Distinguishing within from between individual effects: How to use the within-individual centering method for quadratic pattern

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Abstract

1. Any average pattern observed at the population level may confound two different processes: the within-individual process and the between-individual process. Separating within- from between-individual patterns is critical for our understanding of ecological processes and evolutionary dynamics.

2. The within-individual centering method allows distinguishing within from between individual effects and this method has been largely used in ecology to investigate both linear and quadratic patterns. Here we show that two alternative equations could be used for the investigation of quadratic relationships and explain in which circumstances they are valid.

3. We show that these two alternative equations make different assumptions about the shape of the individual pattern. Reviewing the literature, we find that the inappropriate equation has likely been applied by most of the studies investigated quadratic patterns.

4. To investigate properly quadratic patterns using the within individual centering method, it is critical that the pattern assumed by the equation used is consistent with the biological pattern investigated. We illustrate this statement with the example of age-specific trajectories because age corresponds to the most frequent individual-centered variable used for quadratic pattern. Finally, we give the general equation of the within-individual centering method for any non-linear relationship.

Keywords: age-pattern, individual trajectory, linear mixed models, selective appearance, selective disappearance, senescence.

Introduction

Distinguish the trait variation occurring within-individual from that occurring among-individuals is a recurrent challenge in ecology (Vaupel et al. 1979; Vaupel and Yashin 1985; Bolnick et al. 2011; Vindenes and Langangen 2015; Hamel et al. 2018). In a heterogeneous population, as both within-and between-individual effects drive trait variation, the variation observed at the population level does not necessarily reflect the changes occurring within individual. Similarly, in a set of heterogeneous populations, the overall pattern observed across populations may differ from the pattern occurring within populations due to among population differences. Thus, this problem could be encountered whenever data are aggregated at different scales.

Distinguishing within- from between-individual effects is particularly important when studying age-related changes in a given trait (Vaupel et al. 1979; Curio 1983; van de Pol and Verhulst 2006; Hamel et al. 2018). In a population, the selective appearance or disappearance of individuals with contrasting performance generates between-individual effects. As a consequence, the average age-specific trajectory observed at the population level could differ from the true average individual trajectory. Historically, selective disappearance has been identified quite early as a process that could potentially lead to biased inference in the study of aging (Vaupel et al. 1979). In a heterogeneous population, frail individuals are expected to die first, leaving robust individuals to be overrepresented at old ages (Vaupel and Yashin 1985). This change of the composition of the population generated by selective mortality of frail individuals leads the relationship between longevity (X) and the average individual trajectory of the trait measuring performance (Y) to be positive (Smith 1981; Cam et al. 2002; McCleery et al. 2008; Pigeon et al. 2017). Such positive between-individual effects are expected to be frequent. For

instance, studies on birds and mammals have regularly reported a positive relationship between lifespan and annual reproductive success (Vedder and Bouwhuis 2018). Ignoring the distinction between within- and between-individual effects has for a long time impeded our understanding of age-specific changes in traits at the individual level. For example, the investigation of the age-related individual improvement of breeding success in early life has long-lastingly been limited because most studies considered only the population level pattern (Forslund and Pärt 1995). Similarly the study of senescence that aims to measure the within-individual decline in phenotypic traits across ages inescapably requires the distinction between within- and between-individual effects (Nussey et al. 2008).

More generally, from an eco-evolutionary perspective, it is crucial to separate within- from between-individual variation in traits (Bolnick et al. 2011). For instance, the use of an average trajectory may lead to important biases in various demographic metrics including population growth, generation time and demographic variance (Kendall et al. 2011; Stover et al. 2012; Vindenes and Langangen 2015). Within- and between-individual patterns provide different information and both are of interest to understand the behavior, physiology or demography of biological systems (Reid et al. 2010; Dingemanse and Dochtermann 2013). Within-individual effect may provide information on within-individual phenotypic plasticity, learning or the occurrence of trade-off. On the other hand, between-individual effects depict consistent inter-individual differences and thus suggest among-individual differences in quality, personality or pace of life, for instance.

A statistical method to distinguish within- from between-individual effects is the within-individual centering method (Snijders and Bosker 1999; van de Pol and Verhulst 2006; Van de Pol and Wright 2009). This powerful method is simple to use and has become thereby rapidly

popular right after its introduction to ecologists (Van de Pol and Wright 2009). To date, this work has been cited 483 times and the approach has been used in 284 published studies (research using google scholar in June 2019).While this method has been presented into the context of behavioral studies for linear patterns (Van de Pol and Wright 2009), its use has been extended in various ecological fields including demography, aging, eco-physiology, and parasitology to investigate both linear and quadratic trait variation (Figure 1,Table S1). Two alternative equations, with different assumptions about the shape of the individual pattern, could be used for the investigation of quadratic relationships. We show that a potentially inappropriate equation was used most of the time. Rather than use a quadratic within-individual centering model, most of the previous studies used a quadratic effect of the individual-centered variable (e.g. Westneat et al. 2011; Martin et al. 2019). We illustrate the consequences of the used of the inappropriate equation with the example of quadratic-age patterns which correspond to the most frequent individual-centered variable use for quadratic pattern. Finally, we provide a correct extension of the within-individual centering method to non-linear trajectories.

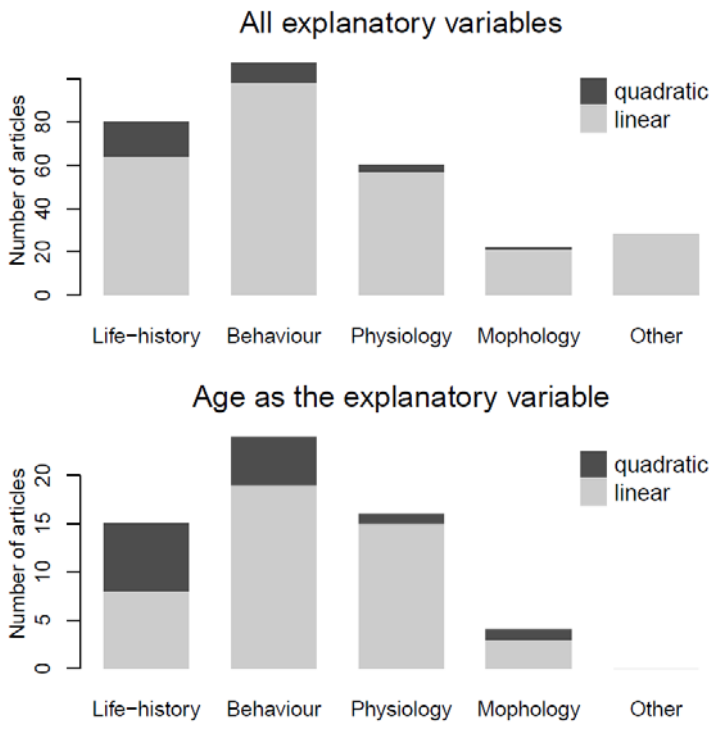

Figure 1: Number of articles citing the van de Pol & Wright (2009)'s work and using the within-individual centering method including all explanatory variables (upper panel) and age in particular with linear (light grey) and quadratic (dark grey) models. The articles have been classified according to the type of response variable(s) used (life-history, behavioral, physiological, morphological, and other traits).

The within-individual centering method

In ecology, linear mixed models are standard tools nowadays to analyze data aggregated at different scales. However, such models may fail to estimate the true within-individual changes because the individual random effect may not capture the total between-individual effects (van de Pol & Wright 2009). The within-individual centering method is an extension of a simple mixed model that allows distinguishing explicitly within- from between-individual variation using

additional fixed effects (van de Pol & Wright 2009). We present only briefly this method and refer to van de Pol & Wright (2009) for further information.

The standard random effect model can be described by the following regression equation:

$$y_{ij} = \beta_0 + \beta_1 x_{ij} + u_{0j} + e_{0ij} \quad (1)$$

where subscripts i and j are the indexes of the data, β_0 is the intercept, β_1 is the slope, x_{ij} is the value of a trait x at measurement i from individual j, u_{0j} is deviation from the intercept for individual j assumed to be drawn from a normal distribution with zero mean and between-subject variance σ_{u0}^2 and e_{ij} is the residual error assumed to be drawn from a normal distribution with zero mean and variance σ_e^2.

Starting from this standard mixed model, the within-individual centering approach decomposes the effect of x in two terms: the within individual and the between individual effects. The between-individual effect is fitted as the average x value for each individual ($\overline{x_j}$). The within-individual effect is fitted as the deviation from the individual mean for a given observation ($x_{ij} - \overline{x_j}$). The previous equation becomes:

$$y_{ij} = \beta_0 + \beta_W(x_{ij} - \overline{x}_j) + \beta_B \overline{x}_j + u_{0j} + e_{ij} \quad (2)$$

where β_W is the slope of the within-individual effect and β_B is the slope of the between-individual effect. Thus, equation 1 correspond to a specific case of equation 2 when $\beta_W = \beta_B$ and consider that between and within individual effect are identical. As demonstrated by van de Pol & Wright (2009), figure 2 shows that simple mixed models do not allow estimating within-individual effect as reliably as the within-individual centering model does. Note that, in this figure, simulated individual patterns emerge directly from equation (2).

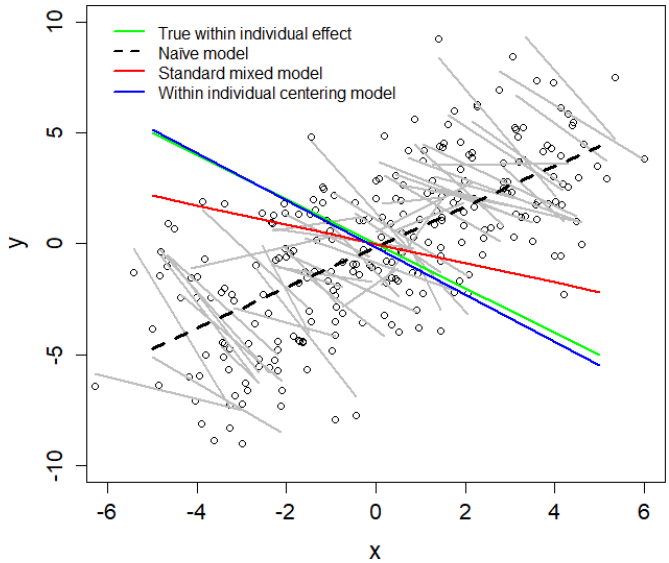

Figure 2. Estimation of the within-individual effect for simulated data considering a linear relationship between X and Y. Each dot is one observation per subject and the gray lines depict observed within-subject trajectories. The green line shows the true within-individual effect, the dashed black line shows the naïve average trajectory in the population, the red line shows the within-individual effect estimated using a standard mixed model (equation 1) and the blue line shows the within-individual effect estimated using the within-individual centering method (equation 2). Data have been generated using the equation 2 with the following parameters: β_0 = 0, β_W = -1, β_B = 1, σ_{u0}^2 = 1 and σ_e^2 = 2.

The within-individual centering method to investigate quadratic patterns

The within-individual centering method has been commonly used in ecology to investigate quadratic changes in traits (10% of all the articles citing van de Pol & Wright (2009) and applying this method, Figure 1). To use an individual centering approach with a quadratic effect, the individual centering should be applied on both linear and quadratic terms. Thus, equations (2) becomes:

$$y_{ij} = \beta_0 + \beta_{W1}(x_{ij} - \overline{x}_j) + \beta_{B1}\overline{x}_j + \beta_{W2}\left(x_{ij}^2 - \overline{x_j^2}\right) + \beta_{B2}\overline{x_j^2} + u_{0j} + e_{ij} \qquad (3)$$

Instead of using equation (3), most of the studies investigating a quadratic individual trajectory rather used a quadratic effect of the individual-centered variable. The equation usually used is:

$$y_{ij} = \beta_0 + \beta_{W1}(x_{ij} - \overline{x}_j) + \beta_{B1}\overline{x}_j + \beta_{W2}(x_{ij} - \overline{x}_j)^2 + u_{0j} + e_{ij} \qquad (4)$$

It should be noted that equations (3) and (4) are not equivalent and would generate very different individual patterns (Figure 3). All studies describing the method with enough detail (n= 17/29) used equation (4), but not equation (3), to investigate quadratic within individual trajectory. Yet, these two equations assume different individual trajectories. The choice of using one equation instead of the other should depend upon the biological hypothesis tested. Although the equation 4 have been applied systematically, this equation seems inappropriate in most cases.

Difference between equations (3) and (4)

Equation (3) and (4) can be reorganized to be easier to compare.

$$y_{ij} = \beta_0 + \beta_{W1}(x_{ij} - \overline{x}_j) + \beta_{B1}\overline{x}_j + \beta_{W2}x_{ij}^2 + (\beta_{B2} - \beta_{W2})\overline{x_j^2} + u_{0j} + e_{ij} \ (3^*)$$

$$y_{ij} = \beta_0 + \beta_{W1}(x_{ij} - \overline{x}_j) + \beta_{B1}\overline{x}_j + \beta_{W2}x_{ij}^2 + \beta_{W2}\overline{x_j}^2 - 2\beta_{W2}(x_{ij}\overline{x_j}) + u_{0j} + e_{ij} \ (4^*)$$

The equation (3), being the natural extension of the within-individual centering method for quadratic patterns, consider that the quadratic effect within an individual could differ from the quadratic effect between individuals. In contrast equation (4) assumes that the quadratic effect is the same at both the between and within-individual level, β_{W2} being the product of both x_{ij}^2 and $\overline{x_j}^2$. Yet, between and within individual effect arise from independent processes and such should be modelled separately from each other. Furthermore, equation (4) include an interaction between the observed value of a trait and the individual mean of the trait individual, $x_{ij}\overline{x_j}$,for which the

biological interpretation is not straightforward. For these reasons, we consider equation (4) to make little biological sense.

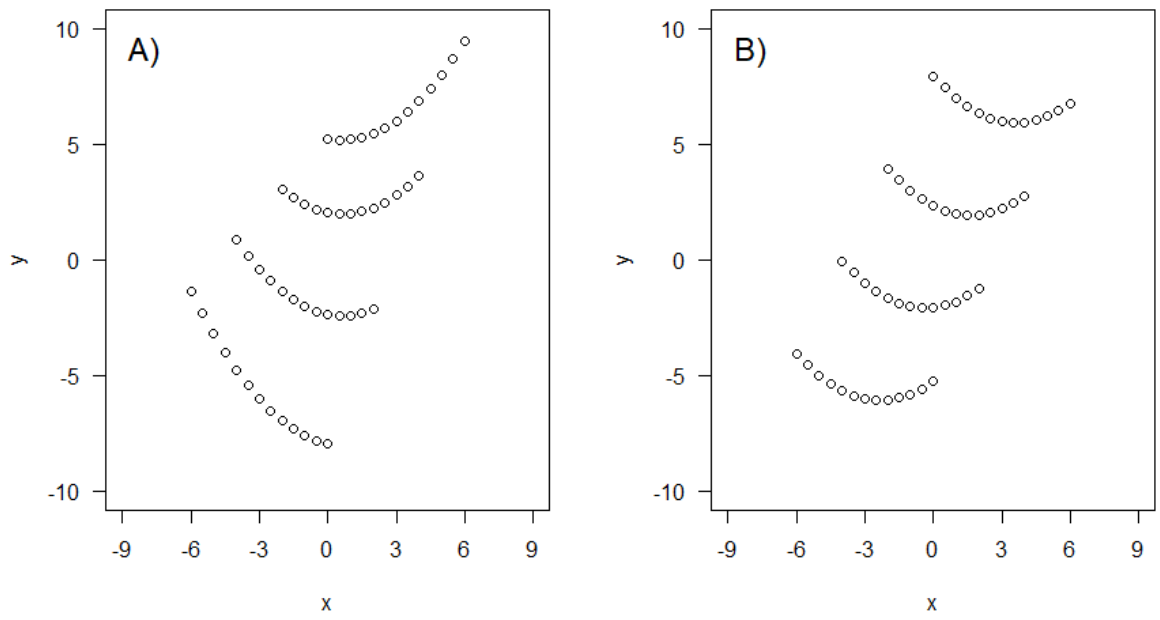

Figure 3. Individual trajectories simulated with equation (3) (A) and (4) (B). In both graphs, the five same individual life histories have been simulated following assumptions of equations (3) and (4), respectively. The equation 3 assumes that all individuals show the same pattern over the range of the explanatory variable. In other word, ignoring the variation in the intercept, equation 3 assumes that the within-individual effect of X on Y is the same for each individual. Sampled individuals on the same size range of X value but with different average will show contrasting pattern (A). In contrast, equation (4) assumes that the intra-individual changes of a given individual are centered on the range of the explanatory variable sampled for this individual. The effect of the variable X on Y is not related to the absolute value of X but to the deviation of X from its average valued for a given individual. Thus, when sampled individuals have the same size range of X value but with different average, they show the same pattern (B).

Individual trajectories assumed by equation (3) and (4) could be very different as illustrated in Figure 3. Equation 4 assumes that all individuals have the same quadratic pattern centered on their individual means (Fig 3B) whereas equation 3 assumes that there is a general

quadratic pattern over the entire range of X of which individuals can deviate as a function of their individual mean. We believe that equation (3) better fits many biological processes than equation (4). For instance, it is reasonable to expect consistent within individual responses to variation in climatic condition, food abundance or parasite load, although individual variations may occur (see last paragraph for more flexible formulation). In many ecological studies, the range of environmental conditions sampled for a given individual is in part randomly determined in relation to the times when an individual has been captured. For instance, if we investigate the individual response to a climatic variable such as precipitation, the range of value considered for each individual will depend on the conditions occurring during the period of observation of those individuals in the field. In natural condition such variables cannot be manipulated. In this example, equation (3) assumes that the definition of good and bad condition is the same for each individual but that individuals were sampled with in different average conditions, however equation (4) assumes that good and bad conditions are relative to the individual average environmental condition. Equation (3) and (4) are thus testing really different hypotheses and it is questionable whether assumption made by the equation 4 i.e. individuals have the same quadratic pattern centered on their individual means, could be met in practice.

As a consequence, the within centering method should be used with caution for non-linear relationships. One needs to be aware of the strong assumptions made by the equation used and to be sure that these assumptions are consistent with the biological pattern, and thus hypotheses, investigated. We illustrate the use of the within centering method and of equations (3) and (4) with the example of quadratic-age patterns which correspond to the most frequent individual-centered variable use for quadratic pattern (Figure 1).

Quadratic age trajectories with selective disappearance

When individual life-trajectories are considered in their entirety including senescence, the observed age patterns generally display a dome-shape. Because the investigation of quadratic relationships with age is often more relevant, 24% of the studies using the within-individual centering method and analyzing age-dependence patterns included a quadratic relationship. Using the within-individual centering method, the age effect is split into two terms: the average individual age whose associated slope estimates the between-individual effect (i.e. the effect due to selective disappearance of certain phenotypes), and the age-related changes (i.e. the difference between the actual and the average age of a given individual), whose slope estimates the within-individual effect. When we compare the individual-trajectories predicted by the two equations, it appears that the equation 4 is not consistent with empirically observed age-pattern (Clutton-Brock 1988; Newton 1998). For the given example, using equation 4 would assumes that the age trajectory of an individual dying at 5 years-old ($\overline{X} = \overline{age} = 3$) is similar to the age pattern between 6 and 10 years old of an individual dying at 15 years-old ($\overline{X} = \overline{age} = 8$). In both cases the age-related changes are the same, ranging from -2 to 2 (Figure 4B). With equation (3), an individual dying young (low average X) is expected to displays a trajectory that differs from that of an individual dying old (high average X). The former would show only the classical early-life increase, whereas the latter would show a more general pattern including an increase, a plateau and a decrease when older due to senescence (Figure 4A). This second pattern (equation 3) is expected to occur according to the theories of senescence. Indeed, the decrease in individual performance should occur in late life and start at the onset of senescence (Williams 1957, Hamilton and Rose1991). Even if the onset of senescence can be variable between individuals, it is not expected to be dependent of individual age at death.

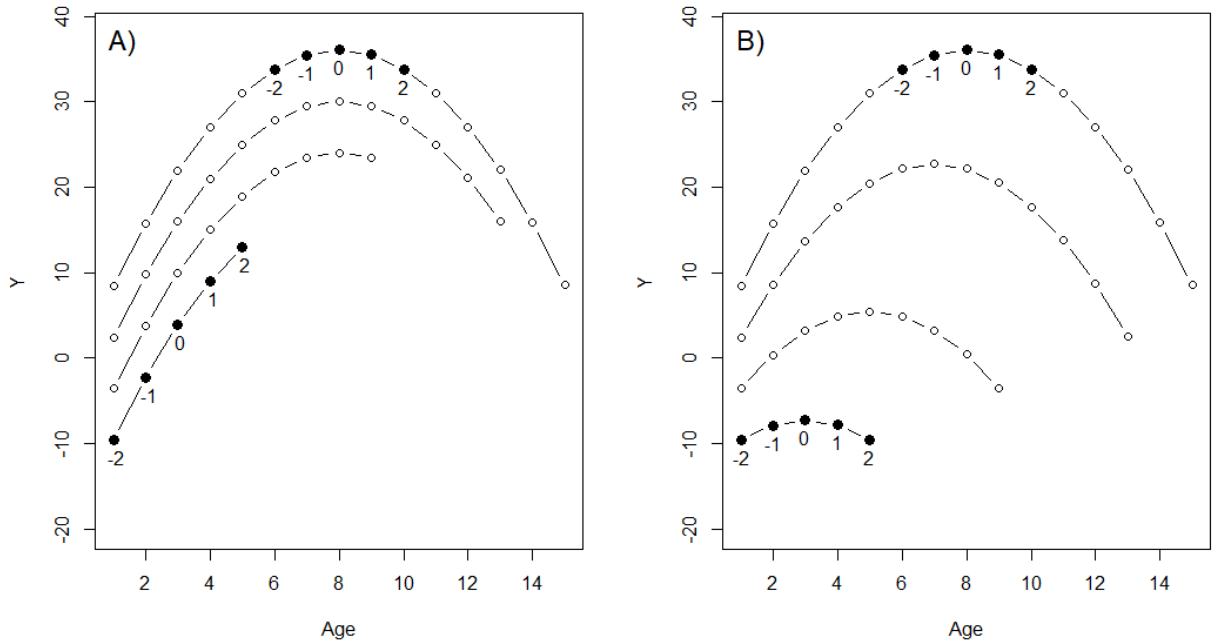

Figure 4. Individual trajectories assuming A) a classical pattern including senescence and B) the pattern expected by the equation 4. The five individual life histories are similar between the graphs regarding the intercept and age range. The equation 4 assumes that the age pattern of an individual dying at 5 years-old is similar to the age pattern between 6 and 10 years old of an individual dying at 15 years-old (black dot with associated age-related changes). Quadratic age-dependence described in panel B is of little biological sense.

We simulated age-specific data with selective disappearance. These data can be considered as any age-specific trait such as age-specific reproductive success on a standardized scale. We simulated 1000 datasets each consisting of 500 individual life-histories over 16 years. The data have been simulated neither from equation (3) nor from equation (4) directly. Instead, we directly simulated individual trajectories with a quadratic age pattern $y_{ij} = \beta_0 + \beta_{W1}(x_{ij}) + \beta_{W2}(x_{ij})^2 + u_{0j}$ where x is age. Individual trajectories differ by their intercept ($\beta_0 + u_{0j}$) that reflected fixed individual performance. Then we introduced selective disappearance by simulated

an age of death for each individual depending on its fixed performance. We used a binomial distribution with probability $p_{0j} = a + bu_{0j}$ to simulate individual annual survival (see appendix S2 for details). We analyses these simulated data with equation (3) and (4). Our results showed that the use of equation (4) is not suitable for the investigation of selective disappearance. With this equation, the within-individual effect estimated is strongly biased (Figure 5, purple line, appendix S1). In contrast the use of equation (3) provides unbiased and accurate estimates of the within-individual age trajectories (Figure 5, blue line, appendix S1). While the estimate of the within individual trajectory provided by the standard mixed model is much less biased than the one provided by a simple regression, it does not allow estimating within-individual effect as reliably as the within-individual centering model does and thus is not fully satisfactory. Moreover, standard mixed model is not able to estimate between individual effects explicitly and thus do not provide any information concerning this meaningful aspect. Although equation (4) has been frequently used to investigate age patterns, only equation (3) is appropriate.

The simulations presented above assumed that the studied population is monitored with perfect detection i.e. the values of the variable of interest are known for each individual each year from birth to death. However, real data often show incomplete histories of individual trajectories i.e. detection probability is typically lower than 1. We reassessed the performance of these models considering incomplete individual capture histories. Results show that missing information within the lifetime of an individual does not change the respective performance of the models previously considered. Even when the detection probability is very low i.e. 0.2, leading to very patchily individual capture histories, the within-centering estimates are accurate whereas those of both the used a quadratic effect of the individual-centered variable and of the standard mixed model are consistently biased (appendix S1).

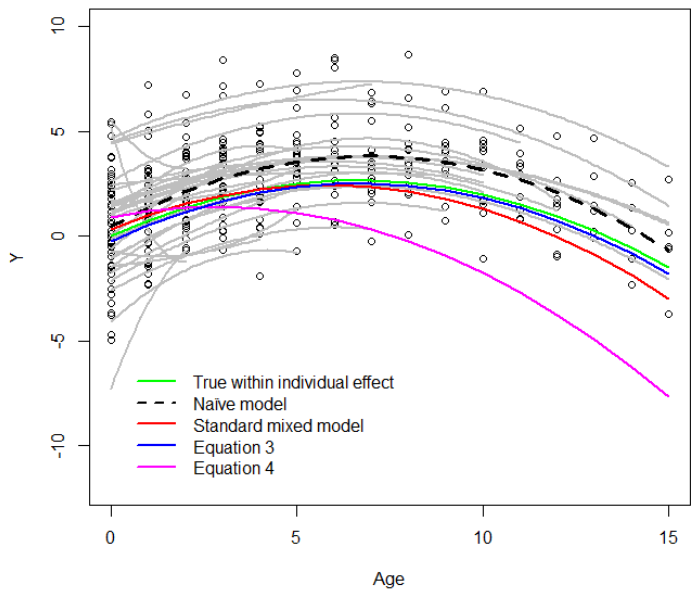

Figure 5. Estimation of a quadratic within-individual effect for simulated age-specific data with selective disappearance. Each dot is one observation per subject and the gray lines depict observed within-subject trajectories. The green line shows the true within-individual effect, the dashed black line shows the naïve average pattern in the population, the red line shows the within-individual effect estimated by a standard mixed model (equation 1), the blue line shows the within-individual effect estimated by the within-individual centering method (equation 3) and purple line shows the within-individual effect estimated by the misused within-individual centering method (equation 4). Scripts used to simulate the data is given in appendix S2.

Quadratic age pattern with both selective appearance and disappearance and alternative methods

In the case of age pattern, the between individual effect may by generated by both selective appearance and disappearance. In this circumstance, a single mean-age variable would not be able to capture the two processes generating the between individual effect. An alternatively method commonly applied is the use of age at first and last reproduction as fixed covariates to model explicitly selective appearance and disappearance, respectively (van de Pol and Verhulst 2006). This method which is derived from the within-individual centering method

allows distinguishing within- from between-individual effects using explicit and biological variables. The equation for the quadratic counterpart is:

$$y_{ij} = \beta_0 + \beta_{W1} age_{ij} + \beta_{W2} {age_{ij}}^2 + \beta_{B1sa} ageFR_j + \beta_{B2sa} ageFR_j^2 + \beta_{B1sd} ageLR_j + \beta_{B2sd} ageLR_j^2 + u_{0j} + e_{0ij} \qquad (5)$$

Where $ageFR_j$ and $ageLR_j$ are the age of first and last reproduction for individual j. $\beta_{B1\ sa}$, $\beta_{B2\ sa}$, $\beta_{B1\ sd}$, and $\beta_{B2\ sd}$ are the linear and quadratic effect for selective appearance and disappearance respectively. This method provides also unbiased estimate for quadratic age-dependence (appendix S1). It can be shown that equation (5) is closely related to the individual centering approach with a quadratic effect (eq. 3) being essentially a reparametrization when only selective disappearance is present (appendix S3). Because this method allow disentangling the selective appearance and selective disappearance and that the estimated parameters are easier to interpret biologically, the use of age at first and last reproduction as fixed covariates seems generally more suitable for the investigation of individual age trajectories (van de Pol and Verhulst 2006). Thus, we strongly encourage its used instead of the more generic within-individual centering method.

Finally, other methods have been proposed to distinguish within- from between-individual effects in age-specific changes of traits. For instance, Rebke et al. (2010) presented a method decomposing the average population change of a trait in each age interval into within-individual change and between-individual differences (selective appearance/disappearance). Cam et al. (2002) proposed to account for the selective disappearance modelling explicitly the covariation between survival and the trait of interest. Using correlated individual random effects from a bivariate normal distribution, this method allows identifying the within-individual effect. However both methods have been seldomly used because they are data expensive and more

complex to implement than the within-individual centering method (van de Pol and Verhulst 2006; Van de Pol and Wright 2009).

The general model for non-linear (polynomial) pattern and further extension

More generally the within-individual centering method following the equation 3 could be used for any non-linear (polynomial) relationship for the within-individual effect as:

$$y_{ij} = \beta_0 + \sum_{t=1}^{n} \left[\beta_{Wt}\left(x_{ij}^{t} - \overline{x_j^t}\right) + \beta_{Bt}\overline{x_j^t}\right] + u_{0j} + e_{ij} \quad (6)$$

Where n is the degree of the polynomial model and β_{Wt} and β_{Bt} are respectively the slope of the within-individual effect and of the between-individual effect for degree t. As shown by van de Pol & Wright (2009), the within-individual centering method could also be fitted using an alternative equation.

An interesting extension of this general equation is the incorporation of random slopes for the within individual effect. The equation becomes:

$$y_{ij} = \beta_0 + \sum_{t=1}^{n} \left[\left(\beta_{Wt} + u_{tj}\right)\left(x_{ij}^{t} - \overline{x_j^t}\right) + \beta_{Bt}\overline{x_j^t}\right] + u_{0j} + e_{ij} \quad (7)$$

Where u_{tj} is deviation from the slope β_{Wt} for individual j assumed to be drawn from a normal distribution with zero mean and between-subject variance $\sigma_{u_t}^2$. The use of random slope allows a deeper investigation of the within individual effect considering individual variation in the underlying ecological process. For instance among individual variation in the within individual effect may provide information on among-individual difference in aging rate or behavioral plasticity (van de Pol and Verhulst 2006; Dingemanse and Dochtermann 2013). It should be

noted however that models including random slopes would require large sample size with a high number of repeated observations per individual over a large range of X to be able to accurately estimate the different parameters. We are not advocating the systematic use of non-linear within-individual centering approach with random slope and merely introduce their potential while suggesting that more investigation should be done to properly assess their suitability. Overall, models using a within-individual approach with both linear and quadratic effects are relatively simple and powerful tools to disentangle within- from between-individual process. We hope that this manuscript will encourage their use promoting correct application for non-linear relationships.

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