# PhD-Dissertation Reviews

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# PhD-dissertation reviews

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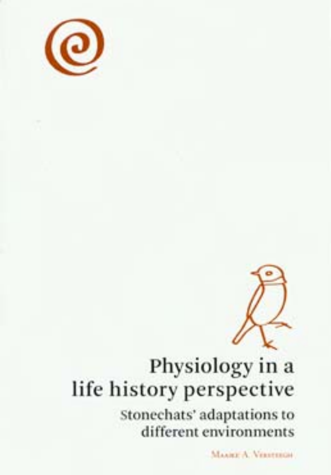
**Versteegh M.A.** 2012. Physiology in a life history perspective. Stonechats' adaptations to different environments. PhD Thesis, University of Groningen, The Netherlands. ISBN 978-90-367-5349-4. Available at http://irs.ub.rug.nl/ppn/340002581.



The life history theory poses that natural selection has shaped the schedule and duration of key events in the lifetime of an organism in such a way that it produces the largest possible number of surviving offspring. Life history traits are the evolved strategies in behaviour, physiology and anatomy that influence reproductive success and survival, key life history factors. Organisms have evolved a large variety in life history traits, but it was early recognized that these strategies can be arranged on a single dominant axis, the Pace-of-Life axis. On the one extreme of this axis are species with a slow Pace-of-Life. Birds with a slow Pace-of-Life have long development times, small clutches, low energy expenditure, long lifespan and live at low latitudes. At the other extreme, the fast Pace-of-Life, species have short development times, large clutches, high energy expenditure, short lifespan and live at high latitudes. The striking latitudinal effect intrigued many researchers. Most explaining hypotheses are based on the idea that an organism has to allocate limited resources between itself and its offspring such that its fitness is optimized, resulting in studies focussing e.g. on variation in food availability and predation risk. Other explaining hypotheses are based on physiological mechanisms, as physiology mediates the relationship between organism and environment. A well-known hypothesis is the oxidative stress theory, posing that energy expenditure produces harmful toxic by-products such as free radicals, which induce senescence and reduce lifespan. Recently two other physiological hypotheses have been developed in relation to other aspects of mortality and physiological maintenance. They involve the endocrine and the immune system.

Generally studies investigating the physiological hypotheses look into only one of the systems. In this thesis, Versteegh combines three physiological systems, and investigates how the metabolic (basal metabolic rate), endocrine (stress-hormones) and immune (constitutive innate response) system relate to each other and to life history traits. But Versteegh takes it a step further. Because the three systems are expected to be linked to each other, the systems might not vary independently. This will constrain their variation, and, consequently, may limit the evolution of life history traits. Therefore Versteegh explored the influence of genes and environment on the correlations between the three systems and life history traits. She used for her studies four Stonechat *Saxicola torquata* subspecies, originating from tropical, continental and temperate environments that differ in many aspects. The Stonechat subspecies were bred and kept in a common garden, yet they displayed the variation in life history traits of their wild counterparts e.g. in clutch size, development time and timing of moult. This indicates that the variation in life history traits has a genetic background, and that hence the stonechat is a good model species for this study.

Chapter 1 provides the background of the study, introducing the Pace-of-Life theory, the three physiological systems, and the Stonechats. In box 1.1 the concept

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of a common garden setup is explained, and box 1.2 provides details about the life history traits of the four subspecies and their hybrids. In Chapter 2, Versteegh investigates if the three physiological systems fall on a single axis, i.e. the Pace-of-Life axis. If this is the case, they should covary with each other at individual and subspecies level. Basal metabolic rate covaried with corticosterone and two of the six immune indices at the individual level, while corticosterone covaried with one immune index at the subspecies level. This indicates that the links between the physiological systems are loose and the results do not support the idea that the systems cannot evolve independently of each other. Therefore environmental factors are more important than links between physiological systems for the evolution of life history traits.

Many life history traits are adapted to seasonal changes in the environment. The resulting annual cycles can be due to phenotypic flexibility of an organism, but they can also be endogenous, i.e. genetically controlled. In Chapters 3 and 4 Versteegh disentangles the effect of phenotypic flexibility and genetic control on the annual cycles of metabolic rate and immunity in three subspecies of Stonechats. The birds were kept in a common garden, while from one subspecies also birds were kept under a temperature regime that mimicked the natural temperature cycles. The annual cycles in metabolic rate, body mass and four of the five immune indices (the exception being haptoglobin) differed between the subspecies, indicating at a genetic basis for the annual cycle of both physiological systems. This was confirmed by the results of the hybrids: their annual cycles differed from the parental subspecies and were often intermediate for metabolic rate though generally not for the immune system. Keeping birds at a varying temperature regime did not affect the shape or variability of the annual cycles of body mass and metabolic rate, but basal metabolic rate was 8% higher under varying temperatures. Hence phenotypic flexibility superimposed a modest variation on the endogenously controlled annual cycle of metabolic rate. The varying temperature regime influenced the annual cycles of only two immune indices, hemolysis and the bactericidal ability against *Escherichia coli*, indicating that the annual cycle of immune indices can be either rigid or more flexible.

In Chapter 5 Versteegh looks into the genetic mechanisms that determine energy expenditure. Metabolic rate, determined often via oxygen consumption, is directly related to mitochondrial function, and mitochondrial DNA may thus have an important genetic influence on metabolic rate. In contrast to nuclear DNA, mitochondrial DNA is solely maternally inherited. By measuring metabolic rate in two types of hybrids with reciprocal parental configurations from three subspecies, Versteegh showed that metabolic rate is affected by a combination of nuclear and mitochondrial DNA. Chapter 6 confirms the genetic basis of metabolic rate by showing that both whole organism and mass-specific basal metabolic rate are repeatable within individuals. Evaporative water loss, a trait that seems to be subject to similar selection pressures as metabolic rate, showed however no significant repeatability within individuals.

The immune system is a complex system which poses two major challenges for ecological immunologists: determining what to measure, and determining how to analyse the data. Chapter 7 provides a helping hand for the latter problem. The here derived new tool to analyse multivariate immunological datasets is used in Chapter 8 together with the repeatability analysis of Chapter 6 to re-analyse the immune and metabolic data of Chapters 3 and 4. In two subspecies, three immune indices showed high repeatability within individuals, indicating that these indices are individual characteristics. In the third subspecies, however, no significant repeatabilities were found and immune indices were not consistent within individuals. The analysis of basal metabolic rate and the immune indices via the method of Chapter 7 showed that the correlations between the immune indices and basal metabolic rate varied within life cycle stage among subspecies, and within subspecies among life cycle stages. This confirms the results of Chapter 2, namely that the immune and metabolic system are unlikely to be constrained within subspecies and that the selection of environmental factors on physiological traits is to a certain degree independent.

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