

**Among-individual differences in predictability in the wild,
its importance and evolutionary consequences.**

PhD Thesis Research Proposal Comprehensive
Exam - Revisions

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Introduction

Over the past decades, we have observed a global and rapid decline of biodiversity (Butchart et al., 2010; MacKinnon, Verkuil, & Murray, 2012). Indeed, biologists even refer to a sixth mass extinction (Barnosky et al., 2011; Estes et al., 2011) and according to the new report published by the World Wildlife Fund (WWF) the Living Planet Index (LPI) estimates a 68% decline in vertebrate populations (mammals, birds, amphibians, reptiles, and fish) monitored since 1970 (Almond, Grooten, & Petersen, 2021). Meanwhile, the Biodiversity Intactness Index (BII) estimates that human land use has reduced species abundance by an average of 15% (Johnson et al., 2017). Another relatively significant example of this biodiversity loss has been assessed in the amphibian group, in which 41% are threatened with extinction (Monastersky, 2014; Wake & Vredenburg, 2008). A major driver of this is a change in land use along with significant habitat loss and degradation (Estes et al., 2011; World Resources Institute (WRI), 2005). Extremely rapid human-induced land transformation exerts strong pressure on biodiversity and the environment (Postma, 2006; Sauve et al., 2022). Issues related to species adaptation and evolution are more than crucial to gain a better understanding of the adaptive responses of individuals and populations. Therefore, we need studies combining ecology and evolution to predict short-term population dynamics (Gonzalez, Ronce, Ferriere, & Hochberg, 2013) and to implement wildlife conservation and management measures (Coltman et al., 2003).

Phenotypic variance

Explaining diversity to understand mechanisms by which species adapt is a major challenge of evolutionary ecology (Charmantier, Garant, & Kruuk, 2014), especially in an ever-changing environment. A key topic for gaining details of how evolution and demography interact is to investigate adaptive variation. Phenotypic variation can be studied at different scales such as among taxa, among species, among populations, among individuals and among instances (Westneat, Wright, & Dingemanse, 2015). Individual differences are the raw material on which natural selection acts and thus the basis for evolutionary adaptation. Understanding the sources of phenotypic variance is therefore an essential feature of biological investigation. In recent decades, two levels of variation have been primarily studied to assess among-individual differences: variation on mean trait values and variation in plastic responses of traits. To describe these different levels of variation, I will use the phenotypic equation which is based on the statement that the phenotype is shaped by a genetic (G) and environmental (E) component ($P = G + E$). Using quantitative genetic models, the phenotypic variance V_P can be

partitioned into genetic variance V_G and environmental and error variance V_E ($V_P = V_G + V_E$) (Falconer & Mackay, 1996; Lynch & Walsh, 1998). Several phenotypic variance patterns have been studied using different versions of the phenotype equation. However, when on the same individual several observations of the same trait are collected the equation can be written as follows:

$$V_P = V_A + V_D + V_S + V_{PE} + V_{TE} + V_R,$$

where V_A represents additive genetic variance effects on V_P , V_D dominance genetic effects, V_S epistatic genetic effects, V_{PE} (developmental plasticity for Westneat et al., 2015) represents permanent environmental effects (V_{PE} includes maternal and paternal effects, epigenetic effects and other contributors that have long-term impacts on phenotypes such as nutritional state during development), V_{TE} represents temporary environmental effects, and V_R the residual variance .

Phenotypic variance can also be decomposed into its among-individual variance and within-individual variance components (V_{among} and V_{within} respectively) (Dingemanse & Dochtermann, 2013). Among-individual variance represents the variation in individual means, i.e. when the average phenotypic attributes of individuals are used to compare them. In recent behavioral ecology literature intrinsic individual differences in the mean expression of a behavior is often referred to as “animal personality” (or consistent behavioral differences among individuals) (Dingemanse, Kazem, Réale, & Wright, 2010; Réale, Dingemanse, Kazem, & Wright, 2010). It is possible to associate this component with certain members of our first equation, as follows: $V_{\text{among}} = V_A + V_D + V_S + V_{PE}$. The second component is the within-individual variance (V_{within}). Part of this variation caused by a response to a temporary and measurable environmental change is called phenotypic plasticity (Gomulkiewicz & Kirkpatrick, 1992; Scheiner, 1993) and is represented by V_{TE} . Another component of within-individual variation is the residual variance V_R which is considered as random noise, and homogeneous between individuals (essentially containing measurement errors) in most behavioral ecology studies unlike fields such as human psychology and quantitative genetics where the importance of modeling residual within-individual variation has already been recognized.

Among-individual variance on mean

There are therefore different scales and levels at which phenotypic variation can be studied. Differences among species and populations have been well studied and, more recently, there has been a growing awareness of the importance to consider among-individual variation.

Indeed, as mentioned above, natural selection occurs at the individual level, so understanding among-individual variation within a population is essential for understanding evolutionary potential. A shift then occurred that consistent variation in behavior between individuals across time or contexts may not be exceptional (Dingemanse et al., 2010; Martin & Réale, 2008) but could be the norm across a large multitude of taxa. We now have evidence that individuals often show consistent differences in the mean of most behavioral traits across time and contexts (Mathot & Dingemanse, 2014).

Furthermore, it has been determined for many labile traits in behavioral ecology that sometimes up to 40% of the variation within a population can be attributed to consistent individual differences, the among-individual variation (Bell, Hankison, & Laskowski, 2009; Dochtermann, Schwab, & Sih, 2015a; Tonsor, Elnaccash, & Scheiner, 2013; Westneat, Hatch, Wetzel, & Ensminger, 2011). Thus, individuals may vary from their conspecifics in their mean trait values (Ramakers, Visser, & Gienapp, 2020; Réale & Dingemanse, 2010), and this among-individual variation is an important component in explaining biological mechanisms of evolution. For example, it has been reported that the aggressiveness of Ural Owl (*Strix uralensis*) females defending their nests each year predicts their aggressiveness in the following year (Konttiainen et al., 2009). Another study showed that docile and bold bighorn sheep rams (*Ovis canadensis*) survived longer than non-docile and shy individuals (Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009). They were also able to show that behavioral traits of the former had a weak negative effect on reproductive success in the early stages of their lives and a strong positive effect for older animals (Réale et al., 2009).

This new approach to analyzing phenotypic variation has led to the emergence of a new field of research in behavioral ecology: adaptive animal personality (Mathot & Dingemanse, 2014; Réale et al., 2010) and intrinsic individual difference in the mean expression of a behavior is called personality (or consistent behavioral differences among individuals) (Dingemanse, Kazem, Réale, & Wright, 2010; Réale, Dingemanse, Kazem, & Wright, 2010). This concept of personality can be extended to a suite of behaviors or traits. Such a suite may have important implications for a range of ecological processes, including species interactions and population dynamics (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012). This approach is an extension of the pace-of-life syndrome (POLS) concept and posits that “consistent behavioral differences among individuals, or personality, covary with life history and physiological differences at intra-, inter-, and interspecific levels” (Réale et al. 2010).

Finally, to characterize consistent among-individual variation of an attribute, we often estimate its repeatability especially for labile traits that can be observed multiple times (Bell et

al., 2009; Nakagawa & Schielzeth, 2010). Repeatability (r) can be defined as follows (Boake, 1989; Dochtermann et al., 2015a):

$$r = \frac{(V_A + V_D + V_S + V_{PE})}{V_P} = \frac{V_{among}}{V_P}$$

And a high trait repeatability value can be interpreted as occurring when the intra-individual variance is low relative to the inter-individual variance (Bell et al., 2009; Stamps, Briffa & Biro, 2012).

Among-individual variance in the within-individual variance: Plasticity

Another well-studied level of phenotypic variance is phenotypic plasticity (or individual-environment interactions). It can be defined as the ability of individuals to change phenotypic trait values through cues across an environmental gradient (Dingemanse & Wolf, 2013) or as the ability of the same genotype to produce different phenotypes in response to environmental variation (Dingemanse & Wolf, 2013b). Plastic response of individuals represents the part of within-individual variation due to measurable environmental change (V_{TE}) and has, in the past decade, generated many studies in animal physiology, animal behavior and evolutionary ecology (DeWitt & Scheiner, 2004; Moczek et al., 2011; Pfennig et al., 2010; Piersma & Gils, 2011; Schlichting & Pigliucci, 1998; Taborsky & Oliveira, 2012; West-Eberhard, 2003). It has been shown that environmental factors can have effects on the phenotype ranging from the short term to the long term (Piersma & Drent, 2003). Indeed, reversible, or permanent aspect of plasticity as well as its selection benefits and limitations have raised many questions about its role in adaptive and evolutionary processes (Abrams & Matsuda, 2004; Pigliucci & Pigliucci, 2001; Vos et al., 2004). As a result, several concepts and terms have emerged to address the different ways in which the environment influences phenotype and its consequences (Gabriel, Luttbegg, Sih, & Tollrian, 2005; Stamps & Groothuis, 2010; Stamps & Groothuis, 2010). An example of a short-term effect of the environment is the time interval between each chick feeding behavior observed in birds. In Bell Miners (*Manorina melanophrys*), it has been found that time between each parental nest feeding depends on chick state (e.g., begging posture) observed during the previous visit, not information on chick state further back in time (Wright, McDonald, te Marvelde, Kazem, & Bishop, 2010). At the other end of the spectrum, some environmental effects occurring during developmental stages may become permanent in adulthood. For example, hatching daphnia populations under water temperature conditions that predict a high level of predation will result in the development of large protective helmets. Conversely, individuals of the same clonal line that hatch under water

temperature conditions that predict a low level of predation develop small protective helmets (Brooks, 1957, 1965). Such permanent variation is defined as developmental plasticity and is included in the variation between individuals in mean (Araya-Ajoy & Dingemanse, 2017; Hertel, Niemelä, Dingemanse, & Mueller, 2020).

It has recently been established that the reversible, short-term plastic response can differ among individuals in the same population (Coppens, de Boer, & Koolhaas, 2010; Dingemanse et al., 2010; Mathot, Wright, Kempenaers, & Dingemanse, 2012; Sih & Bell, 2008; Wolf, van Doorn, & Weissing, 2008) and this response can be studied to assess among-individual variation in plasticity (Dingemanse & Wolf, 2013; Mathot et al., 2012). This is referred to as individual plasticity (Hertel et al., 2020; Westneat et al., 2015). Thus, most of the phenotypic plasticity is contained in the within-individual variance of phenotypic variance. But when we focus more closely on the between-individual variance in plasticity, then we can complexify the previous phenotypic variance equation. As I said before, we have associated plasticity with V_{TE} (temporal variance of the environment), but this can be extended with $V_{I \times E}$ which represents the variance due to individual differences in plasticity or individual by environment interaction ($I \times E$). In some cases, there is a genetic basis of this plasticity which is the genotype by environment interaction ($V_{G \times E}$). $V_{G \times E}$ thus represents the part of the additive genetic variation of phenotypic plasticity in labile traits that can be under selection (Nussey, Wilson, & Brommer, 2007). Analogous to the difference in trait mean, plasticity can have important ecological and evolutionary consequences (Nussey et al., 2007). Among other aspects (Whitman & Agrawal, 2009), plastic response can be adaptive and maladaptive depending on the direction favored by directional selection (see Ghalambor, McKAY, Carroll, & Reznick, 2007). But generally, the ability of a population to cope with rapid and unexpected environmental change is strongly related to the diversity in degree and direction of plastic responses among individuals (Dingemanse & Wolf, 2013).

Study of two levels of among-individual variance: Reaction Norm Framework

What we have seen so far is that we can evaluate phenotypic differences among individuals within a population by differences in the mean of a trait across time and context and by differences in their plastic phenotypic response to adapt to environmental changes. Nevertheless, studying these two levels simultaneously provides a powerful pattern of phenotypic variation between individuals in the same population (Westneat et al., 2011). Indeed, the relationship between mean and plasticity over one or more traits could reflect trade-offs on which selection would act directly and is referred to as coping style or behavioral

syndrome or personality (Coppens et al., 2010; Mathot & Dingemanse, 2014). For example, studies on coping style have shown a propensity for reactive individuals to exhibit a stronger response to environmental cues (i.e. steep slopes) while proactive individuals exhibit greater rigidity in their response (flat or weak slopes) (Bell et al., 2009; Coppens et al., 2010; Koolhaas et al., 1999; Marchetti & Drent, 2000). It has also been argued that individuals with higher levels of aggressiveness often demonstrate lower plastic adjustment of behavior (Benus, Bohus, Koolhaas, & van Oortmerssen, 1991; Kontiainen et al., 2009; Koolhaas et al., 1999). Moreover, several studies emphasize the need to study both components simultaneously (Dingemanse, Barber, Wright, & Brommer, 2012; Dingemanse et al., 2010; Westneat et al., 2011), to obtain a more accurate image of the implication of these two variations on adaption.

The "reaction norm framework" (RN framework) has been developed in evolutionary biology (DeWitt & Scheiner, 2004; Schlichting & Pigliucci, 1998; West-Eberhard, 2003), to study these two levels of variation concurrently. The RN simply describes a function, or series of functions, most of the time a linear regression, of the phenotypic variation which one genotype produces across an environmental gradient (Gomulkiewicz & Kirkpatrick, 1992; Nussey et al., 2007). In behavioral ecology it represents the range of behavioral phenotypes that a single individual produces under different environmental conditions (Hertel et al., 2020). Personality and plasticity association is thus characterized in a linear RN by a combination of a behavioral mean represented by the individual intercept of the reaction norm, a behavioral response to environmental changes which is the individual slope and the covariation among-individuals between the intercept and slope (Dingemanse et al., 2012).

Using RN frameworks to study variation between individuals has several advantages. First, it provides a more detailed overview of the different components of phenotypic variance, namely among-individual variance on mean (RN elevation), among-individual variance on plasticity (RN slope), covariance between both, and error (Dingemanse et al., 2010; Nussey et al., 2007; Westneat et al., 2011). Second, it allows to document and identify on which component selection mechanisms act through fitness studies. Third, through quantitative genetic tools, the heritable fraction of variance in both mean and plasticity of the trait can be quantified. And finally, doing so provides information about evolutionary impact of selection on trait variation and thus information about the different constraints on the adaptive response (Roff, 2012).

In conclusion, the study of among-individual variance on mean and plasticity gives us a framework to obtain a better understanding of evolutionary mechanisms at the individual level and thus assess the evolutionary potential of a population (Dingemanse et al., 2010). However,

until recently, another level to explain phenotypic variance had been poorly considered, even overlooked in ecology: the unexplained part of the within-individual variance.

Among-individual variance in the within-individual variance once corrected by environmental variance: Predictability

Some aspects of within-individual variance (such as plasticity) are nowadays known, studied, and integrated in studies on phenotypic variation. However, full variance partitioning reveals understudied patterns that require explanation (Westneat et al., 2015). These could lead to new insights and hypotheses about the biological processes at work to explain phenotypic variation. Different disciplinary fields of biology have succinctly approached this level of variance and we find in the literature a strong semantic diversity to speak about the same subject, such as micro-environmental variance, hidden genetic variance, residual within-individual variance. “Residual within-individual variance” (Hertel et al., 2020; Westneat et al., 2015) or “unexplained within-individual variance” is the term used in Westneat et al., (2015), and aptly represents the residual part of within-individual variance that remains unexplained. In behavioral ecology, you can find the term “residual intra-individual variability” (rIIV) which refers to the predictability of some individuals around their mean while others are unpredictable (Hertel, Royauté, Zedrosser, & Mueller, 2021; Mitchell, Beckmann, & Biro, 2021). We can also encounter the term “intra-individual variance”, “within-individual variance” (Martin, Pirotta, Petelle, & Blumstein, 2017) or “intraindividual variation” (IIV; Briffa, 2013; Briffa, Bridger, & Biro, 2013; Stamps et al. 2012). The intraindividual variation was originally coined in psychology and refers to the short-term, unpredictable, reversible variability in an individual's behavior measured repeatedly in the same context (Nesselroade, 1991; Ram & Gerstorf, 2009; Salthouse, 2007; Siegler, 1994). Sztepanacz, McGuigan, & Blows (2017) refer to this as “micro-environmental variance” and they define it as the result of unmeasured micro-environmental effects and captures variation in developmental stability (Sztepanacz et al., 2017) (i.e., an individual's ability to buffer its development against random noise and canalization; Sztepanacz et al., 2017). Finally, a last term can be found in the literature, namely the “predictability” of a trait (Cleasby, Nakagawa, & Schielzeth, 2015; Goold & Newberry, 2017; Hertel et al., 2021; Horváth et al., 2017; Martin et al., 2017; O’Dea, Noble, & Nakagawa, 2022; Prentice, Houslay, Martin, & Wilson, 2020) in reference to what is captured by this variance, i.e., the degree to which a trait is predictive within an individual. For this research project I will use the term predictability and residual within-individual variance.

Residual within-individual variance has been a long-known phenomenon in psychology (as intra-individual variation) (MacDonald, Nyberg, & Bäckman, 2006; Ram, Rabbitt, Stollery, & Nesselroade, 2005) and the first elements of understanding have been established in this field. Indeed, after several data accumulations, it has been shown that variability in behavior expressed by the same individual is not simply noise and that the variation could depend on age, experience, while being significantly different between individuals and stable over time (Fiske & Rice, 1955). In addition, laboratory experiments and analyses of breeding animals have recently revealed that within-individual variance is not homogeneous among individuals in a population (Geiler-Samerotte et al., 2013; Hill & Mulder, 2010; Ibanez-Escriche, Sorensen, Blasco, Xicato, & Trocino, 2008; Janhunen, Kause, Vehviläinen, & Järvisalo, 2012; Rönnegård, Felleki, Fikse, Mulder, & Strandberg, 2013; Sonesson, Ødegård, & Rönnegård, 2013; Westneat, Schofield, & Wright, 2013; Wolc, White, Avendano, & Hill, 2009). Moreover, using quantitative genetic models, it has been possible to partition it into an environmental and a genetic component (Hill & Mulder, 2010). In particular, Hill & Mulder (2010) found genetic variation in the within-individual variance on a morphological trait for which they had repeated weight measurements of individual piglets in a litter. Besides increasing the mean of production traits, controlling phenotypic variability presents also a great interest for conventional agriculture (artificial selection) as selecting more predictable genotypes allows reducing the variation of target traits (Hill & Mulder, 2010). Thus, one of the long-standing goals of reducing animal variability and increasing production efficiency is achieved.

A selection experiment in rabbits showed that selection on the genetic component (i.e., breeding value) of the predictability of birth weight, noted environmental variance (V_E) in the study, successfully modified within-litter variability of birth weight (Garreau et al., 2008). Analyses conducted by Wolc et al. (2009) confirm the possibility to act on predictability of a trait through selection to improve uniformity in this case on weight and conformation of broiler chickens at 34 days of age. Despite low heritability estimates, these different studies show non-negligible genetic coefficient of variation (GCV) indicating the selective potential of predictability (microenvironmental variance) in breeding animals (Garreau et al., 2008; Ibanez-Escriche et al., 2008; Janhunen et al., 2012; Mulder, Hill, Vereijken, & Veerkamp, 2009; Ros et al., 2004; SanCristobal-Gaudy, Bodin, Elsen, & Chevalet, 2001; Sorensen & Waagepetersen, 2003; Wolc et al., 2009). Other studies have also estimated genetic variation in within-individual predictability of milk yield in Swedish Holstein dairy cattle (Rönnegård et al., 2013) or within-family body weight in Atlantic salmon (*Salmo salar*) (Sonesson et al., 2013) notably.

In ecology results presented in the meta-analysis by Bell et al. (2009) show that

phenotypic variance is most often due to within-individual variance rather than among-individual variance, the latter accounting for only 37% of the total variance. This suggests the need to explore within-individual variance, which until now has been considered mainly as environmental plasticity due to environmental variation, measurement error and white noise (Westneat, Mutzel, Bonner, & Wright, 2017). Yet, we know that even when correcting for environmental variation (i.e. plasticity), part of the within-individual variance remains unexplained (for graphical depictions of this variation see Martin & Réale, 2008; (Biro, 2012; Carter, Heinsohn, Goldizen, & Biro, 2012; Stamps et al. 2012). But it is still considered as random noise – due to measurement error – and as homogeneous between individuals in the standard mixed models used (Littell, Milliken, Stroup, Wolfinger, & Oliver, 2006; Martin, Nussey, Wilson, & Réale, 2011; West, Ryu, Kwok, & Cham, 2011). Nevertheless evidence that some individuals were more variable than others (Martin et al., 2017) subsequently broke down the assumption of homogeneity and supports the idea that residual within-individual variation is heterogeneous between individuals (Mitchell et al., 2021; Nicolaus, Brommer, Ubels, Tinbergen, & Dingemanse, 2013; Ramakers et al., 2020; Ros et al., 2004; Rowe, White, Avendano, & Hill, 2005; Sorensen & Waagepetersen, 2003; Zhang & Hill, 2005). Several hypotheses have been put forward to explain heterogeneity of within-individual variance between individuals: measurement artifacts (e.g., individual differences in measurement error), inaccurate or incomplete model hypothesis (see Westneat et al., 2015), non-adaptive deviations from an optimal phenotype (e.g., maladaptive inaccuracy: Hansen, Carter, & Pélabon, 2006), or adaptive variation between individuals in their level of variability (e.g., alternative strategies; Wolf, van Doorn, Leimar, & Weissing, 2007). Also, it is essential to underline that some factors may contribute to variation and bias predictability interpretation such as: familiar processes (habituation, sensitization, acclimatization, or motor/sensory fatigue), and other variations not accounted for in environmental conditions such as internal state factors (e.g., circadian rhythms), or instabilities in biological processes (Mitchell et al., 2021).

Recent evolutionary publications have pointed to the necessity of paying more attention to this unpredictable component of the variance and argued that it may represent valuable biological information (Cleasby et al., 2015; Hill & Mulder, 2010; Mulder, Hill, & Knol, 2015; Sae-Lim et al., 2015; Sztepanacz et al., 2017; Westneat et al., 2015). Despite its potential importance for evolutionary questions, predictability has a short history in evolutionary ecology (Stamps et al., 2012) and there are very few studies of predictability in nature. Nevertheless, some studies in evolutionary ecology have evaluated phenotypic variation in residual within-individual variance. They then suggest the existence of distinct variation in predictability

between individuals and that it is a nontrivial component of phenotype (Briffa, 2013; Mitchell, Fanson, Beckmann, & Biro, 2016; Montiglio, Garant, Pelletier, & Réale, 2015; Stamps et al., 2012; Westneat et al., 2013). For example, residual variance difference observed in female red-winged blackbirds (*Agelaius phoeniceus*) on the parental behavior trait (i.e., amount of food delivered per second during each visit) (Westneat et al., 2013). Another example in three-spined sticklebacks (*Gasterosteus aculeatus*) where boldness score shows individual differences in predictability with shy fish less predictable in their behavior than bold fish (Jolles, Briggs, Araya-Ajoy, & Boogert, 2019). Finally, the review by Mitchell et al. (2021) provides a good overview of the magnitude of phenotype-level predictability in different species belonging to different taxa and for multiple trait types (morphological, behavioral, physiological and life history). We can infer that predictability is a component of phenotypic variance that is widespread across many types of traits and species (Mitchell et al., 2021). Nevertheless, to date, very few studies on free-living animal populations have estimated the variation in predictability at the phenotypic and even less at the genetic level. Because a clear understanding of the structure of phenotypic variance and, more importantly, genetic variation in a phenotype is necessary to understand potential evolution and adaptation, it is essential to study the prevalence and importance of predictability variation in natural systems.

Three recent studies have, using data collected on a free-living animal population or from wild animals brought in captivity, initiated a field of possibilities to work further on the evolutionary role of predictability. Indeed, they have shown the existence of a genetic basis for predictability on behavioral traits (Martin et al., 2017; Prentice et al., 2020). Despite a low heritability estimate for predictability of the docility trait in yellow-bellied marmots (*Marmota flaviventris*), Martin et al. (2017) obtained a relatively high coefficient of genetic variation $GCV = \sigma_{av} / \mu * 100 = 35.5\%$ (σ_{av} represent the additive genetic standard deviation and μ the trait mean) reflecting potential for genetic change in response to selection (Hill & Mulder, 2010; Mulder, Bijma, & Hill, 2007). It has also been established that predictability can be associated with fitness variation (Patrick, Martin, Ummenhofer, Corbeau, & Weimerskirch, 2021). This implies that predictability could evolve under natural selection and therefore needs to be considered from an evolutionary, methodological, and statistical perspective. As has been done in studies of livestock and natural systems (Mulder, Gienapp, & Visser, 2016; Sonesson et al., 2013), it should be noted that predictability can be estimated at other data clusters like family or population rather than individual identity (O’Dea et al., 2022). Mulder et al. (2016) did this for fledging weight in a wild great tit (*Parus major*) population where they showed that within-family variance in fledging weight was under stabilizing selection, thus indicating that the trait

was under strong canalization. Not only there is an optimal fledging weight but family with lower variation in fledging weight were surviving better.

We now know that individuals can vary in trait within a similar context (Eriksson, Booth, & Biro, 2010; Stamps et al., 2012) and we can no longer simply say that this is random noise, measurement error, or the result of small-scale environmental fluctuations nested within a given situation (Briffa et al., 2013). Variation in predictability should be considered as part of the wider structure of a trait. Nevertheless, as I have shown, we have very little knowledge about predictability in free-living animals. It is a concept that has a very interesting potential to conduct more comprehensive studies on phenotypic variation and thus better understand adaptive mechanisms. However, most studies on the subject only consider variation in predictability on one or two traits and most often without quantitative genetic analysis. This means a real lack of knowledge exists on the genetic basis of this variation. A reason for this is likely related to the difficulty and time required to construct and collect a full long-term data set. Indeed, a large amount of repeated data on individuals and accurate pedigree knowledge is required to obtain moderate selection accuracy (Sae-Lim et al., 2015). But we have now sophisticated quantitative genetic analysis and long-term datasets on natural populations with known pedigrees that enable this evaluation.

So, I want to set up an integrative study to investigate **the prevalence and importance of variation in predictability in natural systems to better understand among-individual trait variation and comprehend the evolutionary implications of predictability in maintaining or limiting phenotypic variation**. My research project aims to **(1)** conduct a literature review on the state of knowledge on the importance of predictability in evolutionary theory; **(2)** quantify the genetic variance in among-individual differences in predictability across different traits (morphological, physiological, behavioral, and life history) in the yellow-bellied marmot (*Marmota flaviventer*) as well as explore the covariance of among-individual variations between mean, plasticity, and predictability within and among traits; **(3)** estimate the direct and indirect evolutionary implications of individual variation in predictability by analyzing the genetic matrix covariance of mean, plasticity, and predictability across multiple traits with two fitness proxies (lifetime reproductive success and longevity); **(4)** extend the developed framework to several species and traits to obtain a holistic overview of the existence of predictability in free-living animals; and **(5)** conduct methodological work using newly developed statistical tools to establish an adequate sampling method that assesses multiple levels of phenotypic variance (mean, plasticity, and predictability) in various study systems.

General hypothesis

The lack of data, of statistical knowledge and of real consensus around predictability has resulted in a lack of information on its additive genetic basis. Therefore, my project is descriptive and the different axes that will be developed will allow to evaluate the accuracy of my general hypothesis and thus to implement the first results on this subject. First, I hypothesize that a pattern of predictability can be found in different species of different taxa and on several type traits but more importantly that variation on predictability has a genetic basis. Thus, I hypothesize that genetic variation in predictability can impact fitness and is therefore under selection. Furthermore, I suggest that traits subject to strong selection will show less variation. I also posit that phenotypic and genetic covariance exists among the different phenotypic levels (mean, plasticity, and predictability). Finally, I propose that evolutionary trade-offs exist across the different levels of phenotypic variance within and between traits based on ecological and biological constraints for each species. Thus, I argue that predictability is a major level of variation to consider in studies of adaption.

Material and Methods

To conduct this research project, which includes estimating the genetic basis of the among-individual difference in predictability for several types of traits (morphological, physiological, behavioral and life history) and for several species, I need multiple long-term data sets. In a first step, however, my research project will focus on a population of yellow-bellied marmots (*Marmotta flaviventer*), which is the biological model studied by my thesis supervisor Dr. Julien Martin in collaboration with Daniel Blumstein. A long-term study of this population has been conducted at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA since 1962 along a section of the Upper East River Valley (38°57'N, 106°59'W; 2,900 m elevation; Armitage, 2014). Marmots are large, hibernating, subalpine rodents that live in colonies composed by one or more matrilineal typically made up of an adult male, several adult females, and their offspring groups (Armitage, 2014; Frase & Hoffmann, 1980). Individuals are regularly trapped, and morphological measurements are taken (e.g., weighed, measurement of their left hind foot). Behavioral observations are also performed, and experiments are set up to evaluate their behavior (e.g., boldness evaluate through flight initiation distance (FID), docility evaluate through marmots' response to being trapped). Furthermore, the range and topography of the study site allows to group a colony site in “up-valley” (higher altitude) and a second one in “down-valley” (lower altitude). It reflects an elevation difference of 165 m (max range = 332 m) and thus a delayed snowmelt date and

vegetation growth onset in the upper valley (Armitage, 2014; Blumstein, Im, Nicodemus, & Zugmeyer, 2004). Marmots in up-valley emerge on average two weeks later than in down-valley (Blumstein, 2009; Monclús, Pang, & Blumstein, 2014).

In a second step our project will focus on the extent of predictability within other biological systems. Through various collaborations developed by my supervisor Dr. Julien Martin over the last few years, I have access to at least five long-term datasets that fulfill the conditions mentioned above. This dataset gathers over 165 years of combined field data, providing a very rare wildlife dataset to be able to do quantitative genetics. Five biological systems covering two taxa (mammals and birds) studied in research projects conducted by Daniel Blumstein, Marco Festa-Bianchet, Andrew McAdam, Pierre Bize and Denis Réale on yellow-bellied marmots (*Marmotta flaviventer*), bighorn sheep (*Ovis canadensis*), red squirrels (*Tamiasciurus hudsonicus*), alpine swifts (*Tachymarptis melba*) and eastern chipmunks (*Tamias striatus*) respectively. Each population was followed extensively from 15 to 60 years with known demographics and life histories as well as several repeated data on labile traits. In 2018 pedigrees include 4152 yellow-bellied marmots, 1112 bighorn sheep, 7540 red squirrels and 6540 white-bellied swifts. Both maternal and paternal linkage rates are greater than 75% in all pedigrees except for the red squirrel where 55% of the parents are known. As I specified before, a significant amount of repeated data is required for statistical models and this set provides what I need. Being able to work on several species and traits will allow to generate strong results on the existence and importance of the role of predictability for the study of phenotypic diversity (variation) under various ecological conditions and in an evolutionary framework.

I will work on labile traits of different types, such as physiological, behavioral, morphological and life history traits (Araya-Ajoy & Dingemanse, 2017; Briffa et al., 2013; O'Dea et al., 2022; Stamps et al., 2012). A labile trait is defined as a trait that is repeatedly expressed over the lifetime of an individual, allowing them to flexibly adjust their phenotype over a short time scale in response to changing environmental conditions (Araya-Ajoy & Dingemanse, 2017). Furthermore, they can be inherited and affected by early environmental factors, i.e., effects of the permanent environment (Dochtermann, Schwab, & Sih, 2015). Finally, a labile trait can be measured multiple times for the same individual, which is essential for studying within-individual variance.

I will apply Bayesian quantitative genetic methods to analyze our long-term data sets. Our models will then be fitted in a Bayesian framework using stan software (Carpenter et al., 2017), run from R (R Development Core Team 2014) via the brms package (Bürkner, 2018,

2021) or cmdstanr package (Gabry & Češnovar, 2020). To estimate the genetic basis of the predictability of the different traits I will use the “double hierarchical generalized linear model” (DHGLM) combined with quantitative genetics tools to estimate predictability. DHGLM is an extension of the mixed model that jointly estimates the among-individual difference in a trait (i.e., the mean model) and the among-individual variance in predictability while correcting for environmental effects (Cleasby et al., 2015). Conceptually, it can be seen as working in two steps (“Double”), first it models the mean variance distribution of a trait and in a second step it models the residual variance — also known as the dispersion model — distribution by allowing for fixed (e.g., sex) and random (e.g., individual identity) effects (Lee & Nelder, 1996; Youngjo Lee & Nelder, 2006). By combining the DHGLM with the “animal model” of quantitative genetics, we obtain a “double hierarchical animal model” (DHAM). The extension of the animal model estimates the heritability of a trait by assessing the phenotypic covariance between all pairs of parents in a population (Kruuk & Hadfield, 2007; Lynch & Walsh, 1998). It thus allows to estimate the additive genetic and environmental components of the mean variance and the variance in predictability through pedigree knowledge of the individuals. This approach allows us to assess comparable predictability parameters for all traits, environments, and species.

Chapter 1. Extending genetic variation theory

In this first chapter, I want to conduct a literature review of the different hypotheses, ideas, and important concepts in evolutionary ecology by integrating the residual phenotypic variance and its potential evolutionary impact. Indeed, many of these concepts share a very blurred boundary between them and I think some clarification is necessary to illustrate the existing blur and to try to simplify our view of these different evolutionary mechanisms without losing precision. For example, the concepts of plasticity, canalization, bet-hedging, fluctuating asymmetry or developmental instability may overlap with our research on within-individual residual variance. Moreover, it seems that these concepts are prone to confusion, especially between the historical definitions usually used, which do not take into account the latest conceptual and empirical progress (Debat & David, 2001). In addition, these definitions may or may not consider the evolutionary aspect of these phenomena, making the situation more intricate. To date, there does not seem to be any real consensus in the scientific community on the role and definition of these different concepts (Møller & Swaddle, 1997). An explanation of this situation could be derived from the phenotypic equation: $P = G + E$. Indeed, this principle has allowed for distinct definitions of the different components of variance identified, but it has led to overlaps in the different definitions, thus opening these grey areas. For example, some researchers view plasticity and canalization as independent mechanisms (Stearns & Kawecki, 1994), others as opposites (Debat & David, 2001; Ghalambor, Angeloni, & Carroll, 2010), and others show that they can be correlated (Tonsor et al., 2013). One of my point is that these different processes are not exclusive and can cross different levels of phenotypic variance. As Westneat et al. (2015) highlights, a particular trait can be canalized by selection within a single genotype, while promoting a more flexible phenotypic response (i.e. plasticity) to the environment within an individual as well as higher residual within-individual variance. This would suggest a more plastic and less canalized individual while having a more canalized genotype (phenomena occurring at different levels).

In the study by Sztepanacz et al. (2017), variation within individuals is described by within-individual variance (i.e., phenotypic plasticity) and residual within-individual variance. This distinction depends on our ability to measure environmental variation. The former represents macro-environmental variance that can be measured, while the latter represents micro-environmental variance, in other words uncontrollable, unpredictable, or unmeasurable environmental variance. Micro-environmental variance can then be decomposed into an internal and an external component, referring here to developmental instability and

environmental canalization respectively. Developmental instability “is defined as the ability of an organism to develop toward an adaptive endpoint despite perturbations during its ontogeny” (Simons, 2011), and fluctuation asymmetry (i.e., random deviations in the expression of normally two-sided traits) (Leamy & Klingenberg, 2005) is typically used to estimate it. Fluctuation asymmetry would allow the smallest part of the environmental variance to be estimated. On the other hand, canalization represents the suppression of phenotypic variation (Wagner, Booth, & Bagheri-Chaichian, 1997). It can be divided into environmental and genetic canalization. The former is defined as the insensitivity of traits to environmental factors and the latter as the insensitivity of a trait to mutations (Wagner et al., 1997). Canalization and fluctuation asymmetry have always been associated with an adaptive interpretation. It has always been assumed that a phenotype with fluctuation asymmetry (body part) equal to 0 has a beneficial impact on fitness (Møller & Swaddle, 1997). Nevertheless, it has also been shown that in certain biological and ecological settings, deviating from the optimal phenotype can be beneficial for fitness (Briffa, 2013). In other words, part of the residual within-individual variance can be an adaptive response.

Another concept to incorporate into this analysis is the bet-hedging strategy. This theory is based on the fact that natural selection maximizes long-term average fitness and then predicts the evolution of traits to minimize the variance in fitness and the risk of failure during past environmental fluctuations (Simons, 2011). A bet-hedging trait can be either conservative or diversifying. The former is the idea that selection will set a trait that will ensure minimization of fitness variance and risk of failure (Simons, 2002) while the latter, in contrast, will favor a multitude of phenotypes to ensure non-zero survival. Simons (2011) discusses bet-hedging as the third mode of response to environmental change. The first two being adaptive tracking which represents adaptation to a specific environmental change (i.e. constant evolution of the value of the optimal trait) (Bell & Collins, 2008; Bell & Gonzalez, 2009) and phenotypic plasticity which represents adaptation to predictable environmental changes (i.e. range of phenotypes expressed over a range of environments). Here again, we can see that the definitions may overlap. Indeed, the conservative bet-hedging trait appears to be related to canalization while the diversifying bet-hedging trait appears to be related to phenotypic plasticity. Simons (2011) emphasize that the specificity of bet-hedging lies in the fact that it is an adaptation due to long-term fluctuating selection and unpredictability environment or change itself (Simons, 2009). Bet-hedging could then be related to the micro-environmental variance exposed by Sztepanacz et al. (2017) and thus to the residual within-individual variance.

These elements illustrate the confusion that can exist around these different concepts that attempt to explain phenotypic variance and reveal evolutionary processes. Thus, I wish to explore all the nuances of these different concepts in the context of our examination of residual within-individual variance from an evolutionary perspective. Residual within-individual variance as well as all components of phenotypic variance must be integrated into evolutionary studies to clarify the concepts, and micro- and macro-evolutionary processes.

Chapter 2. Magnitude of genetic basis for predictability across multiple traits and relationship to mean and plasticity within a trait in yellow-bellied marmots.

Existence of residual heterogeneity and therefore of within-individual variation between individuals for traits has been shown in some species and on several types of traits such as physiological, behavioral, and morphological (Mitchell et al., 2021). Nevertheless, none has focused on multiple traits at the same time or on the same system, and very few have been able to document the genetic basis of predictability in free-living animals, often due to lack of data or statistical knowledge. In this second chapter, I want through an observational approach to first assess the extent of the genetic basis of the variance in predictability on at least five different traits within a single species. Indeed, I aim to determine if the results obtained on behavioral traits are similar on other types of traits. This analysis is a continuation of the study by Martin et al. (2017) that focused on the behavioral trait of docility in yellow-bellied marmots. The biological system will also be the yellow-bellied marmot and the study will focus on (1) morphological trait – August body mass, (2) a behavioral trait – boldness and (3) docility, (4) a physiological trait – glucocorticoid level and (5) finally life history traits – variations in juvenile mass.

In addition, by a multivariate approach I want to evaluate and establish correlations at three levels of phenotypic variation – variation in mean, plasticity, and predictability – and among the five traits. The Pace of Life Syndrome (POLS) hypothesis suggests that variations in life history strategies are related to a suite of behavioral, physiological, morphological, and life history traits along a continuum of slow to fast pace (Dammhahn, Dingemanse, Niemelä, & Réale, 2018; Denis Réale, Garant, et al., 2010; Ricklefs & Wikelski, 2002). For example, in the same population, "fast" individuals will tend to be more active, bolder, grow faster, live shorter lives, and invest less in immune defense compared to "slow" individuals (Dammhahn et al., 2018). Support for such a hypothesis would help answer ecological and evolutionary questions about the maintenance of phenotypic variation. Various studies testing this hypothesis with specific direction of relationships have worked on trait averaging and contrasting results have been obtained (Montiglio, Dammhahn, Dubuc Messier, & Réale, 2018; Royauté, Berdal, Garrison, & Dochtermann, 2018; Tieleman, 2018). Dammhahn et al. (2018) proposed a more general definition to facilitate the development of multiple hypotheses regarding the evolutionary origin of POLS. I believe that close links and trade-offs exist between variation in the mean, plasticity, and predictability within the same trait (Highcock & Carter, 2014; Jolles

et al., 2019; Martin et al., 2017; Prentice et al., 2020) and between variation in mean trait and predictability of other traits.

In addition, I expect that traits that are highly related in terms of benefits in certain ecological conditions may be genetically correlated in their level of variation. Furthermore, I posit that patterns of variation exist depending on the biological and ecological constraints of the studied model. Thus, traits that are strongly embedded in the life history of marmots and therefore under strong canalization, such as body mass, should present a high level of predictability in contrast to a trait like docility. To support it, Hill & Mulder (2010) argued that genetic component on the mean of a trait was typically more important for morphological traits than for relatively close fitness traits (life history trait). In addition, (Mousseau & Roff (1987) and Stirling, Réale, & Roff (2002) concluded that behavioral traits had similar heritability to physiological traits but were less heritable than morphological traits. Thus, I believe that genetic component of the predictability of boldness and glucocorticoid level will be more important than for variations in juvenile mass, and less important than for body mass.

(1) Body mass will be estimated using August mass data because it is not influenced by past winter, annual and future reproduction. In addition, it reflects the period of maximum growth due to peak vegetation in mid-July (Frase & Armitage, 1989; Frase & Hoffmann, 1980; Ozgul et al., 2010).

(2) Flight initiation distance (FID) can be used to assess whether an individual is bold or not. It is considered an antipredator behavior and is used to quantify boldness (Cooper, 2009). The FID experience consists in measuring the distance at which individuals flee when approached by a human (Blumstein et al., 2004).

(3) An individual's response to being trapped and handled is used to estimate docility (Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013; Réale, Reader, Sol, McDougall, & Dingemanse, 2007).

(4) Corticosterone levels are calculated from fecal material (i.e., fecal corticosterone metabolite levels). Fecal samples from individuals are collected during trapping events. They are either directly sampled from the individuals while they are being handled or freshly harvested from the trap (Blumstein & Munos, 2005; Petelle, Dang, & Blumstein, 2017).

(5) To estimate the variation in pup mass I will use the pup mass measured at emergence.

Chapter 3. Direct and indirect evolutionary implication of predictability: a story of strategy and selection in a yellow-bellied marmot.

In the wild, only two studies (Martin et al. 2017; this should be the guppies study that Prentice conducted in the laboratory) have shown a genetic basis for predictability of behavioral traits. In addition, (Patrick et al., 2021) show that in black-browed albatrosses (*Thalassarche melanophris*), under poor conditions, adult individuals with the greatest variability in foraging behavior had better fitness. They also demonstrate that residual variability changes with environment. Thus, they provide evidence that individual variability is subject to selection and thus highlight its importance for adaptation in nature. These results demonstrate the major potential implication of predictability for the evolutionary causes and consequences of phenotypic variation.

In this chapter, I seek to assess the direct and indirect evolutionary implication of variation in predictability. To do so, I will evaluate the impact of trait predictability on fitness. I will use a multivariate approach to determine the existence of a covariance between fitness and predictability. In order to estimate fitness, we can include a set of traits for which we did not have the ability to examine variation in predictability but for which we know that there is among-individual variation and even genetic variation at the mean level. These traits are proxies for fitness such as number of young, lifetime reproductive success (LRS) and longevity. Following the results on average traits (Hill and Mulder 2010) I assume that predictability of morphology-related traits (e.g., adult size and conformation) or under strong canalization will present a strong effect on fitness compared to traits closely associated with fitness (e.g., litter size, growth). Nevertheless, it cannot be ignored that certain ecological constraints and biological characteristics specific to the biological model may lead to different results.

Chapter 4. An overview of predictability existence in nature across multiple traits in several species.

Can we find similar patterns of predictability across species within a trait?

After having thoroughly developed the analysis system in yellow-bellied marmots that will allow us to: (1) establish the genetic basis of the traits and (2) determine the genetic/phenotypic covariance between the mean and the predictability within a trait (univariate model); but also (3) determine the genetic/phenotypic covariance between different levels of variation among multiple traits (multivariate), I can now extend our integrative approach to other species with the various data sets available. For this chapter I have access to at least 5 long-term data sets including yellow-bellied marmots (*Marmota flaviventer*), bighorn sheep (*Ovis canadensis*), red squirrels (*Tamiascus tamiascus*), striped chipmunks (*Tamias striatus*), and alpine swifts (*Apus melba*). In this chapter, I aim to evaluate the relationship between among-individual variation in predictability and the ecology of each species for the same traits across multiple species. I may find similar patterns among species and/or large differences. I believe that differences in variation in predictability on a single trait may be predicted by the ecological conditions of each. Indeed, the selection pressures that are exerted by the ecological/biological needs/constraints of each species will have a determining role on variation in predictability.

In addition, and as discussed above, I would expect little variation in predictability for traits undergoing strong canalization. For example, yellow-bellied marmots are hibernating sciurid rodents that live in a subalpine habitat. Body condition, which can be estimated by body mass, is therefore a key determinant of winter survival and is subject to strong selection pressure (Armitage, 2014). This trait is consequently subject to strong canalization, in contrast to red squirrels that survive winter by primarily using food caches (Gurnell, 1984). This example illustrates the importance of the ecological conditions of the species' life (life history) on the variation in predictability of a single trait.

Here, I aim to expand our knowledge of among-individual variations in predictability, its genetic basis, and its evolutionary implication in adaptive strategies for different species of different taxa and across multiple traits. It will be important to consider the phylogenetic linkage of some of our biological models studied. Indeed, three species belonging to the subfamily Sciurinae grouping tree squirrels, flying squirrels, and related species. However, all three have very different life histories and strategies in response to ecological conditions.

Chapter 5. Methodological consideration of the new models used.

To conduct our analyses, models will be fitted in a Bayesian framework using stan software (Carpenter et al., 2017), run from R (R Development Core Team 2014) via the package brms (Bürkner, 2018, 2021) or the package cmdstanr (Gabry & Češnovar, 2020). This package has been developed recently and the predictability was until now estimated by fitting the DHGLM with the packages R2OpenBUGS (Sturtz, Ligges, & Gelman, 2005), JAGS (Plummer, 2003) or even ASreml (Gilmour, Gogel, Cullis, & Thompson, 2009). I aim for this last chapter to conduct methodological work on this newly developed statistical tool in order to establish an appropriate sampling method that evaluates several levels of phenotypic variation (mean, plasticity and predictability) in different study systems. Indeed, additional studies must be performed to better understand the analyses and specially to evaluate the adequate type of data and avoid any bias more finely. To do so, I will perform simulation work to estimate the optimal sample size, the number of replications, the number of observations, the duration, but I will also test the different types of distributions, define the limits, the ceiling effects, to obtain sufficient power.

By doing so, I will be able to improve our knowledge of the factors promoting and limiting variability, as well as the evolution and ecological consequences of individuality.

Value of the research and the rationale for conducting it

The value of this project lies in several components. First, the innovative analysis methods used, which used cutting edge statistical analysis in ecology and quantitative genetics. Analysis allowing us to model both the variance in the mean and the residual variance as well as to obtain estimates of the genetic and environmental components of both variances. Second, the collaborative aspect of this project, which provides a combination of rare dataset on natural populations (Clutton-Brock & Sheldon, 2010) but also provides access to expert advice on evolutionary issues, population dynamics, and ecological constraints of each model studied. Most importantly, this project will provide new theoretical and empirical insights into the causes and effects of this component of phenotypic variance on phenotype evolution (Westneat et al., 2015). By using an integrative approach of the predictability with the other components of the phenotypic variation, a more precise insight of the evolutionary process (evolutionary strategies, trade-offs) could be obtained (O'Dea et al., 2022). As seen in farmed animals, genetic variation in predictability in some traits could slow down or speed up artificial selection and also help maintaining genetic variation in a trait under strong selection. Thus, this study will fill an important knowledge gap on the prevalence of predictability in nature and its evolutionary consequences. If similar patterns are found to be widespread for different types of traits and in multiple species, it would demonstrate the need to study predictability thoroughly to assess its importance and role in ecological (predator prey interaction, population dynamics, dispersal, and survival) and evolutionary processes.

Finally, given the ever-increasing human pressure on wildlife (Coltman et al., 2003; Parmesan, 2006), it is crucial to conduct this study to obtain a more complete understanding of the evolutionary mechanisms that influence population size and evolutionary dynamics of species (Gonzalez et al., 2013). Quantitative genetics could effectively enhance our approaches to wildlife management and conservation (Sauve et al., 2022), especially in a rapidly changing environment where evolution, adaptation or extinction are processes that impact the success of many species (Bonnet et al., 2022).

Therefore, we could eventually consider that extreme values of a trait can also influence evolutionary process and thus that individuals do not only impact the world through the mean of their phenotype but also through their variance. Evolution would act on both the mean and the variance of traits.

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