

# QUANTITATIVE GENETICS IN THE WILD



EDITED BY ANNE **CHARMANTIER**,  
DANY **GARANT** & LOESKE E. B. **KRUK**



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# Quantitative Genetics in the Wild

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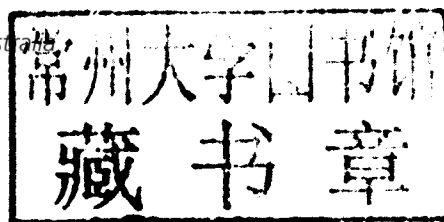
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# Foreword

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Why do individuals differ from each other? How can we tease apart the complex effects of environments, parents, family and genes? What do the size of these effects, and the way that they contribute to differences between populations, mean in terms of the way that evolution has shaped biodiversity? And what do they mean when we think about the rapidly changing world in which we live? Questions of this sort lie at the heart of a vigorous and vibrant field: the application of quantitative genetics to wild populations. This book is both a summary of the state of the art as well as a mission statement for the future.

That this research field has a future, and indeed, one that is brighter and more relevant than ever, is abundantly clear from the work described in this book. The vitality of this field is notable, because it is emerging unscathed, indeed, strengthened, from what might have been considered a major threat derived from other ways of understanding the genetic basis of characters. Quantitative genetics had its origin among the biometricians at the turn of the 19<sup>th</sup> century, at about the time that ‘classical’ (i.e. Mendelian) genetics was rediscovered. Although Fisher showed how the two approaches could be combined almost a century ago, they have, in recent times, with the explosion of molecular genetic and genomic approaches, often been seen as offering competing frameworks. On reflection, ‘competing’ is perhaps the wrong term; at least, for competition to be perceived, both approaches must acknowledge the other! I have lost count of the number of times, in conversation with colleagues working on lab model organisms, that I have been told that, unless I understood the molecular genetic basis of a character, I didn’t know anything about the genetic basis of a trait. On the other hand, I do remember,

quite vividly, how hard I had to argue with a representative of one of the UK research councils that work on quantitative genetics of wild great tits did fall legitimately within their remit of fundamental research into genetics.

Perhaps field ecologists interested in quantitative genetics have been too reticent in the face of such dogmatism. Whilst the past few years have seen several high profile papers in the weekly ‘tabloid’ journals dissecting the single-locus genetic basis of functional traits in wild populations, there is a growing realisation that these may be relatively rare examples. The huge effort expended, for relatively meagre return, in studies of genetics of human quantitative characters and disease is a salutary lesson that even with enormous sample sizes, and genetic marker density at levels that are only just within reach of studies of wild organisms, relatively little variance in quantitative traits may be attributable to the effects of specific identifiable loci. Aulchenko *et al.* (2009) illustrated this with the case of human height, showing that genotyping the (at the time) 54 SNPs with largest effect, in a sample of 5748 people, explained only about a tenth as much variance as did the ‘Victorian’ method developed by Galton, which simply used the parental mid-point as a prediction. There is something simultaneously remarkable and encouraging about the fact that a centuries-old method requiring no more than a ruler, a pencil and (I suppose) a slide rule, outperformed, by an order of magnitude, the fruits of the genomic revolution. This gap will continue to narrow, of course, but this example, many others like it, and emerging evidence from wild populations of the highly polygenic nature of many quantitative characters, serves to legitimise the quantitative genetic approach.

As the chapters in this book demonstrate, the great strength of a quantitative genetic approach is that it is a flexible way to ask questions about the causes of variation and their effects: I share the editors' enthusiasm for viewing the application of quantitative genetics to wild populations as providing a broader analytical framework to think about all sorts of causes of variation, including environmental, genetic and developmental processes. As a consequence, we can fit questions about the adaptive influence of mothers on offspring, about epigenetics, about the developmental processes associated with ageing, about mechanisms of sexual selection, about effects of climate change, and about the influence of social processes within one coherent framework, and doing so provides a much richer understanding of the role of genetics in evolution and ecology.

This book is also forward-looking, and there are two particular aspects of this, among many, that I wish to highlight. First, it is clear that there are huge opportunities to be gained by combining classical 'phenotype-based' quantitative genetics with molecular genomics. These range from the ability to determine relatedness in systems where this has been impossible, or impractical, via deriving true measures of pairwise relatedness, rather than expected ones, to combining pedigrees with markers to test models of genetic architecture. Ironically, because it gets ever easier and cheaper to derive genetic information, the limiting step in such combined studies, and in quantitative genetic studies of wild populations generally, may be the quality and extent of phenotypic data. In many cases, long-term studies are limited by the decisions made by previous generations about which phenotypes to study. Digital techniques and remote- or automated-tracking of organisms offer the scope to collect very rich phenotypic data, including that relating to social and behavioural traits, and we should perhaps be thinking harder about how we can lay the foundation, in terms of phenotypic data, for the (academic) generations that may follow us.

Second, the current foundations of quantitative genetics in the wild are based almost entirely on vertebrate populations, with a disproportionate number of estimates derived from a very limited sample of species. It is very encouraging to see active

consideration being given here as to how these taxonomic blinkers can be lifted, and very stimulating to think about how the experimental approach to quantitative genetics that typifies work in invertebrates and plants can inform these more ecologically framed studies.

Whilst the history of application of quantitative genetics in the wild is almost four decades old at the time of writing, the explosion of interest is more recent. There are probably many reasons for that, some of which are outlined in the following chapters, but one that I think should not be neglected is the series of meetings held among a group of practitioners of this approach, at 2–3 year intervals since the first in 2004. These meetings (known as the Wild Animal Model Biennial Meeting) have always been held in quite remote locations (Rum, Scotland 2004; Gotland, Sweden 2007; Dejioz, Italy 2009; Corsica 2011), far from the usual big-city hotel milieu of conference centres, and always close to a study site that hosted a population that was an active model for quantitative genetics in the wild. Informal, and with a timetable that was sufficiently elastic to incorporate extended, sometimes very extended, discussions of the points made by speakers, these have been among the most intellectually satisfying and invigorating of meetings, with the feeling that, after each one, genuine progress had been made in the field. Many, but by no means all, of the authors of the chapters that follow have also been key participants in these meetings (indeed, two of the editors organised a meeting each), and the feeling on reading the chapters here is not unlike that of attending one of those meetings: real progress has been made, and there are tremendous opportunities for more work in the future.

**Ben Sheldon**  
Oxford & Uppsala  
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Many contributors to this book have gathered over the years in informal biennial meetings to discuss methodological, theoretical and empirical advancements in quantitative genetics applied to wild populations. These meetings, held in remote study sites across Europe (the Isle of Rum, Scotland; the island of Gotland, Sweden; Gran Paradiso National Park, Italy; and Fango Valley in Corsica, France) have been incredibly inspiring for the exchange of ideas and techniques, and for triggering new collaborations. We thank all the past organisers and attendees of these meetings.

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Finally, we thank our families for their love and support, and dedicate this book to our children, Vincent, Laetitia, Alexanne, Émilien, Saskia, Lyndon and Edward.

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# **The study of quantitative genetics in wild populations**

Loeske E. B. Kruuk, Anne Charmantier and Dany Garant

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## **1.1 Why study quantitative genetics?**

A core aim of evolutionary biology is to explain the biological diversity of natural populations. This diversity occurs at multiple levels: between species or higher taxonomic groups, between populations of the same species, between individuals of the same population, or between different time points in an individual's life. Quantitative genetics, the study of the genetic basis of complex (or 'quantitative') traits, is concerned with these lower levels, and in particular with the diversity between individuals in a population, and the extent to which it is determined by genetic vs non-genetic causes (Fisher 1918; Wright 1921). In addition to addressing the fundamental question of the relative contribution of 'nature' vs 'nurture' to variation, knowledge of levels of genetic variance is critical for assessing the extent to which changes in phenotypic traits due to selection are passed on from one generation to the next—i.e. the microevolutionary dynamics of traits. Plant or animal breeders therefore use quantitative genetics to determine how artificial selection can change the distribution of phenotypes within a population (Lush 1937; Falconer & Mackay 1996). Evolutionary biologists also want to understand and even predict the effects of selection, but with a focus on natural or sexual selection: quantitative genetic analyses provide information about the raw material on which selection can work (Roff 1997; Lynch & Walsh 1998). The application of quantitative genetics to evolutionary biology has generated a large and rapidly changing field (for an

excellent history of the subject, see Lynch & Walsh 1998). In this book, we aim to provide an overview of one particular area of this wide field: quantitative genetic studies of wild populations inhabiting natural environments, motivated by evolutionary ecologists wishing to address core evolutionary questions in realistic ecological settings.

The last decade has seen a rapid expansion in quantitative genetic studies in natural environments (see Chapter 2, Postma), fuelled by methodological advances in molecular genetics and statistical techniques (Kruuk *et al.* 2008), and by increasing availability of suitable long-term datasets, especially in animals (Clutton-Brock & Sheldon 2010). As a result, studies of 'wild quantitative genetics' have provided insights into a range of important questions in evolutionary ecology, some in well-established fields such as life-history theory, behavioural ecology and sexual selection, others addressing relatively new issues such as the response of populations to climate change, or the process of senescence. This work is motivated in part by the increasing appreciation of the need to quantify the genetic—rather than just phenotypic—diversity in key traits, and the genetic basis of the associations between traits (Roff 2007): phenotypic associations may not be accurate representations of the underlying genetic associations that will ultimately determine evolutionary dynamics, especially in studies of populations experiencing natural environmental heterogeneity (Kruuk *et al.* 2008).

We use the term 'quantitative genetics' somewhat loosely, to cover a range of aspects of the

evolutionary ecology of populations—in fact a more accurate (if even less appealing) term might have been ‘variance component analysis’. Thus, whilst a core aim is often to estimate levels of genetic variance and heritability for particular traits, as well as the structure of the multivariate genetic relationships between them, we are also interested in the other sources of variation that may be important for a wild population: for example, effects of environmental variation due to phenotypic plasticity, maternal effects (genetic or environmental), genotype–environment interactions, dominance variance, or the effects of ageing. The statistical tools of quantitative genetics, and the pedigree data required to estimate levels of genetic variance, fortunately provide efficient ways of exploring these fascinating questions.

### 1.1.1 Ten big questions

A research field is driven by the central questions or hypotheses it aims to address. Below is a (non-exhaustive) list of what we see as core questions in current evolutionary quantitative genetics.

1. What is the genetic basis of variation in phenotypic traits, and of covariation between traits?
2. Is there heritable genetic variance for fitness? Across traits, how is genetic variance maintained in the face of erosion by selection?
3. To what extent do genetic trade-offs shape the evolution of life histories? More generally, how widespread are evolutionary genetic constraints?
4. Can we predict evolutionary responses to selection pressures? Or, why does artificial selection generate predictable evolutionary responses, but natural selection does not?
5. To what extent is the phenotype of an individual shaped by the genotypes of other individuals in the population—for example by maternal effects?
6. Do individuals vary in their response to environmental conditions, and is this variation genetically based: how prevalent are genotype–environment interactions? Do other components of variance change with environmental conditions?

7. Why does senescence occur?
8. Why does sexual dimorphism occur?
9. How much inbreeding and inbreeding depression are there in a population?
10. How will climate change affect the evolutionary dynamics of natural populations?

These questions can be addressed with many types of study populations, but as we discuss below—and as we hope this book illustrates—they address issues into which studies in natural environments can provide valuable insights.

### 1.1.2 Why in the wild?

Quantifying genetic effects in artificial (domestic or laboratory) populations under controlled conditions is undoubtedly easier than in wild populations experiencing natural environments, and obviously provides invaluable insights into evolutionary processes (Roff 1997). However, the importance of genetic variation is arguably best assessed relative to other causes of variation, requiring an understanding of both genetic and environmental variation, and by extension a need for relevant environmental conditions. Furthermore, there is increasing evidence for the impact of environmental conditions both on the selection processes in which we are interested (Endler 1986; Wade & Kalisz 1990) and on the expression of genetic variance (Hoffmann & Merilä 1999; Charmantier & Garant 2005)<sup>1</sup>. This suggests that extrapolation of estimates from artificial conditions to more realistic ecological contexts may be difficult. Third, simple theoretical

<sup>1</sup> One point to note here is that in referring to estimates in ‘wild’ populations, we mean exactly that: phenotypes are typically measured in individuals inhabiting natural environments. Previous comparisons of ‘lab’ vs ‘field’ heritabilities (e.g. Simons & Roff 1994; Roff 1997; Hoffmann 2000) have involved ‘field’ populations in which individuals have been collected in the field and brought into and bred in the lab, so that the ‘field’ vs ‘lab’ contrast lies in the source of the population, not in the location in which phenotypic variation is expressed. Although some of these comparisons suggest that lab heritabilities provide good surrogates for field heritabilities (Roff 1997), we believe it is worth bearing this distinction in mind. Comparison of lab with true field heritabilities is inevitably difficult given that lab studies tend to involve shorter-lived and smaller organisms, predominately invertebrates, whereas field studies tend to involve relatively longer-lived species in which individuals are easily monitored in the field.

predictions for the expected cross-generational responses to selection (the ‘breeder’s equation’, see Box 1.1), which work for artificial selection on single traits in controlled conditions (Roff 2007), do not seem to hold when considering natural selection in wild populations (Merilä *et al.* 2001). Multiple explanations for this mismatch have been proposed, but most centre on the fact that real-world natural selection, involving multiple traits, is likely to be much more complex than artificial selection (Rausher 1992; Kruuk *et al.* 2008; Walsh & Blows 2009; Morrissey *et al.* 2010). Fourth, there are arguably many important traits, for example life-history or behavioural traits, which will not be expressed properly in artificial conditions, but which are critical components of a species’ biology. In particular, estimates of natural variation in individual fitness, comprising natural variation in survival and fecundity, may only be feasible in field studies. Fifth, increased appreciation of the potential feedbacks between the ecological and evolutionary dynamics of a population underlines the value of investigating evolutionary parameters in a relevant ecological setting (Pelletier *et al.* 2009). In relation to this, it is worth noting that almost all of the quantitative genetic analyses of field data discussed in this book have arisen as extensions of ecological or behavioural studies (see below), reflecting a rapid expansion of activity at the interface between evolutionary biology and ecology.

However, despite these arguments, we do not wish to imply any artificial distinction between evolutionary quantitative genetic studies under artificial or natural conditions. Clearly some of the interesting aspects of the latter, such as natural (i.e. uncontrollable) environmental heterogeneity, can also constitute serious drawbacks, and opportunities for experimental manipulation are greatly reduced. As the following chapters illustrate, research in the field is motivated by general questions such as those above, and in evaluating empirical evidence we need to consider results drawn from both artificial and ‘wild’ populations.

In this chapter, we first outline briefly the basic principles of a quantitative approach and of the most commonly used statistical tools, by way of introduction to the subject for readers with less familiarity with the concepts (Section 1.2). Box 1.1 contains a glossary of important terminology which

appears repeatedly throughout the book. We then provide an overview of the different chapters in the book (Section 1.3), and finally we discuss some recurrent challenges (Section 1.4) and then consider some emerging topics in the field (Section 1.5).

## 1.2 How? The basic tools of quantitative genetics

### 1.2.1 Estimating similarity between relatives

At the core of a quantitative genetic analysis is estimation of the extent of genetic control of traits and of the associations between different traits, i.e. levels of genetic variance, its magnitude relative to the overall phenotypic variance or the trait’s heritability, and the genetic determinants of correlations between traits (Falconer & Mackay 1996, see Box 1.1 for definitions). This estimation relies on the concept that if a complex (or continuous, or ‘quantitative’) trait is genetically determined, then individuals who share the same genes should have similar phenotypes: in other words, the degree of phenotypic similarity between relatives should reflect the genetic control of that trait. A trait can be any measure on an individual, for example body size, number of babies, antibody levels, aggression score, plumage colouration, or when it breeds. The approach relies on an assumption that quantitative traits are likely determined by very large numbers of genes spread across the genome, an assumption that (reassuringly) appears to be upheld by both the results of selection experiments and recent molecular data (Hill & Kirkpatrick 2010; Hill 2012). The degree to which two individuals share the same genes depends on their relatedness, which can be quantified either via knowledge of a pedigree (or family tree, constructed from knowledge of each individual’s parents), or with appropriate genomic marker data (Lynch & Walsh 1998).

The similarity (covariance) between pairs of individuals for a given phenotypic trait is therefore determined by i) the relatedness of the pair and ii) the degree of genetic variance underlying the trait. The phenotypic covariance can be observed and the relatedness can be estimated, so we can solve statistically for an estimate of the additive genetic variance (see Box 1.1). These calculations can be done in different ways, the simplest being to use

only relatives of a certain type and consider, for example, the similarity of offspring to their parents (a 'parent-offspring regression'), or among groups of full or half siblings. In practice, if we have phenotypic information on individuals in a population, it is most efficient to consider the covariance between as many pairs as possible, which is feasible using a form of mixed-effect model known as an 'animal model' (Henderson 1975; Lynch & Walsh 1998). An animal model partitions the phenotypic trait of an individual into contributions from predictable effects (e.g. sex, age, climate), termed 'fixed effects', and other effects for which we wish only to estimate the overall variance in individual effects, known as 'random effects'. For the latter, given pedigree or relatedness information, we can fit an additive genetic term which exploits the fact that the effect of an individual's genotype (or specifically, the additive genetic value of its genotype; see Box 1.1) will be similar to that of its relatives, and the degree of similarity will scale with the degree of relatedness. Box 1.2 contains a brief overview of animal models; for more details, see Lynch & Walsh (1998).

For no particularly clear reason, other than possibly computational demands, application of the animal model to evolutionary quantitative genetic studies outside plant and animal breeding is surprisingly recent (for a brief history, see Kruuk 2004): the earliest applications to data from free-ranging populations being for rhesus macaques (*Macaca mulatta*; Konigsberg & Cheverud 1992), and three populations of ungulates: bighorn sheep (*Ovis canadensis*; Réale *et al.* 1999), Soay sheep (*Ovis aries*; Milner *et al.* 2000) and red deer (*Cervus elaphus*; Kruuk *et al.* 2000). The late arrival of the animal model in studies of the quantitative genetics of wild species, relative to its ubiquity in applied research, is especially surprising given that some of its strongest advantages are in dealing with the problems posed by data from natural populations: it is relatively tolerant of unbalanced designs, missing trait data and pedigree links, and the complexities of heterogeneous environmental conditions (Kruuk 2004; Wilson *et al.* 2010). However, despite the late start, it has now been applied to dozens of different populations (see Chapter 2, Postma), and this application has provided great impetus to the current interest in wild (and also non-wild)

evolutionary quantitative genetics. For a practical guide to application of the animal model for ecologists, see Wilson *et al.* (2010).

### 1.2.2 Role of long-term studies

The vast majority of quantitative genetics in the wild has to date been conducted on populations that have been the subject of long-term study, in many cases over several decades (Clutton-Brock & Sheldon 2010). Clearly such studies offer many advantages, one of which is that most were set up by ecologists and have been used for extensive investigations into the effects of natural environmental variation as well as the mating systems and behavioural ecology of the study species: quantitative genetic analyses are therefore generally founded in a thorough understanding of a population's ecology. However, reliance on long-term studies has obvious drawbacks: a new study on a new species cannot obviously be created and used immediately, funding bodies do not work to delivery points several decades away, and continuous maintenance of ongoing studies in a harsh funding environment can be difficult. The ability to estimate relevant genetic parameters from genomic data will change this dependence on historical information to some extent, but even if it removes the need for a multigenerational pedigree, it still cannot generate estimates of the impact of temporal environmental variation, nor of any interaction of environmental and genetic variance. Use of historical data from long-term studies also generally relies on correlational associations between traits, despite the value of experimental manipulations such as cross-fostering for separating genetic and non-genetic causes of similarity between relatives (Merilä & Sheldon 2001).

The timeline of analyses in one study population of our cover species, the great tit (*Parus major*), illustrates the development of quantitative genetic studies of wild populations. The long-term study of the great tit population in Wytham Woods, Oxford, UK (running since 1947, Lack 1964) generated possibly the earliest field heritability estimate from a wild population, the inheritance of clutch size (Perrins & Jones 1974). Subsequent analyses have progressed from single-trait models

using either parent–offspring regressions (van der Jeugd & McCleery 2002) or the animal model (McCleery *et al.* 2004), to bivariate models (Garant *et al.* 2008), random regressions to test for genotype-by-environment interactions (Charmantier *et al.* 2008; Husby *et al.* 2010), tests for environmentally induced variation in inbreeding depression (Szulkin & Sheldon 2007) and senescence (Bouwhuis *et al.* 2010), analysis of trends in breeding values (Garant *et al.* 2008) and subsequent reanalysis with more appropriate methods (Hadfield *et al.* 2010), and most recently, genomic marker-based partitioning of variances and covariances (Santure *et al.* 2013). Studies have therefore progressed from simple estimates of heritability to much more sophisticated tests of some of the key hypotheses at the heart of quantitative genetics.

### 1.3 Overview of chapters

In this book we invited a range of researchers in the field to illustrate how quantitative genetics research in the wild has developed over the years and to provide an up-to-date resource covering the most important topics addressed by this area of research.

Defining the heritable basis of a trait was the main goal of most early studies of quantitative genetics in the wild (see the great tit examples above; Boag & Grant 1978; and reviews in Mousseau & Roff 1987; Merilä & Sheldon 2001; Visscher *et al.* 2008). The book thus starts with an in-depth analysis of the variation in heritability estimates published over the last four decades from wild populations (Chapter 2, Postma). Postma analysed 1600 heritability estimates from over 50 species and traits, showing that heritabilities have become more precise and less biased over time. This seems to result from both the application of the animal model, and the inevitable strengthening of datasets over time, with resultant improvements in the quality of pedigree information. Postma also assesses the relationships between the estimates of heritability and the coefficient of additive genetic variance, and shows that it is weak at best (and even negative) and thus that there is little concordance between the two metrics (see also Houle 1992; Hansen *et al.* 2011), re-emphasising the need to report and compare both in future studies.

Chapters 3 to 5 illustrate that the methods associated with quantitative genetic analyses have now been successfully applied in natural populations for the study of a variety of fundamental ecological and evolutionary processes. In Chapter 3, Reid shows how quantitative genetics can be applied to deriving and testing pertinent sexual selection theory in wild populations experiencing natural genetic and environmental variation. She uses two case studies in birds to illustrate how quantitative genetics can bring new insights in the evolutionary causes and consequences of mate choice and sexual selection, as well as trait and mating system evolution. In Chapter 4, Dingemanse and Dochtermann show how the theory and tools already adopted by quantitative geneticists can be used by behavioural ecologists interested in the adaptive nature of between-individual variation in behaviour. They further show that theory and empirical research in behavioural ecology might inform quantitative geneticists as to how and why trait variation is distributed, thus illustrating how these fields would gain from a more integrative approach and sustained exchange of ideas (Owens 2006). Finally, the authors suggest how we can bridge the gap between the two disciplines by presenting theoretical and empirical demonstrations of the statistical language familiar to quantitative geneticists in order to explain behavioural patterns of current interest. Charmantier, Brommer and Nussey (Chapter 5) follow with a review of the concepts and analyses related to senescence in the wild. They start by discussing the main classical evolutionary theories of ageing, emphasising the importance of estimating age-dependent patterns of genetic (co)variance ( $G \times \text{Age}$  interactions). They then outline a detailed statistical framework with which to quantify  $G \times \text{Age}$ , and review the literature supporting evidence for individual differences in senescence rates in wild vertebrates. They conclude their chapter by identifying important statistical issues, forthcoming challenges, and recommendations for future work in this field of research. In particular they call for higher standards of analysis and reporting to facilitate generalisation about senescence patterns across populations and species.

Besides the assessment of additive genetic variance and heritabilities, the importance of



quantifying other variance components that are relevant for evolution has been increasingly recognised (see Crnokrak & Roff 1995; Mousseau & Fox 1998; Keller & Waller 2002; Räsänen & Kruuk 2007). As a result, there is a growing interest in estimating these components in the wild, as emphasised by the following two chapters. In Chapter 6, McAdam, Garant and Wilson emphasise the importance of considering 'indirect genetic effects' (Box 1.1) for studies of evolutionary dynamics. In particular, they provide conceptual and analytical background to the importance of maternal effects, the best studied type of indirect effects. They point out important emerging questions in the field such as the need to explore the evolutionary implications of social interactions across a wider range of contexts and scenarios. In the next chapter, Wolak and Keller (Chapter 7) review the main issues related to the estimation of non-additive variance, especially dominance variance. They present an overview of empirical estimates obtained in laboratory and agricultural populations, and conclude that dominance variance is a major contributor to phenotypic variation, and may even rival additive genetic variance. As estimates of dominance variance in the wild are still lacking, the authors explore the practical considerations for quantifying these effects in wild populations. They conclude their chapter by discussing how inbreeding affects estimates of non-additive genetic variance.

It is evident from the literature content of the field that, despite several years of research in quantitative genetics in the wild, most studies are still based on a rather limited number of species/populations (see below, and also Chapter 2, Postma). Yet, several systems offer promising perspectives for future developments in order to reach a broader taxonomic coverage in this field. For example, Stinchcombe (Chapter 8) provides an original and constructive approach comparing studies published on long-lived mobile animals in the wild with those focusing on short-lived plants mainly performed on a single generation and/or under common garden conditions. In particular, he explores the conceptual, analytical, and biological insights that might be obtained from applying lessons and techniques of experimental studies in plant evolutionary ecology to studies of wild vertebrate populations, and vice

versa. This chapter reviews important findings in plant evolutionary ecology and their potential implications for wild animals, and also assesses the main challenges that have so far prevented the potential application of wild quantitative genetic approaches in free-living plant populations. In Chapter 9, Zajitschek and Bonduriansky consider recent developments in assessing genetic variation in fitness-related traits in wild populations of arthropods. The life-history characteristics of insects—which made them typical model species for many laboratory studies—have resulted in a near complete absence of genetic parameter estimates from wild populations. They suggest potential ways to fill this gap, and discuss some examples of suitable systems for doing so. They emphasise that much will be gained from studies of quantitative genetic parameters for natural populations of invertebrates as they will allow for comparison with the enormous literature on captive invertebrate populations, as well as extend our knowledge of quantitative genetics in the wild to a broader array of taxonomic coverage.

Development of research in quantitative genetics in the wild has resulted in a transition from studies conducted on single traits to applications of multivariate analyses (Arnold *et al.* 2008; Walsh & Blows 2009). As such, both theoretical and empirical considerations of the *G*-matrix in nature are presented in the next three chapters. In Chapter 10, Kruuk, Clutton-Brock and Pemberton present an empirical case study to illustrate recent developments in applications of quantitative genetic analyses, using 40 years of data to apply a multivariate quantitative genetic approach to sexually selected antler traits in a red deer population from the Isle of Rum, Scotland. Despite computational constraints due to the demanding nature of multivariate analyses, they find significant positive covariances between antler traits, positive phenotypic selection, and genetic variance for annual breeding success. However, their results also reveal that environmentally driven associations between traits and components of fitness can generate the appearance of selection which has no evolutionary relevance because of the lack of appropriate genetic covariance between trait and fitness component. In Chapter 11, Badyaev and Walsh consider the

contribution of epigenetic developmental dynamics to the maintenance of multivariate genetic variation in complex traits that are subject to strong natural selection. They combine geometric and developmental perspectives to the understanding of the evolution of genetic architecture that reconciles precise adaptation, evolutionary diversification, and environmentally contingent developmental variation. As a case study, they assess the importance of forces that shape the current *G*-matrix of beak traits for a population of house finches (*Carpodacus mexicanus*) studied over several generations. In doing so, they show that the dimensionality estimated at the genetic level of a structure is often far smaller than is expected from the dimensionality of its phenotype. Finally, Teplitsky, Robinson and Merilä (Chapter 12) provide an overview of our current knowledge and limitations in the study of evolutionary potential and constraints in wild populations. They then examine available data regarding the stability of genetic architecture across different ecological timescales. They focus especially on the current state of the field in dealing with the assessment of multivariate evolutionary potential, the evaluation of genetic constraints and the effect of evolutionary forces on the structure of *G*-matrices. Finally, they use a simulation-based approach to compare several matrix comparison statistics with respect to their capacity to detect differences in *G*-matrices.

Quantitative genetics in the wild is still expanding as a field of research, and the final three chapters suggest promising avenues for future developments. First, Jensen, Szulkin and Slate (Chapter 13) tackle important aspects related to the newly emerging field of molecular quantitative genetics by showing how high-throughput genomic approaches are increasingly being applied to evolutionary quantitative genetics research. They first describe how newly available molecular approaches promise to enhance our understanding of the genetic architecture and evolutionary dynamics of fitness-related traits in non-model species in the wild. They then examine how the integration of genomic data is allowing detailed population genetic analyses of natural populations and emphasise how these approaches are highly complementary to quantitative genetics;

for instance, they allow identification of genes and/or genomic regions that are under selection. Morrissey, de Villemereuil, Doligez and Gimenez (Chapter 14) then provide an overview of Bayesian statistics and their applications to quantitative genetic analyses of empirical data in the wild. They focus primarily on how Bayesian Markov Chain Monte Carlo (MCMC) algorithms are particularly suitable for such analyses. They provide examples of models in the BUGS statistical programming language which aim to demystify some aspects of these methods. They then discuss ways in which Bayesian tools can be used to make quantitative genetic inferences of complex data from natural populations and outline a range of benefits afforded by such applications. In particular, they emphasise that more direct inference of key evolutionary parameters and their associated error can be achieved than is often possible in frequentist frameworks. Finally in Chapter 15, Gienapp and Brommer emphasise the importance of improving our understanding of how climate change affects selection and the genetic variation in important traits in wild populations. To do so, they explore evidence for selection on phenological traits driven by climate change and then review quantitative genetic studies of these traits. They emphasise that very few studies reporting presumed evolutionary changes in response to climate change also considered phenotypic plasticity as a possible mechanism for such change, despite the need to assess whether observed changes related to climate are plastic and/or genetic. Their overview of the field suggests that evidence for genetic changes in response to climate change is scarce, yet it is still unclear if such absence also stems from a lack of statistical power and/or appropriate methods in previous studies.

## 1.4. Challenges

This book demonstrates that the field of quantitative genetics applied to populations studied in natural environments has extended substantially in the last two decades, providing fundamental insights into a wide range of topics in evolutionary ecology. Nevertheless, almost every chapter of this book contains discussion of problems inherent