CHAPTER 1

Introduction

This book is primarily about physiological mechanisms, but it also addresses the specific question of what we know about the physiological, metabolic, energetic, and hormonal mechanisms that regulate, and potentially determine, *individual*, or phenotypic, variation in key *reproductive life-history traits*, *trade-offs* between these traits, and *trade-offs* and *carry-over effects* between different life-history stages. Initially I will focus on the avian reproductive cycle (from seasonal gonadal development, through egg-laying and incubation, to chick-rearing), and then I will expand this view to consider reproduction in the broader context of the annual cycle and over an individual's entire lifetime (incorporating early developmental effects, maternal effects, and late developmental effects such as senescence). Throughout I will focus on and develop two major themes: that we need to consider reproductive physiology and ecology from a *female perspective* and that we need to consider the causes and consequences of *individual (phenotypic) variation* in reproductive life-history traits.

1.1. Structure of the Chapters

Although this book is about physiology I have rooted the book's organization firmly in the domain of evolutionary biology, or life-history, by asking the question, Which reproductive life-history traits contribute most to individual variation in lifetime fitness? An increasing number of long-term, individual-based population studies of birds and mammals are providing answers to this question, measuring differences in fitness between individuals, and assessing the causes of these disparities (Clutton-Brock and Sheldon 2010). Figure1.1 shows an example for multiple life-history traits for a pedigree of more than 2,100 individual female great tits (*Parus major*) studied across 39 years in Wytham Wood, England (McCleery et al. 2004). This study, and numerous others cited in this book, shows that the traits most strongly correlated with lifetime fitness (estimated as total number of offspring *recruited* to the breeding population) are lifetime fledging success (the total number of young *fledged* from all breeding attempts), longevity, clutch size, and laying date. Traits such as egg size, nestling mass, natal dispersal, and body size do not significantly influence total fitness. This approach is, admittedly, not perfect: only traits for which large amounts of individual data are available can be entered into these models. As an example, a major focus in avian biology in the last 10–15 years has concerned yolk hormones, antioxidants, and antibodies as potential determinants of offspring quality (see chapter 4). Given sufficient data, which currently do not exist, it is *possible* that these traits could prove to be important components of variance in lifetime fitness. Similarly, as I will highlight in chapter 6, it is much easier to obtain simple, reliable metrics for laying date, egg size, and clutch size than it is to measure the multiple, composite traits that characterize individual variation in incubation and chick-rearing effort (e.g., incubation onset, duration, constancy, provisioning rate, load size, and foraging distance), so the latter are not currently included, explicitly, in these analyses of lifetime fitness. Nevertheless, variation in incubation and chick-rearing effort is presumably subsumed within the trait of lifetime number of fledglings, implying that these *are* important components of variance in fitness. Taking this approach also highlights other important, unresolved evolutionary and mechanistic questions; for example, why are other traits, such as egg mass, highly variable among individuals if this variation is *not* related to variation in fitness?

Taking the approach outlined above, the main chapters of this book deal with timing of breeding (chapter 3), egg size and egg quality (chapter 4), clutch size (chapter 5), and parental care (incubation and chick-rearing, chapter 6). Each of these chapters is structured in the same way. I describe variation in the trait of interest (e.g., clutch size) or the composite traits that make up more complex reproductive behavior (e.g., variation in on-nest and off-nest bouts in relation to incubation). I focus on *individual* variation within a population or species, and, with one or two exceptions, this book does not take a comparative approach. Having described how variable these traits are, I ask if, and how, this variation is related to fitness and if there is evidence that selection is acting on these traits. Finally, having provided an evolutionary context for individual variation in these key reproductive life-history traits, I ask what we know about the physiological, metabolic, energetic, and hormonal mechanisms that regulate, and potentially determine, trait variation. Each chapter ends with a summary, and readers might like to start with it to get a quick overview of the main points. Reproduction does not occur in isolation; rather, an individual's fitness is dependent on successful integration of multiple life-history stages (non-breeding, breeding, molt, and migration) across the complete life cycle. In chapter 7 I place breeding in this broader context and consider linkages between different life-history

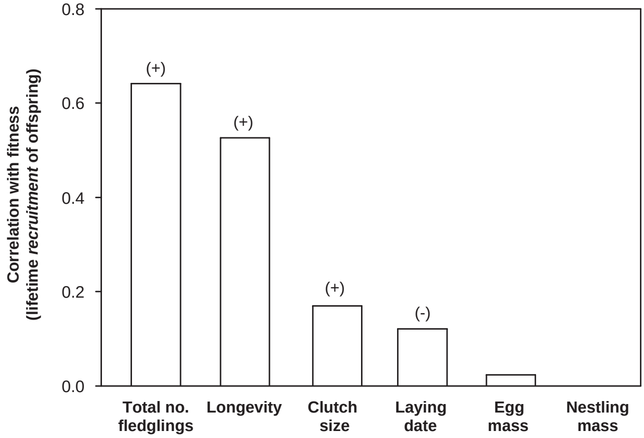

Fig. 1.1. Correlations of different life-history traits with total fitness (lifetime recruitment) in the great tit. (Based on data in McCleery et al. 2004.)

stages, including carry-over effects, costs of reproduction, and other trade-offs. How does an individual's activity during the non-breeding or pre-breeding period influence the subsequent reproductive period, and how, in turn, does reproduction influence late-season events such as post-fledging parental care, molt, migration, and ultimately future fecundity and survival? As in the previous chapters, having considered individual variation in these linkages between life-history stages, I then ask what we know about the physiological mechanisms that regulate potential trade-offs and carry-over effects.

1.2. A Primer on Reproduction in *Female* Birds

The reproductive traits that contribute most to lifetime fitness are either directly (laying date, clutch size) or indirectly (e.g., number of fledglings, where the upper limit is set by the clutch-size decision) related to a female's decision on *when* to breed and what *level* of primary reproductive investment to make during egg-laying. Furthermore, a female's decision on when to initiate a breeding attempt has important consequences for many components of reproductive effort much later in the season, for example, the probability of multiple brooding, the probability of breeding-molt overlap, and perhaps sex-specific survival. Chapter 2 provides a comprehensive overview of the physiological and endocrine control of female reproduction, focusing on the mechanisms underlying egg production, which must be involved in regulating and generating individual variation in these traits. The female perspective that pervades this book, and in particular chapter 2, stems from what I perceive as a disconnect in avian biology between physiological research on free-living or non-poultry species, where much of the focus has been on male birds, avian ecology, which *has* focused on female traits (e.g., egg and clutch size), and poultry studies, which *have* focused on females and egg production. Seasonal breeding provides one clear example. *Female-specific* physiological processes, such as vitellogenesis, yolk deposition, follicle growth, and oviduct development, are critical determinants of the timing of breeding, but in the majority of studies on environmental control of seasonal reproduction and gonadal development, male birds have been the model of choice! This disconnect has been long-standing: more than 40 years ago Farner et al. (1966) stated that "the accumulation of data on the ovarian cycle, both in the field and the laboratory, has been necessarily at a much slower rate [than for testis function]." G. Ball and Ketterson's recent review (2008) pointed out just how little we know about control of seasonal reproduction in *females* and highlighted the fact that "sex differences in relation to the environmental control of reproduction are [still] not a major research focus for the field overall." Therefore, I believe that bringing a female-specific perspective to bear within a life-history framework will help to move the field forward.

1.3. Individual Variation

It is almost axiomatic that heritable, individual variation is the raw material for natural selection. Darwin's *Origin of Species* (1872) is replete with references to *variability* and to *individual differences*, and he highlighted the fact that "these … afford materials for natural selection to act on and accumulate" (p. 34). Interestingly, Darwin fully recognized that these differences could be physiological in nature, describing studies of individual variation in the branching of nerves and in the structure of muscles in insects. The analysis of individual variation has been embraced by many areas of ecology and evolutionary biology (Biro and Stamps 2008; Clutton-Brock and Sheldon 2010; Dingemanse et al. 2010; Hamel et al. 2009; Nussey et al. 2007; A. Wilson and Nussey 2010), but until recently, physiology and endocrinology have all but ignored individual variation (A. Bennett 1987; T. Williams 2008). A consideration of individual variation forces us to ask a different set of questions with regard to regulatory mechanisms underlying reproductive traits. The question, What is the physiological difference between non-breeding and egg-producing females? might be satisfactorily answered by showing that the former has baseline plasma estrogen levels, whereas the latter has highly elevated plasma estrogen levels. These results would be taken as evidence that estrogens play a role in regulating egg production. However, in understanding individual variation we need to ask the question, Does a female with a high egg-producing phenotype (many, large eggs) have higher plasma estrogen levels than a low egg-producing phenotype (few, small eggs)? In other words, do estrogens, or estrogen-dependent mechanisms, explain *individual* variation in the reproductive phenotype? As a further example, although elevated plasma prolactin levels are generally associated with parental care, is prolactin causally related to individual, phenotypic variation in the *amount* of parental care? This approach therefore gets at the heart of a mechanistic understanding of phenotypic variation.

1.4. What Is *Not* in This Book?

As a consequence of the specific perspective described above, there are many topics that are *not* covered in this book. I have not considered male-specific topics, such as testis structure and function, sperm competition, song, testosterone-immune function trade-offs, etc. I have tried to avoid any extensive consideration of social behavior per se since this topic has been comprehensively covered in Elizabeth Adkins-Regan's excellent book, *Hormones and Animal Social Behavior* (2005). I have also not included behavioral syndromes or avian personalities, although these represent other areas where ecological studies are rapidly outpacing any mechanistic understanding (Biro and Stamps 2008; Dingemanse et al. 2010; Reale et al. 2010). There is relatively little genomics in this book, even though it is considered by some to be one of the "hotter" areas of avian biology (Bonneaud et al. 2008). Sequencing of the zebra finch (*Taeniopygia guttata*) genome is indeed a "major step forward for avian ecology and evolutionary biology" (Balakrishnan et al. 2010), and genomics might indeed "revolutionize our understanding of birds" (Edwards 2007). However, most work to date has focused on comparative genomics, population genetics, speciation, and systematics, and genomics work on natural bird populations is still in its infancy (Ellegren and Sheldon 2008). In particular, application of genomic approaches to questions of plasticity, phenotypic variation, and adaptation has hardly begun, especially for reproductive and life-history traits (but see, e.g., Abzhanov et al. 2004; Abzhanov et al. 2006; Cheviron et al. 2008; Fidler et al. 2007). A main conclusion of this book very much supports Edwards' (2007) statement that "ornithologists [should] maintain focus on the age-old questions in ecology." However, my own view is that the "age-old questions" considered in this book, such as why clutch size, or parental effort varies among individuals, and the consequences of this variation, have *not* remained intractable simply because of a dearth of non-genomic approaches. Rather we have just stopped focusing on certain fundamental questions even though they remain unresolved and can be tackled with traditional, *experimental* approaches (albeit enhanced and aided by genomics knowledge and techniques). Identifying the genes or DNA sequences underlying variation is life-history traits is an important goal (Ellegren and Sheldon 2008), but unveiling the *physiological mechanisms* linking genotypes to phenotypes, and ultimately to fitness, in natural populations is even more important.

1.5. Avian Reproduction in a Changing World

Global climate change is currently impacting all aspects of the annual cycle of birds, from the tropics, through the temperate zone, to the Poles (Gaston et al. 2005; Nevoux et al. 2010; Visser, et al. 2004; S. Williams et al. 2003). Climate change is affecting the phenology of breeding in birds, the timing of migration, demography, population dynamics, and species' distributions and ranges (Carey 2009; Visser 2008; Visser, et al. 2004). Since the timing of breeding determines the timing and pattern of subsequent breeding stages (see chapter 3), climate change affects all components of the reproductive cycle, including incubation, nestling development time, and probability of second clutches (e.g., Husby et al. 2009; Møller et al. 2010; Matthysen et al. 2010) via effects on a suite of correlated life-history traits (Both and Visser 2005; Garant, Hadfield, et al. 2007). Regional differences in climate change (e.g., between breeding and non-breeding areas) and variation in responses to climate change at different trophic levels (e.g., between birds and their insect prey) have led to mismatching of resource availability and arrival dates in migratory birds (T. Jones and Cresswell 2010) and to mismatching of peak food availability and chick-rearing in some breeding birds (Gaston et al. 2005; Visser et al. 1998; Visser et al. 2004). However, population responses to climate change are complex, and shifts in the timing of breeding and migration have varied markedly between species, occurring in some populations but not others (Carey 2009; Parmesan 2006). Several studies have reported or predicted negative effects of climate change on population dynamics of certain species (e.g., Both et al. 2006; Jenouvrier et al. 2009), but some studies have also suggested there might be positive effects of climate change on other populations, at least in the short-term (D'Alba, Monaghan, and Nager 2010; Gaston et al. 2005). Long-term monitoring studies of bird populations provided some of the earliest and clearest evidence for changes in phenology associated with climate change (Crick et al. 1997). However, to date most studies have simply, though importantly, documented change after it has occurred; a critical goal is to develop the ability to predict how *future* climate change will affect avian populations. This capacity, in turn, will require that we obtain a far better understanding of the *physiological response mechanisms* that link environmental cues and environmental conditions to reproductive and life-history decisions, and it is therefore essential that research on phenological, life-history events integrates both mechanistic and evolutionary perspectives (Visser et al. 2010). Physiological or mechanistic hypotheses can themselves provide a valuable approach for predicting future effects of climate change *provided we know enough about the basic, underlying physiology* (Portner and Farrell 2008; Portner and Knust 2007; Sinervo et al. 2010). As this book demonstrates, this is at present not the case for most of the key reproductive life-history traits in birds, a situation that adds urgency to the need to refocus our research efforts. Hopefully, by focusing on the basic physiological, metabolic, energetic, and hormonal mechanisms underlying female-specific reproductive traits within a broader life-history context, this book will contribute to advancing our progress in this area.