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Age-Dependent Traits: A New Statistical Model to Separate Within- and Between-Individual Effects

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ABSTRACT: Evolutionary questions regarding aging address patterns of within-individual change in traits during a lifetime. However, most studies report associations between age and, for example, reproduction based on cross-sectional comparisons, which may be confounded with progressive changes in phenotypic population composition. Unbiased estimation of patterns of age-dependent reproduction (or other traits) requires disentanglement of within-individual change (improvement, senescence) and between-individual change (selective appearance and disappearance). We introduce a new statistical model that allows patterns of variance and covariance to differ between levels of aggregation. Our approach is simpler than alternative methods and can quantify the relative contributions of within- and between-individual changes in one framework. We illustrate our model using data on a long-lived bird species, the oystercatcher (*Haematopus ostralegus*). We show that for different reproductive traits (timing of breeding and egg size), either within-individual improvement or selective appearance can result in a positive association between age and reproductive traits at the population level. Potential applications of our methodology are manifold because within- and between-individual patterns are likely to differ in many biological situations.

Keywords: random effects models, aging, age-dependent reproduction, selection hypothesis, *Haematopus ostralegus*.

Phenotypic traits can change as a result of within-individual changes (phenotypic plasticity) and between-individual changes, as selection may favor some individuals over others. When quantifying how population values of phenotypic traits change over time or differ between groups of individuals, it is therefore important to realize that both within- and between-individual processes might be underlying causal mechanisms. The aim of this study is to introduce a novel statistical method that allows the disentanglement of the within-individual from the between-individual components of phenotypic change in a population. Our study will focus on differences in phenotypic traits between age classes, but in principle the methodology applies to many biological problems where within- and between-individual patterns might differ.

Reproductive performance of iteroparous animals is generally positively associated with age, at least over the first part of animals' lives (Clutton-Brock 1988; Forslund and Pärt 1995). Many studies have quantified patterns of age-dependent reproduction and survival because such patterns allow the construction of age-structured population models. Understanding how mutations and phenotypic changes in age-specific schemes affect population dynamics and individual fitness is crucial for the study of the evolution of aging, age at maturity, the optimization of reproductive effort during a lifetime, and conservation issues. The relationship between age and reproduction is thus at the core of population demography (Caswell 2001), life-history evolution (Stearns 1992), and population genetics (Charlesworth 1980).

Evolutionary questions in age-structured populations specifically address patterns of within-individual changes in reproduction during a lifetime (fig. 1*A*). However, many studies report an association between age and reproduction at the population level (cross-sectional analysis), which does not necessarily imply within-individual change. Correlations at the population level might also result from progressive changes in the phenotypic composition of higher age classes because of the selective appearance or disappearance of certain phenotypes. Selective appearance of good reproducers might occur when individuals queue for high-quality breeding position; in such queuing systems, a late onset of the reproductive career will be associated with producing many offspring annually (e.g., Ens et al. 1995; East and Hofer 2000; fig. 1*B*). In contrast, selective appearance of poor reproducers might occur when low-quality individuals are competitively inferior and start reproducing later in life (fig. 1*C*). Selective

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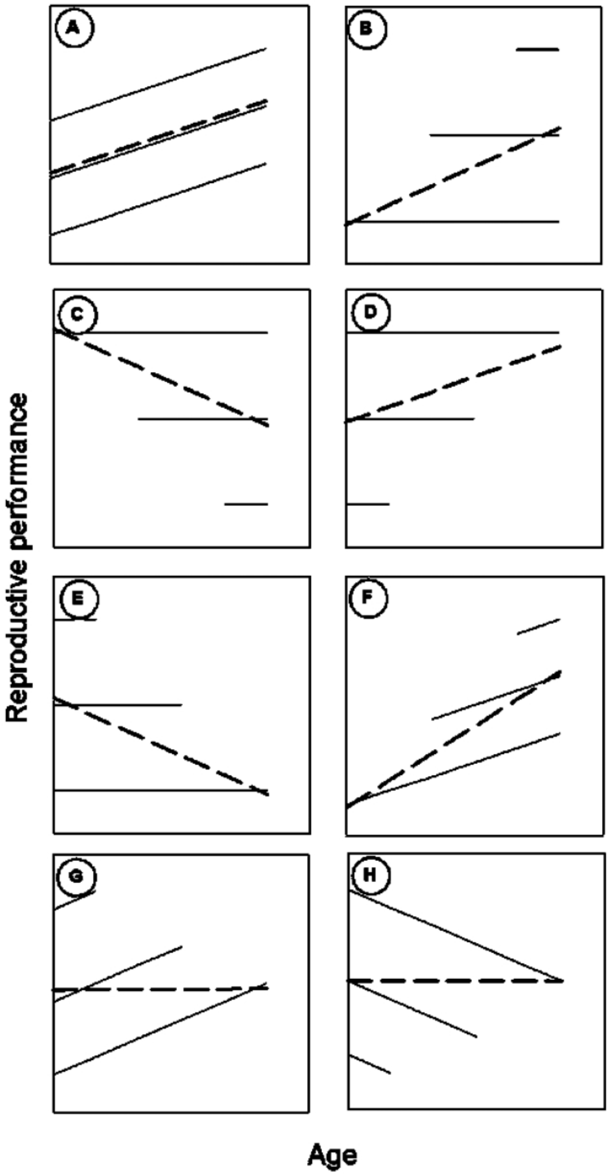

Figure 1: Relationship between age and reproduction in a hypothetical population of three individuals (*solid lines*) of different phenotypic quality, compared with ordinary regression lines (*dashed lines*) fitted through all points of all individuals. Possible scenarios are within-individual improvement (*A*), selective appearance of good reproducers (*B*), selective appearance of poor reproducers (*C*), selective disappearance of poor reproducers (*D*), selective disappearance of good reproducers (*E*), within-individual improvement and selective appearance of good reproducers (*F*), within-individual improvement and selective disappearance of good reproducers (*G*), and senescence and selective disappearance of poor reproducers (*H*).

disappearance can also take two forms: when individuals vary mainly in their resource acquisition, poor reproducers might live shorter lives and progressively disappear (fig. 1*D*); conversely, when individuals vary mainly in their resource allocation, producing many offspring might come at the cost of a shorter life span, and good reproducers might progressively disappear (cf. van Noordwijk and de Jong 1986; fig. 1*E*). Such hypotheses describing patterns of life-history covariation have been referred to as selection hypotheses (Nol and Smith 1987), bad-quality hypotheses (Curio 1983), and delayed-breeding hypotheses (Hamann and Cooke 1987). All these effects result in correlations between age and reproduction in cross-sectional analyses, without reflecting within-individual changes. Within-individual changes can be caused by factors intrinsic to the individual, such as increasing experience (Curio 1983), restraint as part of reproductive tactics (Pianka and Parker 1975), and physiological deterioration (Medawar 1952), or by extrinsic factors, such as changes in habitat quality. Within- and between-individual changes are not mutually exclusive. Often, within- and between-individual changes will affect the relationship between age and reproductive performance at the population level in the same direction (fig. 1*F*). However, within- and between-individual changes might work in opposite directions, and between-individual changes can mask patterns of improvement (fig. 1*G*) or senescence (fig. 1*H*) at the population level.

The difference between within- and between-individual effects on age-dependent reproduction is well recognized in the literature, and when an association between age and reproduction at the population level is found, additional analyses are often performed to test whether within- or between-individual changes occurred. Separate longitudinal analyses are used to investigate whether reproductive performance changes within individuals (e.g., Rattiste 2004). Additionally, any selective appearance or disappearance is investigated by relating reproductive performance to either longevity (survival) or age at first reproduction (e.g., Berube et al. 1999). However, such post hoc analyses of a correlation between age and reproduction do not allow the quantification of the relative contributions of within- and between-individual changes, although this has been named as one of the major challenges in the study of age-dependent reproduction (Forslund and Pärt 1995).

In this note, we introduce and illustrate a new statistical model that we implement using a random effects approach to simultaneously test and compare between-individual and within-individual age effects within one framework. The idea to analyze age-dependent processes with random effects models is in itself not new (e.g., Reid et al. 2003; Krüger 2005). Random effects at the individual level can account for variation in reproductive performance between individuals, and in survival analyses, this approach is generally known as a frailty model (Vaupel et al. 1979). However, the selective appearance and disappearance hypotheses suggest not only that individuals vary in their phenotypic quality but also that individual quality covaries with the probability that an individual will appear in or disappear from the (breeding) population that is sampled. To our knowledge, Cam et al. (2002) were the first to analyze age-dependent reproduction while specifically modeling an association between an individual's reproductive performance and its survival propensity. They used a multivariate approach to explicitly model a covariance between reproduction and survival and thereby were able to account for selective disappearance (but not for selective appearance). The multivariate approach they used is quite complex and poses some technical challenges because survival and reproductive variables generally have different distributions (see also Wintrebert et al. 2005 for a time-to-failure approach). In this study, we introduce a novel univariate approach that is much simpler and is able to test for selective appearance as well as selective disappearance. Moreover, the method we introduce explicitly quantifies the relative effects of within-individual change and selective appearance and disappearance on age-dependent reproduction (or other traits) in one model.

Random Effects Models

The statistical model that we introduce below is a specific parameterization of a random effects model. Specific applications of such models are also known as mixed models, generalized linear mixed models, hierarchical linear mixed models, and multilevel models. In most biological studies, observations are collected on individuals within the same population or year or are collected repeatedly on the same individual. Random effects models not only account for heterogeneity between such sources of aggregation but also allow the partitioning of total variation among these sources (e.g., Goldstein 1995; Verbeke and Molenberghs 1997; Snijders and Bosker 1999; McCulloch and Searle 2000). For example, by modeling individuals and their longitudinal measurements as nested random effects, we can split total variance into a between-individual (σ_u^2) and a within-individual (σ_e^2; residual variance) component. Consequently, this method specifically accounts for the fact that measurements from the same individual might be intercorrelated (i.e., nonindependent).

More important for our purpose is that random effects models also allow patterns of covariance to differ between multiple levels of aggregation because different hypotheses of age-dependent reproduction deal with covariation at different levels. Improvement and senescence hypotheses assume a covariation between age and reproductive performance within individuals. In contrast, selective appearance and disappearance hypotheses assume that there is a between-individual covariance between the moment an individual enters (or leaves) the reproductive population and its individual quality. More specifically, the selective appearance hypothesis assumes a correlation between age of first reproduction (α) and individual quality (fig. 1*B*, 1*C*), while the selective disappearance hypothesis assumes a correlation between age of last reproduction (ω) and individual quality (fig. 1*D*, 1*E*). Note that covariations between age of first or last reproduction and individual quality can be either positive or negative, depending on the underlying mechanisms (see the introduction to this note). Individual quality can be measured as an estimate of reproductive performance (r) over a lifetime.

We formalized our approach in the following random effects regression model:

$$r_{ij} = \beta_0 + \beta_W \times \text{age}_{ij} + \beta_S \times \alpha_i + u_{0i} + e_{0ij}, \tag{1}$$

a two-level random intercept model with individual as the highest level i and the annual measurement of reproductive performance as the lowest level j. The random intercept term, u_{0i}, and residual error term, e_{0ij}, are assumed to be drawn from a Gaussian distribution with mean 0 and variance σ_u^2 and σ_e^2, respectively. Subscripts refer to the level at which parameters are variable; age is variable within and between individuals; age of first reproduction (α) varies only between individuals. This model specifically tests for within-individual change ($\beta_W \times \text{age}_{ij}$) in the presence of a selective appearance effect ($\beta_S \times \alpha_i$) and vice versa. It is crucial to test for an effect of selective appearance in the presence of a within-individual effect because when individuals improve with age, those that start reproducing at a later age are expected to do better because they are older. Thus, the effect of age of first reproduction (β_S) estimates the additional effect of selective appearance, given the estimated within-individual change with age. The independent effect of between-individual differences in age of first reproduction on reproductive performance can be obtained by adding β_W and β_S, giving β_B. Alternatively, the regression equation (1) can be rewritten to the equivalent

$$r_{ij} = \beta_0 + \beta_W \times (\text{age} - \alpha)_{ij} + \beta_B \times \alpha_i + u_{0i} + e_{0ij}. \tag{2}$$

Using within-group deviation scores (age $-$ α), we obtain a model in which β_B and β_W can be quantified and tested directly (*sensu* within-group centering; Snijders and Bosker 1999).

Models 1 and 2 investigate selective appearance; effects of selective disappearance can be incorporated in a similar way by adding ω_i (age of last reproduction) to the model. Furthermore, nonlinear effects of age can be investigated by using various other nonlinear functions of age (or of age of first or last reproduction) in the model, although all such covariates might not be orthogonal. Our approach is robust to intermittent breeding or missing values, as long as they occur at a random age. However, uncertainty about the exact age of first or last reproduction (e.g., because of dispersal) will reduce the power to correctly identify selective between-individual processes. Although models 1 and 2 are not specific with respect to sex, separate age effects of both sexes can be incorporated by replacing the individual level with separate female and male levels (cross-classified structure).

Two Examples on Oystercatchers

To illustrate the use of models 1 and 2, we analyzed data from a 21-year study on oystercatchers (*Haematopus ostralegus*), a long-lived bird species with large variation in age of first reproduction (3–10 years; see van de Pol et al. 2006 for general information on the fieldwork protocol). We analyzed the effect of age on two reproductive parameters: the annual timing of reproduction (laying date) and egg volume (using clutch averages). Both of these parameters are associated with annual reproductive output and are strongly intercorrelated within individuals (Heg 1999). Experiments indicated that early laying is causally related to higher reproductive success (Heg 1999), while producing large eggs probably is not causally related to reproductive output but is associated with another measure of phenotypic quality of individuals (territory quality; van de Pol et al. 2006).

A group of 69 individuals, with ages varying from 3 to 19 years, was followed. We selected these individuals out of all known breeders because they were ringed as juveniles, so their ages and ages of first reproduction were known exactly. We succeeded in measuring the reproductive performance of all individuals in most years ($N = 283$ reproductive attempts, on average 4.1 yearly attempts per individual, range 1–11). There were no indications of sex differences in age effects (data not shown), and sexes were therefore pooled in the analyses. We present analyses of a model for within-individual improvement with age and selective appearance. Analyses of nonlinear effects of age and effects of selective disappearance (ω_i) are not presented because they were far from significant. Values were standardized for annual variation in laying date and egg volume by subtracting annual population mean from each value. Analyses were performed in MLwiN 2.0 using the restricted iterative generalized least squares algorithm (Rasbash et al. 2004).

Laying date was negatively associated with age and egg volume was positively associated with age at the population level, as determined by ordinary cross-sectional regression (β_P; fig. 2*A*, 2*D*; table 1). At first glance, this result was consistent with expectation; both laying early and producing large eggs are generally thought to increase reproductive output (i.e., older individuals did better). However, when we pooled individuals of similar age of first reproduction and plotted longitudinal patterns, the results suggested that different mechanisms might be at work (note that the age grouping in fig. 2 is for graphical purposes only—ungrouped integer age data were entered in the analysis). Laying date advanced with age within individuals, independent of age of first reproduction (fig. 2*B*). In contrast, egg volume was independent of age within individuals, but individuals that started breeding late in life (high age of first reproduction) produced larger eggs than individuals that started breeding early in life (low age of first reproduction; fig. 2*E*).

To quantify the relative effects of within-individual improvement and selective appearance in one model, we applied models 1 and 2 to this data set. As expected, laying date significantly improved within individuals; individuals advanced laying by 0.74 days every year they aged (β_W; fig. 2*C*; table 1). Individuals laid 0.56 days earlier (β_B; fig. 2*C*; table 1) for each year they delayed age of first reproduction. Although the latter effect bordered on significance ($P = .075$), it is important to note the similarity in slope to the within-individual effect (fig. 2*C*). The difference in slope between the within- and between-individual effects in figure 2*C* is exactly the effect of selective appearance ($\beta_S = \beta_B - \beta_W$), which was very small for laying date. Thus, individuals that started breeding later in life laid earlier because they were older; there was no additional selective appearance of early-laying individuals (β_S; table 1). Between-individual differences in laying dates explained 25.4% of total variance (calculated by $\sigma_u^2/[\sigma_u^2 + \sigma_e^2]$ from a model without covariates), indicating that laying dates were strongly intercorrelated within individuals. A graphical representation of the final model for laying date (fig. 2*C*) fit the plotted longitudinal patterns well (fig. 2*B*). In the case of laying date, the selective appearance hypothesis was not supported, but within-individual improvement did occur, consistent with the scenario depicted in figure 1*A*. As a consequence, a reduced model without an effect of age of first reproduction (the standard random effects approach) would have produced the same results (table 1).

Individuals did not increase the size of their eggs during their lives (β_W; fig. 2*F*; table 1). However, individuals laid eggs 0.51 cm^3 larger (1.2%) for each year that they delayed the start of reproduction (β_B; fig. 2*C*; table 1). Individuals that delayed their first breeding attempt did not lay larger eggs because they were older but because of selective appearance of individuals that laid large eggs (β_S; table 1). This can be seen in the large difference in slope between the within- and between-individual effects (fig. 2*C*). Between-individual differences explained 45.6% of total variance, indicating that egg volume was highly intercorrelated within individuals. A graphical representation of

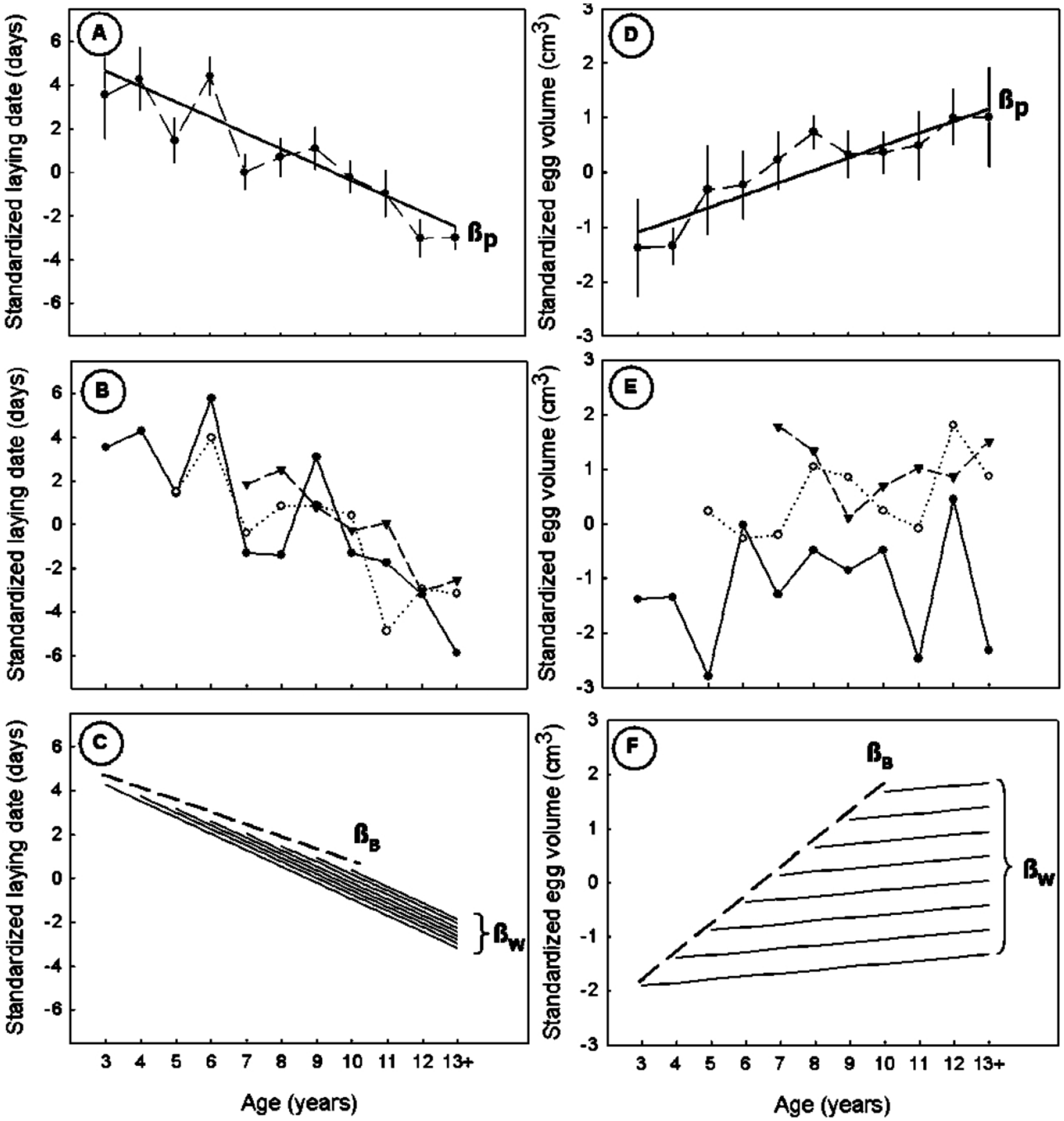

Figure 2: Relationships between age and laying date (*left*) and between age and egg volume (*right*) in oystercatchers. For both parameters, a significant relationship with age was observed at the population level (*A*, *D*). Longitudinal patterns of individuals differing in age of first reproduction were similar to the cross-sectional pattern for laying date (*B*) but different from that for egg volume (*E*). In *B* and *E*, individuals were grouped by age of first reproduction (3–4 years, *filled circles*; 5–6 years, *open circles*; 7–10 years, *triangles*) for graphical reasons. The models that best fit the data (see table 1) are depicted in *C* and *F*. Each solid line gives the average within-individual slope (β_w) of individuals grouped by age of first reproduction (3–10 years); the dashed line depicts the between-individual slope (β_B;table 1). Note that age classes 13 years and older were grouped for graphical reasons because of low sample sizes (ungrouped data were used in analyses).

Table 1: Results of the effects of age on standardized laying date and standardized egg volume (deviations from annual mean)

	Standardized laying date (days)				Standardized egg volume (cm^3)			
Parameter	B	SE	χ^2 (df = 1)	P	B	SE	χ^2 (df = 1)	P
Model 1:								
Intercept (β_0)	5.9	2.1			−3.44	1.06		
Age$_{ij}$ (β_W)	−.74	.14	29.9	<.001	.06	.06	.89	.34
α_i (β_S)	.18	.35	.29	.59	.45	.17	7.5	.006
Individual variance (σ_u^2)	39.8	14.7			3.86	1.06		
Residual variance (σ_e^2)	106.3	13.1			5.58	.67		
Model 2:								
Intercept (β_0)	5.9	2.1			−3.44	1.06		
(Age − α)$_{ij}$ (β_W)	−.74	.14	29.9	<.001	.06	.06	.89	.34
α_i (β_B)	−.56	.31	3.17	.075	.51	.16	11.3	<.001
Reduced model:								
Intercept (β_0)	6.7	1.3			−.54	.63		
Age$_{ij}$	−.70	.15	25.6	<.001	.11	.06	3.5	.063
Individual variance (σ_u^2)	43.0	14.8			4.34	1.15		
Residual variance (σ_e^2)	107.4	13.1			5.56	.678		
Ordinary regression model:								
Intercept	6.8	1.3			−1.78	.62		
Age$_{ij}$ (β_P)	−.71	.12	33.1	<.001	.23	.06	10.0	.002

Note: Within-individual slope (β_W), between-individual slope (β_B), difference in slope between β_B and β_W (β_S), and slope at the population level (β_P) are interpreted in the text. The reduced model with only age as a covariate is equivalent to the more standard random effects models used in several other studies.

the final model for egg volume (fig. 2*F*) fit the plotted longitudinal patterns well (fig. 2*E*). In the case of egg size, there was strong evidence in favor of the selective appearance of good reproducers hypothesis, but there was no evidence for within-individual change (cf. fig. 1*B*). A reduced model without an effect of age of first reproduction (the standard random effects approach) did not describe the data very well because it produced an estimate of an age effect ($\beta = 0.11$) that described neither the within-individual (β_W) nor the between-individual (β_B) age effect very well (table 1). This is because the random effect at the individual level can account only for heterogeneity in phenotypic quality between individuals, not for a covariation between age of first reproduction and phenotypic quality. This comparison shows that our method systematically accounts for the effects of selective appearance, which contrasts with previously used random effects approaches.

The slopes at the population level (β_P; fig. 2*A*, 2*C*; table 1), as obtained using ordinary regression (or the standard random effects approach), are weighted averages of the within- and between-individual slopes (β_W and β_B; fig. 2*C*, 2*F*). The contributions of β_W and β_B (or β_S) to β_P depend on several factors. Most important are the ratio between the number of individuals and the number of measurements per individual as well as the variance within and between individuals. The population slope of laying date on age was quite similar to that of the within-individual effect; however, the population slope of egg volume was much lower than that of the between-individual effect and much higher than that of the within-individual effect. This difference is probably caused by the fact that individuals were more consistent in egg size than in laying date; consequently, effects of selective appearance (β_S) on egg size have a larger impact on correlations at the population level.

Further Extensions

Models 1 and 2 are very simple and allow the testing of most hypotheses of interest, but some simple extensions can be incorporated to further enhance our understanding of underlying processes. For example, some individuals might improve reproductive performance more strongly during their lives than others. Random slope models allow slopes of covariates (such as age) to vary between individuals and estimate the total variation in these slopes (e.g., Rasbash et al. 2004). In our example, the advancement of laying date with age within individuals did not vary much between individuals in our data ($\sigma^2_{\text{slopes}} = 1.8 \pm 1.6$), especially compared to the considerable variation in intercepts between individuals ($\sigma_u^2 = 39.8 \pm 14.7$). This suggests that most oystercatchers advanced laying date at the same rate during their lives, which is an interesting result because little is known about individual variation in the improvement of reproductive performance with age.

Several authors have argued that reproductive performance does not necessarily increase with age but that correlated increases in breeding or mate experience might be causally responsible for age-dependent reproduction (e.g., Forslund and Pärt 1995; Fowler 1995). By adding the years of breeding experience or pair-bond duration to the model, we can use a multiple regression approach to statistically disentangle these intercorrelated parameters. Potentially, only good reproducers are able to become very experienced breeders or pairs. Such effects of selective disappearance can be further investigated by adding the maximum breeding experience or pair-bond duration of each individual as a covariate to the model.

Conclusion

The statistical model we introduced provides a simple but powerful tool to disentangle within- and between-individual change. The differences from the more often used random effects models with age as the only covariate are small but nonetheless crucial. Our example on oystercatchers illustrates that using cross-sectional comparisons in the study of age-dependent reproduction can sometimes be misleading (as illustrated by the analysis on egg size) and that a random effects approach in combination with the parameterization we suggested yields novel insights in the underlying mechanisms.

To our knowledge, this is the first study to show that selective appearance of certain phenotypes (individuals that lay large eggs) generates a correlation at the population level between age and a measure of reproductive performance in the absence of within-individual changes. In contrast, laying date improved with age primarily as a result of within-individual changes. Thus, the mechanisms underlying patterns of age-dependent reproduction can vary between different measures of reproductive performance within the same population. Within-individual changes in laying date may result from foraging efficiency improving with age and experience (Goss-Custard and le V. dit Durell 1987), which may affect the individual's condition and timing of breeding (Heg 1999). Conversely, egg size might depend on adult body size (e.g., Nol et al. 1984). When large birds start reproducing late in life, for example because they were queuing for high-quality territories (Ens et al. 1995), the selective appearance of individuals that lay large eggs could be a by-product of this settlement behavior.

It seems likely that the degree to which effects of age on reproductive performance at the population level might be caused by within- or between-individual changes is also related to a species' life history. For example, for short-lived species, which usually have low variation in age of first reproduction, the reported patterns of age-dependent reproduction are probably little affected by selective appearance of individuals in the population. However, the effects of selective disappearance may be important in both short- and long-lived species because both types of species can have substantial variation in age of last reproduction. Our approach will result in the correct interpretation independent of the life history of the species or the various underlying mechanism (as described in fig. 1). We hope our study will further encourage other researchers to compare the effects of within- and between-individual change on age-dependent reproduction in a variety of species, enabling a comparative study of different life-history strategies.

We see many other potential applications of the statistical model we present in this note because selective appearance and disappearance of certain phenotypes is a common phenomenon that can result from temporal as well as spatial processes. Progressive selective changes in phenotypic population composition might be important in the study of any other behavior or trait that is expressed differentially over time. Growth may be a particularly suitable trait because selective disappearance through death or dispersal typically depends on growth. Similarly, to study the effects of environmental changes on long-term changes in phenotypic traits, equivalent models can be used to disentangle change as a result of phenotypic plasticity (within individuals) from selection against certain phenotypes (between individuals). Alternatively, selective changes in phenotypic composition as a result of spatial processes might occur when the probability of entering or leaving a group of individuals measured is associated with the phenotypic quality of individuals. For example, in examinations of performance of individuals on leks, migration stopover sites, or foraging sites, selective appearance or disappearance due to movement of individuals into and out of the sampled population is the norm and might strongly affect estimates of time trends of phenotypic traits.

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