 and 2007 (*Methods*). Over this period, recapture rates have been exceptionally high in the considered age groups, being almost 100% thanks to marking with passive implanted transponder (PIT) tags and an automatic detection system (51). We only have information for the breeding season. Data come from the philopatric part of the breeding population, most of which were marked as hatchlings. Immigrants are not marked. Selective appearances are therefore birds that are born in the colony that returned to breed at an age greater than the modal age of 3 (i.e., delayed

recruitment) and those >3 years old that were present at the beginning of the study. The common tern is a monogamous long-distance migrant. Breeding pairs typically remain together for many years. Adults, on average, fledge one chick per year (range 0–3). Most individuals start breeding at 3 years (52, 53). Maximum longevity from our study is 21. The average life expectancy at age 3, 6.8 years, is much shorter than the length of the study.

We consider two measures of performance. First, we decompose change in the absolute number of fledglings y_x produced between age x and $x + 1$. Because environmental variation generates temporal fluctuation in reproductive success in this population (54), we next decompose change in relative (or residual) reproduction (as, e.g., in refs. 28, 51, 55, and 56). Relative reproduction r_{ixt} gives the reproduction of an individual in relation to the averaged reproduction of the population in a given year. More specifically, relative reproduction is defined as the number of fledglings y_{ixt} produced by an individual i at age x in a specific year t minus the average fledgling rate in that year t for all known-age birds j with age z between 3 and 21:

$$r_{ixt} = y_{ixt} - \frac{\sum_{z=3}^{21} \sum_{j=1}^{N_{zt}} y_{jzt}}{\sum_{z=3}^{21} N_{zt}}. \quad [10]$$

The number of all known-age birds at age z and year t is N_{zt} .

We then examine differences between the sexes by decomposing change separately for females and males. Next, we identify reasons for the age-specific patterns we observe by calculating decompositions and fitting various mixed models (57) to each individual's changes in reproductive performance at each age (*Mixed Models in SI Methods*) with age replaced by (*i*) the past number of breeding attempts, (*ii*) the past number of successful breeding events, and (*iii*) the length of the pair bond.

Example. To understand our approach, consider the following example of the change in the number of fledglings from age 5–6 years (Fig. 1). The change at the level of the population is given by the difference between mean number of fledglings of all individuals at age 6 (0.57) and the same average at age 5 (0.42). The difference between these values is $P = 0.57 - 0.42 = 0.15$. Assuming that no new birds enter the study at age 6, all birds alive at age 6 have to be survivors from age 5. We can follow these surviving individuals back and calculate their mean number of fledglings at age 5 (0.44). The difference for the survivors is $s = 0.57 - 0.44 = 0.13$; this quantity captures the change in the mean trait among survivors—i.e., average ontogenetic development. The difference between the two means at age 5 ($c = 0.44 - 0.42 = 0.02$) measures the change in the composition of the population due to differential survival.

Results

At the population level, relative reproduction increases with age until approximately age 14 before decreasing (Fig. 2). Results for both absolute and relative change are similar. Furthermore, there is no linear relationship between the mean age in the population and year ($r^2 = 0.01145$, 14 df, $P = 0.6933$); such a relationship might have removed part of the age effect when yearly means in reproductive success are corrected for relative reproduction. We report results for relative reproduction (see Fig. S2 for absolute reproduction). By applying our approach we calculate that, averaged over all individuals and all ages, 86.6% of the age-related change is attributable to average change in performance among surviving individuals and 14.7% to selective disappearance (Fig. 3A). Selective appearance at ages after 3 years does not play an important role, with a contribution of -1.3% (Fig. 3A), and is subsequently not reported. Each average relative reproduction

with caution because of high variability around the average individual change contributions at advanced ages.

Our results provide evidence that the age-specific pattern of reproduction in the common tern is mainly due to changes in the mean among survivors. That average reproductive ability improves over an extended period of their life also holds for females (Fig. S4) and males (Fig. S5) when considered separately, and when relative reproduction is replaced with the number of fledglings produced (Fig. S2). Males on average seem to improve to a greater extent at young and middle ages and decline more slowly at advanced ages than females, with selective disappearance playing an even smaller role than in females.

Breeding performance not only increases with age but also with past breeding experience, the number of past breeding successes, and mate familiarity measured by the length of pair bond (Table S1). Changes in individual reproductive performance among surviving individuals are best explained by the number of years an individual produced fledglings, both for males and females. This is mainly attributable to a large improvement when having the first successful reproduction (Table S2).

Discussion

The problems of inferring average individual-level processes from population-level patterns when there is selective disappearance are well known. Several researchers tacked onto population-level studies further analyses to elucidate individual-level change (refs. 18–20; see *SI Discussion* for details). In addition, an array of methods have been derived to correct for selective disappearance or selective appearance (refs. 5, 20, 22, 24, 25, 27, 33–35, 38, 42, 45, 46, 58–61; see *SI Discussion* for details).

The use of a random individual intercept is the only method proposed so far that can account for unobserved heterogeneity within the population. The combination with some fixed effect controlling for the quality of individuals is currently the approach most widely used to correct for selective disappearance or selective appearance (5, 22, 24, 25, 27, 33–35, 42, 45, 60, 61). The method assumes that, with appropriate fixed effects, individual random intercepts can be interpreted as a latent variable often termed “frailty” and that corrected estimates are no longer biased by a compositional change and can be interpreted as the expectation of individual performance (1, 5, 62). The choice of the fixed effect can affect the results (61). Our approach does not require the estimation of, and correction for, latent variables. Our simple approach provides a powerful way of exactly quantifying contributions of various processes to observed age-specific population-level patterns. Previous approaches were not able to decompose the population change exactly into the contributing components.

In addition to being a confounding factor in longitudinal studies of fertility changes over age, heterogeneity is a pervasive challenge in biology and demography. Therefore, our formula is of broad interest in a wide range of different applications to decompose population change into average change of the surviving individuals and change in the population’s composition (1, 2, 7). The approach is not limited to quantitative traits; the formula holds for means in general. It is therefore also possible to additively decompose categorical variables, in which case the means in the equation are substituted by proportions. For the specific case of a binary variable, this is the proportion of successes—i.e., the mean number of successes is considered.

If the contribution of selective disappearance and selective appearance to population patterns of age-specific reproductive performance is small, inferences from previous analyses of the study population that do not account for these biases are broadly correct (21, 28, 53, 55, 63). In cases where selective disappearance and selective appearance—including immigration—are influential, a failure to correct for them could substantially bias results. In our study, averaged over all reproductive ages, 87% of the

population-level change is explained by average ontogenetic development. Although population-level change and average ontogenetic development show a similar pattern over age, the difference between them is not consistent (Fig. 2 and Fig. S3). However, the single-age patterns need to be treated with caution because of high variability in the data.

Our findings show that average individual improvement characterizes a long period of life and senescence appears only to become important at old ages in the common tern. Only 20% of all mature birds reached the age when senescence may become important. As a result, the reproductive life of most individuals is characterized by an improvement in individual performance with age.

Are these results likely to be general? There are only a few comprehensive analyses that appropriately account for unobserved heterogeneity. For reproductive improvement in early life these studies are: reindeer *Rangifer tarandus* (25, 35), barn swallows *Hirundo rustica* (27), common gulls *Larus canus* (22), mute swans *Cygnus olor* (42), wood thrushes *Hylocichla mustelina* (33), the laying date in oystercatchers *Haematopus ostralegus* (5), and the breeding probability in black-legged kittiwake *Rissa tridactyla* (46). We found only two studies that do not show any improvement in certain reproductive performance measures when accounting for compositional change, although there was an apparent improvement when not accounting for the bias. In the black-legged kittiwakes, the entire apparent improvement in breeding success (success or failure) was due to selective appearance and selective disappearance (60). The apparent improvement in egg volume for the oystercatcher in the study of van de Pol and Verhulst (5) was entirely explained by the selective appearance of individuals laying larger eggs at older ages. Our results thus seem typical of findings from other vertebrates suggesting that reproductive improvement may be a widespread phenomenon.

In some of the studies listed in the previous paragraph and in some additional studies accounting for unobserved heterogeneity, reproductive senescence was previously found for red deer *Cervus elaphus* (24, 34), barn swallows (27), black-legged kittiwakes (22), mute swans (42), wood thrushes (33), great tits *Parus major* (45), and reindeer (35). Note that none of these studies of reproductive improvement and senescence decompose change at the population level into average individual change and compositional change.

In our study, the age-specific patterns in average improvement among survivors in reproductive performance between age 3 and 14 may be due to a gain in experience (25, 31, 64, 65)—individuals may get better at raising fledglings, possibly through improved foraging ability (28, 65, 66). Alternatively, older birds may be less likely to reduce parental care when stressed (26, 67). For long-lived species it is unlikely that increasing reproductive effort because of a small probability of successful future reproduction is responsible for increasing fertility early in life (16, 64).

What do our results tell us about evolution? Different models have been developed to estimate optimal life-history strategies by optimal allocation of resources among maintenance, growth, and reproduction, starting with the work of Gadgil and Bossert (68). Increasing fecundity with age is typically predicted in indeterminate growers (69–71). Birds, however, are determinate growers, and most species reach their final size before they start to fly—long before the onset of reproduction (72). Only a few models address reproductive performance rather than reproductive effort for determinate growers (73–76). Baudisch (76) shows that, depending on the returns of investment in reproduction or maintenance and growth up to maturity, different reproductive strategies are optimal, including improvement at all ages, improvement followed by senescence, and senescence at all ages. The other models (73–75) predict a triangular pattern in reproductive performance over age.

In the classic evolutionary theory of aging, performance is generally predicted to decline because the strength of selection

against deleterious mutations decreases with age after maturity. Mortality reduces cohort size even if there is only extrinsic mortality. This leads to a decrease with age in the net effect of a mutation for the population (77, 78), implying that individuals should suffer senescence after maturity (77, 79–81). As Williams (79) put it, “the time of reproductive maturation should mark the onset of senescence,” at least for species reaching their final size at or before maturity. This corresponds to the predictions of Hamilton (80). Even though these theories are generally discussed with a focus on mortality, the same reasoning should hold for reproductive performance (80). According to the equations of Hamilton (80) and Emlen (82), the force of selection on age-specific mutations that act on fertility declines with age, which implies that fertility should decrease over the adult lifespan (83, 84). Even though Emlen (82) unconvincingly argues later in his article that fertility should first increase after maturity, he arrives at the direct conclusion of his equation that “traits increasing fecundity will be pushed to earlier and earlier ages until stopped by opposing factors.” In aging research, this classic viewpoint based on a declining selection pressure with age is still widely accepted (85).

Application of our method to common terns provides strong support for the predictions of life-history theory with a triangular shape in reproductive performance over age. The classic view of senescent declines from maturity is not observed. Our results add to the view that reality is more complicated than the classic evolutionary theory of aging suggests. We conclude that, in common terns, reproductive senescence occurs, but only after a prolonged period of improved age-related performance beyond the age at maturity.

Methods

Study Details. We used a total of 4,307 observations of reproduction of 959 individually marked common terns of known age between age 3 and 21 years. The data were collected in a common tern colony in the Banter See in Wilhelmshaven (German North Sea coast, 53°27'N, 08°07'E). The Banter See colony is monospecific. The common terns nest there on six artificial islands, which are arranged in a distance of 0.9 m to the neighboring island, each 10.7 × 4.6 m and surrounded by a 60-cm wall.

Common terns have been ringed since 1980 at other places in Wilhelmshaven and when the colony started to establish in 1984, at the Banter See. Since 1992, all fledged chicks have been ringed and marked with subcutaneously implanted transponders (TROVAN ID 100; TROVAN). Antennae on 44 elevated resting platforms read the individual specific alphanumeric code automatically every 5–10 s for each individual within a distance ≤11 cm. Additional antennae were placed temporarily for 1–2 days during the breeding season around every incubated clutch. The details of this automatic detection system are described by Becker et al. (51, 52). Only chicks and 101 breeders have been PIT-tagged since 1992. Therefore, there are birds at the colony that do not have an implanted transponder; they are mainly immigrants. As ringing commenced in 1980, 12 years before PIT-tagging started, the ages of most residents in the population were known at the beginning of the 16 years of data we use with a wide age range present in all years.

The colony was checked for new eggs, hatched chicks, and fledged chicks every 2–3 days during the remainder of the breeding season. A chick was defined as fledged when it reached an age of 18 days and was not found dead during the rest of the breeding season. Further details of this ongoing long-term study, restricted to the philopatric segment of the population, are described by Becker et al. (52).

Because we are interested in adult life, the starting age in our analysis is 3 years. The last age considered is 21, the age of the oldest bird. Reproduction occurs in discrete birth pulses during a 3-month period every year. Most individuals have only one clutch per breeding season with a maximum of three eggs. However, in the case of complete clutch failure, some pairs lay additional eggs. Here, we consider the overall number of fledglings per year, which exceeded 3 in only one case. We excluded birds with unknown breeding status and unknown age. Nonbreeding birds entered the dataset with zero fledglings. We further assumed that birds that were not detected in a given year but reappeared in following years did not breed in that particular year. However, this number was small and did not influence the results. To study the sensitivity of the results to changes in the data, we used jackknifing to estimate 95% confidence intervals.

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