

Editorial

General conclusion to the special issue Moving forward on individual heterogeneity

Sandra Hamel, Jean-Michel Gaillard, Nigel G. Yoccoz, Ron D. Bassar, Sandra Bouwhuis, Hal Caswell, Mathieu Douhard, Eric J. Gangloff, Olivier Gimenez, Phylis C. Lee, Isabel M. Smallegange, Ulrich K. Steiner, Oscar Vedder and Yngvild Vindenes

S. Hamel (<http://orcid.org/0000-0003-1126-8814>) (sandra.hamel@uit.no) and *N. G. Yoccoz* (<http://orcid.org/0000-0003-2192-1039>), Dept of Arctic and Marine Biology, UiT The Arctic Univ. of Norway, Tromsø, Norway. – *J.-M. Gaillard*, CNRS-UMR 5558, Univ. Claude-Bernard, Lyon, France. – *R. D. Bassar*, Dept of Biology, Williams College, Williamstown, MA, USA. – *S. Bouwhuis* and *O. Vedder* (<http://orcid.org/0000-0003-4689-8568>), Inst of Avian Research 'Vogelwarte Helgoland', Wilhelmshaven, Germany. *OV also at: Groningen Inst. for Evolutionary Life Sciences, Univ. of Groningen, Groningen, the Netherlands.* – *H. Caswell* (<http://orcid.org/0000-0003-4394-6894>) and *I. M. Smallegange* (<http://orcid.org/0000-0001-6218-7358>), Inst. for Biodiversity and Ecosystem Dynamics, Univ. of Amsterdam, Amsterdam, the Netherlands. – *M. Douhard*, Dépt de biologie, Univ. de Sherbrooke, Sherbrooke, QC, Canada. – *E. J. Gangloff* (<http://orcid.org/0000-0002-9074-8009>), Station d'Ecologie Théorique et Expérimentale du CNRS, Moulis, France. – *O. Gimenez* (<http://orcid.org/0000-0001-7001-5142>), CEFÉ UMR 5175, CNRS, Univ. de Montpellier, Univ. Paul-Valéry Montpellier, Montpellier, France. – *P. C. Lee*, Psychology, Faculty of Natural Sciences, Univ. of Stirling, Stirling UK. – *U. K. Steiner* (<http://orcid.org/0000-0002-1778-5989>), Max-Planck Odense Centre on the Biodemography of Aging, and Dept of Biology, Odense, Denmark. – *Y. Vindenes* (<http://orcid.org/0000-0003-1197-5818>), Dept of Biosciences, Univ. of Oslo, Norway.

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Introduction

The aim of this Oikos special issue entitled 'Individual heterogeneity: the causes and consequences of a fundamental biological process' was to provide a balanced view of individual heterogeneity as a biological process relevant for a broad range of ecologists and not simply as a noisy process that needs to be accounted for to get reliable estimates of biological parameters. The methodological and empirical contributions included in this special issue provide a synthesis of the recent advances in measuring and quantifying individual heterogeneity. These contributions also provide a broad range of perspectives on the ecological and evolutionary causes and consequences of individual heterogeneity. The works compiled in this special issue emphasize the relevance of individual heterogeneity as a biological process that shapes a substantial proportion of observed variation in traits, which can drive population demography and eco-evolutionary dynamics. Following discussions held during the workshop ('Ontogeny, adaptation, and chance in life-history trajectories: do individual differences matter?' UiT The Arctic University of Norway, 13–15 October 2015) dedicated to this special issue, we propose a way forward in the study of individual heterogeneity in ecology and evolution, by identifying research gaps that still need to be filled and challenges that remain to be solved, both from a methodological and an empirical viewpoint.



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Methodological developments

The importance of individual heterogeneity for ecological understanding is nothing new. Non-random variation in fitness traits has been acknowledged for some time, for instance in classic model species like Darwin's finches *Geospiza scandi* (Grant and Grant 2000). Such pioneer studies typically focused on summary measures of individual heterogeneity over the entire lifetime, such as variation in longevity, in the number of breeding occasions, or in lifetime reproductive success. Nowadays, methodological progress such as the development and easy implementation of generalized mixed modelling has allowed researchers to examine individual heterogeneity in more detail throughout an individual's lifetime, i.e. within life-history trajectories. The three methodological papers included in this special issue go a step further (Caswell and Vindenes 2018, Gimenez et al. 2018, Hamel et al. 2018). Together, they provide an overview of the recent statistical methods and theoretical developments for taking into account two major issues that have been so far largely overlooked: first, that individual heterogeneity is more structured than is generally assumed, both within and among traits, and second, that individual heterogeneity might result from stochastic processes and not necessarily be adaptive.

The contributions in this special issue clearly demonstrate that using mixture or joint modelling to account for the structure of individual heterogeneity improves our understanding of the causes and consequences of individual heterogeneity. Individual heterogeneity is commonly modelled using mixed models that include a random effect, which typically assume a single normal distribution of individuals in relation with a single variable or trait (Pinheiro and Bates 2000, Gelman 2006). Mixture models can account for the presence of groups or subpopulations within a population (McLachlan and Peel 2000), whereas joint models can account for the shared latent correlation that commonly occurs across traits as a result of individual heterogeneity (Henderson et al. 2000). The enthusiasm for such models is growing in ecology. For instance, mixture models are increasingly used to uncover life-history tactics that may occur within a population (Authier et al. 2012, Chevallier et al. 2013, Fay et al. 2016, Hamel et al. 2017, 2018) and to partition the variance in lifetime demographic traits into components due to heterogeneity fixed at birth and heterogeneity generated by stochasticity during a life course (Hartemink et al. 2017, Jenouvrier et al. 2017, Hartemink and Caswell 2018). Joint models are used to assess the full co-variation among traits, thereby improving our understanding of positive and negative relationships among numerous traits (Cam et al. 2002, Pavitt et al. 2016, Careau and Wilson 2017, Hamel et al. 2017). Still, progress is required in terms of both developing these modelling frameworks and communicating them to enhance knowledge transfer. For example, criteria used in mixture modelling for determining the number of subgroups or tactics occurring within a population do not always agree, in particular when the focal traits do not follow a normal distribution (Brame et al. 2006, Everitt et al. 2011, Cubaynes et al. 2012,

Stahl and Sallis 2012, Hamel et al. 2017). Furthermore, even though mixture and joint models are increasingly accessible to researchers, they remain complex tools, which still limits their use. The ecological community would therefore benefit from increasing availability of tutorial examples (Hamel et al. 2017, Gimenez et al. 2018). Such examples would also help prevent potential misuse of statistical methods, which is unfortunately commonplace in ecology. For example, Houslay and Wilson (2017) pointed out that researchers still frequently extract best linear unbiased predictors (BLUPs) from mixed models as a measure of individual differences and then use these BLUPs as independent data in subsequent analyses. This approach is flawed because it ignores the uncertainty in individual values estimated from BLUPs, a point that has been clearly demonstrated years ago in the context of ecological and evolutionary studies (Hadfield et al. 2010). Using a joint modelling approach to model the covariance among traits is a more appropriate way to assess how individual heterogeneity in one trait affects another trait (Hadfield et al. 2010, Houslay and Wilson 2017).

The special issue is also highlighting that, although individual heterogeneity can play a fundamental role in many aspects of ecology and evolution, some variation can result from stochastic processes, i.e. neutral heterogeneity, and may not necessarily be adaptive (Caswell and Vindenes 2018, Jouvét et al. 2018). We have known since Darwin that variation is the fuel for the evolution of any given trait (Darwin 1871). We thus need to understand which processes give rise to individual heterogeneity and assess reliably whether individual heterogeneity is adaptive (i.e. individual differences leading to differences in fitness due to heritable genetic variation) or not (i.e. individual differences only driven by random factors). Nowadays, nobody doubts that both types of variation co-occur in most populations (Caswell 2009, Tuljapurkar et al. 2009, Steiner et al. 2010, Mauck et al. 2012, Plard et al. 2012, Cam et al. 2013, Hartemink et al. 2017). Unfortunately, there is as yet no method that allows teasing apart adaptive versus neutral individual heterogeneity to quantify their respective contributions (Bonnet and Postma 2016, Cam et al. 2016, Authier et al. 2017, Jouvét et al. 2018). In addition, it is important to note that neutral heterogeneity might also be adaptive, because large amounts of neutral heterogeneity can slow adaptive processes and hence might buffer against environmental disturbance (Steiner and Tuljapurkar 2012). However, we do not have the possibility to evaluate this in the modelling frameworks currently available. We might therefore need a new methodological approach to be able to untangle adaptive and neutral heterogeneity to move forward and be able to assess whether individual differences are adaptive. Recently, new perspectives to incorporate multiple kinds of heterogeneity have been presented (Jenouvrier et al. 2017). Nonetheless, because parameters for estimating the different kinds of heterogeneity are competing for the same information in the models (Nerlove 2014), we might be unable to really solve this question due to identifiability issues. Resolving this, however,

would provide a promising avenue to be able to determine when individual differences are important and when they can be neglected, and at which stage of the life-history trajectory individual differences are most pronounced and influential in determining adaptation.

Moreover, in the current context of climate change, we must start considering whether and how adaptive individual heterogeneity influences responses to changes in environmental conditions, and then assess the impacts of variable environments on the abundance and persistence of populations. Pioneering demographic analyses have shown that ignoring individual heterogeneity leads to erroneous conclusions in terms of population dynamics (Johnson et al. 1986). Increased individual differences can lead to an increase in the persistence probability of small populations through selection of individuals surviving better under adverse/new conditions (Conner and White 1999, but see Vindenes et al. 2008). In fact, we could expect the magnitude of adaptive individual heterogeneity to affect the probability of a population to persist under variable conditions similarly to the influence of phenotypic plasticity or bet-hedging. Still, it is unsure whether phenotypic plasticity promotes or hinders adaptation to climate scenarios in the long run (Chevin and Lande 2015). Phenotypic plasticity can provide a buffer to environmental changes, but there is likely a limit depending on the rate of changes and the costs of phenotypic plasticity (Chevin et al. 2010). Correlation among multiple environmental variables can also result in maladaptive plasticity or may constrain adaptation (Chevin and Lande 2015). For example, the phenotypic response to environmental changes on the wintering grounds of common terns *Sterna hirundo* likely hindered phenotypic responses to environmental changes on their summer breeding ground (Dobson et al. 2017).

To our knowledge, models aiming to project how climate change will affect populations and ecosystems have not yet included the influence of individual heterogeneity and its potential interaction with other processes in their projections, as done for phenotypic plasticity (Chevin et al. 2010). The work by Vindenes and Langangen (2015) is a notable exception and has opened the way to such population projections by demonstrating that accounting for individual heterogeneity can change predicted population responses to climate warming. Using pike *Esox lucius* as a case study, these authors showed that demographic responses to climate warming were reversed once they accounted for the high heritability of the focal trait, i.e. for the high variation in the trait transmitted genetically. To perform population projections including individual heterogeneity, we need modelling approaches that reliably capture the factors shaping the magnitude of both adaptive and non-adaptive individual heterogeneity and how individual heterogeneity may or not respond to changes in conditions over time. We thus need models that can include both factors enhancing variation – like spatiotemporal variation in environmental conditions, genetic diversity (Lindström 1999, Senner et al. 2015, Westneat et al. 2015,

Crone 2016) – and those limiting it – like viability/fertility selection and compensatory growth (Vaupel et al. 1979, Conover and Munch 2002, Coulson and Tuljapurkar 2008, Ozgul et al. 2009, Hamel et al. 2016).

Finally, even using the best models available, the results we can currently obtain are limited by available data. Studying individual heterogeneity requires a large amount of data because we usually need repeated measures of individuals, which ideally requires the monitoring of individually identifiable animals from birth to death. Some level of genetic information is also required to separate out heritable components (e.g. selective and neutral heterogeneity). It also requires following a large enough number of individuals to ensure that parameters (e.g. variance) are estimated accurately. The amount of data needed is not always easy to determine, but some tools like SQuID (Allegue et al. 2017) provide to researchers the opportunity to simulate complex data sets that can guide for determining the required sample size for a specific question. Moreover, in the context of estimating variation in different environmental conditions, the modelling will require not only estimating random intercepts, but also random slopes and their correlation with random intercepts (Schielzeth and Forstmeier 2009, van de Pol and Wright 2009). Unless the study design consists of manipulating wide-ranging conditions, a long time series will often be required to reach a large enough sample size that also captures a sufficiently broad range of conditions to be able to estimate the random slopes. In addition, missing values in the individual time series remain an important issue, with missing values of over 25% being shown to have the potential to bias estimates (Hamel et al. 2012, Brooks et al. 2017). Therefore, although studies should always be designed according to the questions to be answered, we need to remember that studying individual heterogeneity is data-hungry and relies heavily on long-term, individual-based studies. This highlights the limits of the questions that can be addressed, but also reemphasizes the need for protecting and pursuing these extremely valuable long-term studies (Clutton-Brock and Sheldon 2010). For instance, there are now unprecedented opportunities for using vital rates collected in demographic databases (e.g. compadre/comadre: < www.compadre-db.org >) and conduct comparative analyses, such as comparing demographic contributions to demographic variance (Caswell and Vindenes 2018). Nonetheless, individual level data is still not commonly available in such databases, and we therefore call for more data sets at the individual level to be made available.

Origin and maintenance of heterogeneity and its impacts on life histories and population dynamics

The special issue includes four empirical studies based on very different model systems, i.e. bacteria, mites, snakes, and birds (Gangloff et al. 2018, Jouvet et al. 2018, Smallegange et al. 2018, Vedder and Bouwhuis 2018). In addition, the methodological papers include examples from plants, ungulates and humans (Caswell and Vindenes 2018, Gimenez et al.

2018, Hamel et al. 2018). Together, these studies clearly show that each model species is more suitable for answering some questions than others. For instance, Jouvét et al. (2018) used bacteria to disentangle adaptive and neutral heterogeneity because bacteria can be cloned and are easy to work with in laboratory experiments, which make them perfectly suited to control for genotype and environmental differences. Fast-living species with short generation times like mites (Smallegange et al. 2018) facilitate a faster gain of insights into evolutionary consequences of individual heterogeneity than slow-living species with long generation times. One classic, fast-living model species studied in ecology and evolution is *Drosophila* spp. Although *Drosophila* are usually not individually tracked, groups of individuals have been followed to show that the observed plateaus for late fecundity can be due to heterogeneity and not to a real levelling off at old ages (Khzaeli and Curtsinger 2014, Curtsinger 2015). In contrast, individuals of more long-lived species often experience widely varying conditions throughout their lifetime, which offer opportunities to study cumulative effects and their causes and consequences at different life-history stages over the lifespan. Interestingly, although slow organisms are less sensitive than fast organisms to environmental variability (Morris et al. 2008, Dalgleish et al. 2010, Gamelon et al. 2014), they are limited by their lower evolutionary potential (Vedder et al. 2013). This suggests that contrasting slow-fast species could provide far-reaching insights on the influences of changes in environmental conditions (Smallegange et al. 2014). In addition, extremely long and detailed time series have been collected for some species like humans (Briga et al. 2017), primates (Bronikowski et al. 2016), ungulates (Festa-Bianchet et al. 2017), or seabirds (Wooller et al. 1992), making it possible to also study gradual changes in individual heterogeneity through time (Hartemink et al. 2017, Caswell and Vindenes 2018).

The life-history contrast between short-lived and long-lived species is especially interesting because the data collected from these different species sometimes must be investigated using models with different distributions. For instance, short-lived mammals like voles can produce several large litters within a year (Lambin and Yoccoz 2001, Speakman 2008). Thus, the most appropriate distribution for their annual fecundity (sensu Allainé et al. 1987) is a Poisson or generalized Poisson regression (Kendall and Wittmann 2010). Conversely, long-lived mammals, like elephants, whales, or humans, usually produce only a single offspring per reproductive attempt, with long inter-birth intervals (Kraus et al. 2001, Hayward et al. 2015, Lee et al. 2016). In such cases, annual fecundity is usually modelled with a logistic regression. Comparing variation in reproductive success between short- and long-lived animals is therefore challenging because individual heterogeneity will be modelled differently and the estimation of the amount of individual heterogeneity is sensitive to these modelling choices (Hamel et al. 2012). To circumvent this, reproductive success

of all species can be expressed as a simple binary variable, e.g. successful or not. This, however, will underestimate the amount of individual heterogeneity in reproductive success, especially in short-lived species where individuals typically do not skip any potential reproductive attempts (Speakman 2008). Hence, individual heterogeneity will be found in the number of offspring produced or raised successfully (Bouwhuis et al. 2009) rather than in the probability of producing offspring at each reproductive attempt. Individual heterogeneity in plant reproductive success is expected to be even more complex. Although we currently lack accurate measurements of demographic heterogeneity for plant species, the lower explanatory power of the slow-fast continuum to explain life-history variation observed in plants (Salguero-Gomez et al. 2016) should lead to consider other axes of life-history variation to assess the role of demographic heterogeneity in these organisms.

Nonetheless, recent developments in stochastic models (so-called Markov chains with rewards) provide a powerful and general approach to analyzing lifetime reproductive success for age-classified, stage-classified, and multistate models, for any kind of reproductive output distributions, and including a general sensitivity analysis (van Daalen and Caswell 2017). These analyses have shown that the stochasticity within the individual life cycle produces much more variation in lifetime reproductive output than might be expected (Caswell 2011, van Daalen and Caswell 2017), with consequences to be explored at the population level (Caswell and Vindenes 2018).

Much discussion on heterogeneity centers on the identification of the type of heterogeneity, and to some degree on the consequences of such heterogeneity over one generation (Steiner and Tuljapurkar 2012, Cam et al. 2016). Even if we have means to accurately quantify components of fixed and dynamic heterogeneity – and overcome additional challenges related to heritable heterogeneity in phenotypic plasticity, bet-hedging, and epigenetically driven heterogeneity –, we still lack understanding of how heterogeneity influences evolutionary dynamics over multiple generations. If traits related to fixed heterogeneity are heritable, as for instance reproductive rates in Weddell seals *Leptonychotes weddellii* (Chambert et al. 2014), selection should remove individuals with low reproductive rates. But then, how is heterogeneity in reproduction maintained in the following generations? New directions leaning on population genetic theories or quantitative genetics, building for instance on mutation-selection balance equilibria (Wachter et al. 2013) or the development of quantitative genetic integral projection models (Coulson et al. 2017, Janeiro et al. 2017) depict promising avenues. These new directions help to understand how heterogeneity can be maintained but are not necessarily having an individual level focus. Nevertheless, these directions illustrate how synthesising concepts from these different fields and aiming to combine approaches across fields will be an important step forward.

Conclusion

We still have far to go before we reach a deep understanding of the causes and consequences of individual heterogeneity. As discussed here, many challenges lie ahead but this special issue provides an overview of our current knowledge on the ecological and evolutionary causes and consequences of individual heterogeneity. We hope this special issue will clarify some of the issues surrounding individual heterogeneity and establish foundations for future work within this timely topic, which currently attracts increasing attention from ecologists and evolutionary biologists. This increasing enthusiasm is not specific to our field. In economics, for instance, the Bank of Sweden Prize in Memory of Alfred Nobel was awarded to Heckman in 2000 for his work on the importance of individual heterogeneity in the field of economics (Heckman 2001). As he made clear in his Memorial Lecture, this work started with the availability of new sources of data on individual behaviour after the Second World War, leading to the development of new analytical models, which then both influenced economic theory as well as the evaluation of the impacts of public policy. This pattern is similar to what we have seen in quantitative genetics and ecology, and we hope this special issue will inspire evolutionary ecologists to continue developing and using new analytical frameworks to improve our understanding of the causes and consequences of individual heterogeneity at all scales of biological organization.

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References

- Allainé, D. et al. 1987. The relationship between fecundity and adult body weight in homeotherms. – *Oecologia* 73: 478–480.
- Allegue, H. et al. 2017. Statistical quantification of individual differences (SQuID): an educational and statistical tool for understanding multilevel phenotypic data in linear mixed models. – *Methods Ecol. Evol.* 8: 257–267.
- Authier, M. et al. 2012. Foraging fidelity as a recipe for a long life: foraging strategy and longevity in male southern elephant seals. – *PLoS One* 7: e32026.
- Authier, M. et al. 2017. Wolf in sheep's clothing: model misspecification undermines tests of the neutral theory for life histories. – *Ecol. Evol.* 7: 3348–3361.
- Bonnet, T. and Postma, E. 2016. Successful by chance? The power of mixed models and neutral simulations for the detection of individual fixed heterogeneity in fitness components. – *Am. Nat.* 187: 60–74.
- Bouwhuis, S. et al. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. – *Proc. R. Soc B* 276: 2769–2777.
- Brame, R. et al. 2006. Exploring some analytical characteristics of finite mixture models. – *J. Quant. Criminol.* 22: 31–59.
- Briga, M. et al. 2017. What have humans done for evolutionary biology? Contributions from genes to populations. – *Proc. R. Soc. B* 284: 20171164.
- Bronikowski, A. et al. 2016. Female and male life tables for seven wild primate species. – *Sci. Data* 3: 160006.
- Brooks, M. E. et al. 2017. Estimation of individual growth trajectories when repeated measures are missing. – *Am. Nat.* 190: 377–388.
- Cam, E. et al. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. – *Am. Nat.* 159: 96–105.
- Cam, E. et al. 2013. Looking for a needle in a haystack: inference about individual fitness components in a heterogeneous population. – *Oikos* 122: 739–753.
- Cam, E. et al. 2016. The conundrum of heterogeneities in life history studies. – *Trends Ecol. Evol.* 31: 872–886.
- Careau, V. and Wilson, R. S. 2017. Performance tradeoffs and ageing in the “world's greatest athletes”. – *Proc. R. Soc. B* 284: 20171048.
- Caswell, H. 2009. Stage, age and individual stochasticity in demography. – *Oikos* 118: 1763–1782.
- Caswell, H. 2011. Beyond R_0 : Demographic calculation of variability in lifetime reproductive output. – *PLoS One* 6: e20809.
- Caswell, H. and Vindenes, Y. 2018. Demographic variance in heterogeneous populations: matrix models and sensitivity analysis. – *Oikos* 127: 648–663.
- Chambert, T. et al. 2014. An evolutionary perspective on reproductive individual heterogeneity in a marine vertebrate. – *J. Anim. Ecol.* 83: 1158–1168.
- Chevallier, C. et al. 2013. Use of mixture models to characterize site quality in philopatric animals: a case study with Bonelli's eagle. – *Anim. Conserv.* 16: 198–206.
- Chevin, L.-M. and Lande, R. 2015. Evolution of environmental cues for phenotypic plasticity. – *Evolution* 69: 2767–2775.
- Chevin, L.-M. et al. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. – *PLoS Biol.* 8: e1000357.
- Clutton-Brock, T. and Sheldon, B. C. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. – *Trends Ecol. Evol.* 25: 562–573.
- Conner, M. M. and White, G. C. 1999. Effects of individual heterogeneity in estimating the persistence of small populations. – *Nat. Resour. Model.* 12: 109–127.
- Conover, D. O. and Munch, S. B. 2002. Sustaining fisheries yields over evolutionary time scales. – *Science* 297: 94–96.
- Coulson, T. and Tuljapurkar, S. 2008. The dynamics of a quantitative trait in an age-structured population living in a variable environment. – *Am. Nat.* 172: 599–612.
- Coulson, T. et al. 2017. Modeling adaptive and nonadaptive responses of populations to environmental change. – *Am. Nat.* 190: 313–336.
- Crone, E. E. 2016. Contrasting effects of spatial heterogeneity and environmental stochasticity on population dynamics of a perennial wildflower. – *J. Ecol.* 104: 281–291.
- Cubaynes, S. et al. 2012. Assessing individual heterogeneity using model selection criteria: how many mixture components in capture-recapture models? – *Methods Ecol. Evol.* 3: 564–573.

- Curtsinger, J. W. 2015. On the analysis and interpretation of late-life fecundity in *Drosophila melanogaster*. – *Exp. Gerontol.* 72: 22–28.
- Dalgleish, H. J. et al. 2010. Can life-history traits predict the response of forb populations to changes in climate variability? – *J. Ecol.* 98: 209–217.
- Darwin, C. 1871. The descent of man, and selection in relation to sex. – John Murray.
- Dobson, F. S. et al. 2017. Plasticity results in delayed breeding in a long-distant migrant seabird. – *Ecol. Evol.* 7: 3100–3109.
- Everitt, B. S. et al. 2011. Cluster analysis. – Wiley.
- Fay, R. et al. 2016. Variation in the age of first reproduction: different strategies or individual quality? – *Ecology* 97: 1842–1851.
- Festa-Bianchet, M. et al. 2017. Successes and challenges of long-term field studies of marked ungulates. – *J. Mammal.* 98: 612–620.
- Gamelon, M. et al. 2014. Influence of life-history tactics on transient dynamics: a comparative analysis across mammalian populations. – *Am. Nat.* 184: 673–683.
- Gangloff, E. et al. 2018. Among-individual heterogeneity in behaviour and physiology interact to influence fitness in a model ectothermic amniote, the garter snake *Thamnophis elegans*. – *Oikos* 127: 705–718.
- Gelman, A. 2006. Multilevel (hierarchical) modeling: what it can and cannot do. – *Technometrics* 48: 432–435.
- Gimenez, O. et al. 2018. Individual heterogeneity and capture-recapture models: what, why and how? – *Oikos* 127: 664–686.
- Grant, P. R. and Grant, B. R. 2000. Non-random fitness variation in two populations of Darwin's finches. – *Proc. R. Soc. B* 267: 131–138.
- Hadfield, J. D. et al. 2010. The misuse of BLUP in ecology and evolution. – *Am. Nat.* 175: 116–125.
- Hamel, S. et al. 2012. Statistical evaluation of parameters estimating autocorrelation and individual heterogeneity in longitudinal studies. – *Methods Ecol. Evol.* 3: 731–742.
- Hamel, S. et al. 2016. Cohort variation in individual body mass dissipates with age in large herbivores. – *Ecol. Monogr.* 86: 517–543.
- Hamel, S. et al. 2017. Assessing variation in life-history tactics within a population using mixture regression models: a practical guide for evolutionary ecologists. – *Biol. Rev.* 92: 754–775.
- Hamel, S. et al. 2018. Quantifying individual heterogeneity and its influence on life-history trajectories: different methods for different questions and contexts. – *Oikos* 127: 687–704.
- Hartemink, N. and Caswell, H. 2018. Variance in animal longevity: contributions of heterogeneity and stochasticity. – *Popul. Ecol.* in press.
- Hartemink, N. et al. 2017. Stochasticity, heterogeneity, and variance in longevity in human populations. – *Theor. Popul. Biol.* 114: 107–116.
- Hayward, A. D. et al. 2015. Early-life reproduction is associated with increased mortality risk but enhanced lifetime fitness in pre-industrial humans. – *Proc. R. Soc. B.* 282: 20143053.
- Heckman, J. J. 2001. Micro data, heterogeneity, and the evaluation of public policy: Nobel lecture. – *J. Polit. Econ.* 109: 673–748.
- Henderson, R. et al. 2000. Joint modelling of longitudinal measurements and event time data. – *Biostatistics* 1: 465–480.
- Houslay, T. M. and Wilson, A. J. 2017. Avoiding the misuse of BLUPs in behavioural ecology. – *Behav. Ecol.* 28: 948–952.
- Janeiro, M. J. et al. 2017. Towards robust evolutionary inference with integral projection models. – *J. Evol. Biol.* 30: 270–288.
- Jenouvrier, S. et al. 2017. Interacting effects of unobserved heterogeneity and individual stochasticity in the life history of the southern fulmar. – *J. Anim. Ecol.* doi:10.1111/1365-2656.12752.
- Johnson, D. H. et al. 1986. The role of heterogeneity in animal population dynamics. – *Int. Biometrics Conf.* 13.
- Jouvet, L. et al. 2018. Demographic variability and heterogeneity among individuals within and among clonal bacteria strains. – *Oikos* 127: 728–737.
- Kendall, B. E. and Wittmann, M. E. 2010. A stochastic model for annual reproductive success. – *Am. Nat.* 175: 461–468.
- Khazaeli, A. A. and Curtsinger, J. W. 2014. Heterogeneity's ruses: how hidden variation affects population trajectories of age-dependent fecundity in *Drosophila melanogaster*. – *Demogr. Res.* 30: 313–332.
- Kraus, S. D. et al. 2001. Reproductive parameters of the North Atlantic right whale. – *J. Cetacean Res. Manage.* 2: 231–236.
- Lambin, X. and Yoccoz, N. G. 2001. Adaptive precocial reproduction in voles: reproductive costs and multivoltine life-history strategies in seasonal environments. – *Anim. Ecol.* 70: 191–200.
- Lee, P. C. et al. 2016. The reproductive advantages of a long life: longevity and senescence in wild African elephants. – *Behav. Ecol. Sociobiol.* 70: 337–345.
- Lindström, J. 1999. Early development and fitness in birds and mammals. – *Trends Ecol. Evol.* 14: 343–348.
- Mauck, R. A. et al. 2012. Experience versus effort: what explains dynamic heterogeneity with respect to age? – *Oikos* 121: 1379–1390.
- McLachlan, G. J. and Peel, D. 2000. Finite mixture models. – Wiley.
- Morris, W. F. et al. 2008. Longevity can buffer plant and animal populations against changing climatic variability. – *Ecology* 89: 19–25.
- Nerlove, M. 2014. Individual heterogeneity and state dependence: from George Biddell Airy to James Joseph Heckman. – *Oeconomia* 4: 281–320.
- Ozgul, A. et al. 2009. The dynamics of phenotypic change and the shrinking sheep of St Kilda. – *Science* 325: 464–467.
- Pavitt, A. T. et al. 2016. Testosterone and cortisol concentrations vary with reproductive status in wild female red deer. – *Ecol. Evol.* 6: 1163–1172.
- Pinheiro, J. C. and Bates, D. M. 2000. Mixed-effects models in S and S-plus. – Springer.
- Plard, F. et al. 2012. Modeling reproductive trajectories of roe deer females: fixed or dynamic heterogeneity? – *Theor. Popul. Biol.* 82: 317–328.
- Salguero-Gomez, R. et al. 2016. Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. – *Proc. Natl Acad. Sci. USA* 113: 230–235.
- Schielzeth, H. and Forstmeier, W. 2009. Conclusions beyond support: overconfident estimates in mixed models. – *Behav. Ecol.* 20: 416–420.
- Senner, N. R. et al. 2015. An ontogenetic perspective on individual differences. – *Proc. R. Soc. B* 282: 20151050.
- Smallegange, I. M. et al. 2014. Correlative changes in life-history variables in response to environmental change in a model organism. – *Am. Nat.* 183: 784–797.
- Smallegange, I. M. et al. 2018. Population consequences of individual heterogeneity in life histories: overcompensation in

- response to harvesting of alternative reproductive tactics. – *Oikos* 127: 738–749.
- Speakman, J. R. 2008. The physiological costs of reproduction in small mammals. – *Phil. Trans. R. Soc. B* 363: 375–398.
- Stahl, D. and Sallis, H. 2012. Model-based cluster analysis. – *WIREs Comput. Stat.* 4: 341–358.
- Steiner, U. K. and Tuljapurkar, S. 2012. Neutral theory for life histories and individual variability in fitness components. – *Proc. Natl Acad. Sci. USA* 109: 4684–4689.
- Steiner, U. K. et al. 2010. Dynamic heterogeneity and life history variability in the kittiwake. – *J. Anim. Ecol.* 79: 436–444.
- Tuljapurkar, S. et al. 2009. Dynamic heterogeneity in life histories. – *Ecol. Lett.* 12: 93–106.
- van Daalen, S. F. and Caswell, H. 2017. Lifetime reproductive output: individual stochasticity, variance, and sensitivity analysis. – *Theor. Ecol.* 10: 355–374.
- van de Pol, M. and Wright, J. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. – *Anim. Behav.* 77: 753–758.
- Vaupel, J. W. et al. 1979. The impact of heterogeneity in individual frailty on the dynamics of mortality. – *Demography* 16: 439–454.
- Vedder, O. and Bouwhuis, S. 2018. Heterogeneity in individual quality in birds: overall patterns and insights from a study on common terns. – *Oikos* 127: 719–727.
- Vedder, O. et al. 2013. Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. – *PloS Biol.* 11: e1001605.
- Vindenes, Y. and Langangen, Ø. 2015. Individual heterogeneity in life histories and eco-evolutionary dynamics. – *Ecol. Lett.* 18: 417–432.
- Vindenes, Y. et al. 2008. Individual heterogeneity in vital parameters and demographic stochasticity. – *Am. Nat.* 171: 455–467.
- Wachter, K.W. et al. 2013. The age-specific force of natural selection and biodemographic walls of death. – *Proc. Natl Acad. Sci. USA* 110: 10141–10146.
- Westneat, D. F. et al. 2015. The biology hidden inside residual within-individual phenotypic variation. – *Biol. Rev.* 90: 729–743.
- Wooller, R. D. et al. 1992. Long-term population studies of seabirds. – *Trends Ecol. Evol.* 7: 111–114.