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THE PHYSIOLOGY OF LIFE HISTORY TRADE-OFFS IN ANIMALS

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■ **Abstract** The functional causes of life history trade-offs have been a topic of interest to evolutionary biologists for over six decades. Our review of life history trade-offs discusses conceptual issues associated with physiological aspects of trade-offs, and it describes recent advances on this topic. We focus on studies of four model systems: wing polymorphic insects, *Drosophila*, lizards, and birds. The most significant recent advances have been: (*a*) incorporation of genetics in physiological studies of trade-offs, (*b*) integration of investigations of nutrient input with nutrient allocation, (*c*) development of more sophisticated models of resource acquisition and allocation, (*d*) a shift to more integrated, multidisciplinary studies of intraspecific trade-offs, and (*e*) the first detailed investigations of the endocrine regulation of life history trade-offs.

INTRODUCTION

Life history traits are often negatively associated with each other (Clutton-Brock et al. 1982, Reznick 1985, Stearns 1989, 1992, Roff 1992, Rose et al. 1996). Classic examples include decreased early fecundity in lines of *Drosophila melanogaster* selected for increased longevity, and reduced overwintering survivorship in lactating (reproductive) red deer, *Cervus elaphus*. These negative associations, referred to as life history trade-offs, have played a prominent role in theory and interpretation of life history studies. For example, trade-offs are a key assumption of optimality models of life history evolution, and they provide an explanation for the widespread occurrence of variable life history traits in natural populations (Reznick 1985, Roff 1992, Stearns 1992).

The physiological causes of life history trade-offs have been a central topic in life history studies for more than six decades (Fisher 1930, Tinkle & Hadley 1975, Townsend & Calow 1981, Dunham et al. 1989, Adolph & Porter 1993, Stearns 1992, Roff 1992, Zera et al. 1998). The ultimate goal of physiological studies has been to illuminate the mechanisms of life history evolution by identifying functional interactions among the various components of life history traits. In many cases, life history trade-offs have been thought to result from competition among

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different organismal functions for limited internal resources. Hence, traditional physiological studies of life history trade-offs have focused almost exclusively on the differential allocation of limiting internal nutrients to reproduction, maintenance metabolism, growth, and storage within single species or variation in these processes among populations or species (Calow 1979, Townsend & Calow 1981, Congdon et al. 1982).

During the past decade, significant advances have been made in understanding the physiological mechanisms that underlie life history trade-offs. For example, while retaining focus on individual species or variation between populations or species (Bernardo 1994, Niewiarowski 2001), studies of trade-off physiology have recently expanded to include comparisons between phenotypes or genotypes within populations (Rose et al. 1996, Zera & Huang 1999, Salmon et al. 2001, Zera & Cisper 2001). This expansion has provided the first data on genetic variation and covariation for physiological traits and their relationship to trade-offs at the demographic level. In addition, trade-off studies have recently expanded to include non-energetic aspects of resource allocation, such as the hormonal control of antagonistic traits that comprise trade-offs (Ketterson & Nolan 1992, 1999, Sinervo & Basolo 1996, Sinervo 1999, Zera & Cisper 2001).

The past decade also has seen the development of more complex models of trade-offs (Houle 1991, de Jong 1993, Reznick et al. 2000). These models underscore the importance of functional studies as opposed to the sole use of phenotypic or genetic correlation to identify the existence of trade-offs, and the necessity of taking into account nutrient input in studies of nutrient allocation. Finally, more sophisticated genetic, environmental, endocrine, and molecular approaches have been used to investigate classic trade-offs such as the cost of reproduction (Ketterson & Nolan 1992, 1999, Sinervo & Basolo 1996, Zera et al. 1998, Sinervo 1999, Salmon et al. 2001, Stearns & Kaiser 1993).

Physiological aspects of life history trade-offs have been reviewed previously (e.g., Townsend & Calow 1981, Bell & Koufopanou 1986, Sibley & Calow 1986, Ricklefs 1991, Sibley & Antonovics 1992). However, many of the recent developments in trade-off physiology described above have never been reviewed or have been reviewed in a limited manner. The literature on functional aspects of life history trade-offs is considerable, and no single review can adequately cover all aspects of this topic in all major groups of organisms. In this review, we focus on three topics that have been especially prominent in recent physiological studies of intraspecific trade-offs: (*a*) the influence of nutrient acquisition on the trade-off of internal resources, (*b*) hormonal control of trade-offs, and (*c*) genetic and experimental analyses of trade-offs. We also focus on four model systems that have been especially prominent in physiological studies of life history trade-offs: wing-polymorphic crickets, *Drosophila melanogaster*, lizards, and birds. These models were chosen because they illustrate a diversity of approaches that have been used to investigate a range of central issues in trade-off physiology in taxonomically diverse organisms studied in the laboratory or in the field.

CONCEPTUAL BACKGROUND

Definitions and Basic Principles

Definitions of key trade-off terms such as costs, constraints, and trade-off often vary among studies, which could lead to confusion (Antonovics & van Tienderen 1991). For example, in some cases trade-off is defined as the result of physiological or fitness costs (Leroi et al. 1994b, see below), while in other cases the term cost is used to define a trade-off (Reznick 1985, 1992). The classic example of the latter usage is the cost of reproduction, which is the term used to define the trade-off between current and expected future reproduction (Reznick 1985, 1992). The term cost of reproduction requires special attention because it has been used in many different ways. For example, this term can refer to either a price (e.g., amount of calories required to produce an egg) or penalty of reproduction, that is measured in physiological (i.e., calories), demographic (survivorship), or fitness units. Moreover, the cost of reproduction can refer to a direct penalty of current reproduction or to a penalty exacted in the future.

If internal resources are limited and are insufficient to pay all construction and maintenance costs for two life history traits that share a common resource pool, then a trade-off results: an increment of resources allocated to one trait necessitates a decrement of resources to another trait (the traditional "Y" model of resource allocation; van Noordwijk & de Jong 1986) (Figure 1). In the absence of variation in resource input, two traits linked in a functional trade-off are negatively correlated (more complex situations involving more than two traits and variation in resource input are described below). For example, if internal reserves allocated to current reproduction limit resources available for future reproduction, a trade-off between current and future reproduction exists for physiological reasons (Calow 1979, Bell & Koufopanou 1986). Trade-offs can occur between physiological traits expressed during the same or different times in the life cycle (Chippindale et al. 1996, Zera et al. 1998, Stevens et al. 1999), and they can result from variation in genetic factors (e.g., pleiotropy), environmental factors, or combinations of these two types of factors that give rise to negative interactions between traits. If the trade-off results from a negative genetic correlation, then short-term evolutionary change in one phenotype constrains (i.e., limits) evolutionary change in the other phenotype. Ecological factors, such as predation (Reznick et al. 1990), or behavioral factors, such as time-based conflicts between activities (Marler & Moore 1988, Marler et al. 1995) can be a primary cause of life history trade-offs. Thus, assessing the importance of variation in internal physiological factors on a life history trade-off is most appropriately done by taking into account the relative importance of variation in external ecological or behavioral factors.

Appropriate Use of the Term "Trade-Off"

Implicit in the term trade-off, used in a physiological context, is the notion that a negative functional interaction is the cause of the negative association between

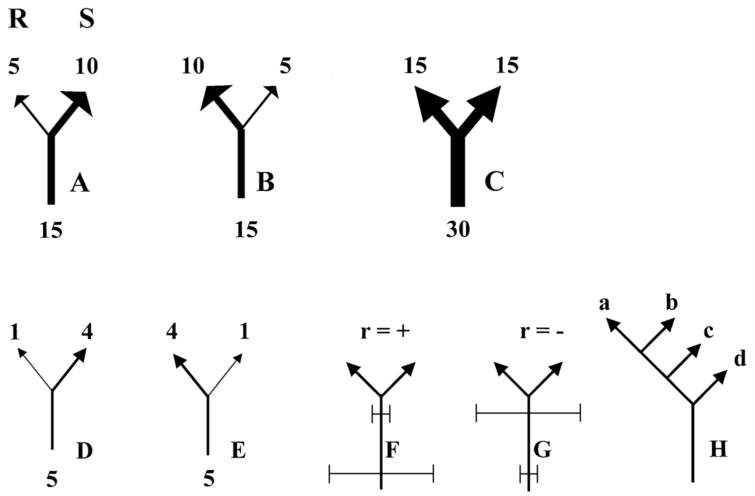

Figure 1 Diagrammatic representation of trade-offs. Each "Y allocation tree" illustrates the amount of resource input (acquisition; number at the base) and the pattern of resource allocation (numbers at the tips of the branches) for a particular phenotype or genotype. R denotes allocation to reproduction, while S denotes allocation to soma. In trees *A–E*, maximal allocation to (maximal physiological cost of) R or S is 15 resource units. Trees *A* and *B* illustrate a standard trade-off (differential allocation of a limiting internal resource). Relative to trees *A* and *B*, tree *C* illustrates the obviating effect of increased resource input on a trade-off (resource input matches physiological costs of both traits), while trees *D* and *E* illustrate the exacerbating effect of decreased nutrient input on a trade-off. Trees *A* and *B*, relative to *D* and *E*, illustrate plasticity of a resource-based trade-off. Trees *F* and *G* illustrate the influence of relative variation in resource input (length of the bar at the base of the tree) versus variation in resource allocation (length of bar at the branch of the tree) on the sign of the correlation between two traits involved in a trade-off. Tree *H* illustrates a more complex allocation tree with multiple dichotomous branches. See text for additional explanation and references. Trees *F* and *G* were redrawn from van Noordwijk & de Jong (1986), while tree *H* was redrawn from de Jong (1993).

two traits under consideration. However, the term trade-off has often been applied to trait associations for which only minimal or no information is available as to whether the traits interact functionally (e.g., see Mole & Zera 1993). Traits might be negatively associated for a variety of reasons other than functional interaction, such as genetic linkage (Mole & Zera 1993, Zera et al. 1998, Zera & Cisper 2001). In our view, the term trade-off, used in physiological studies of life history variation, should represent a hypothesis concerning the cause of a negative trait association, just as the term adaptation is a hypothesis concerning the role of natural selection in shaping the form or function of a trait. It is inappropriate to apply the term evolutionary adaptation to a trait for which there is no strong evidence that its form or function was shaped by natural selection (Lauder 1996). In the future, we anticipate that the term trade-off will be restricted to cases where data indicate a negative functional interaction between traits. When little or no functional information is available, the terms negative association, or potential trade-off, are preferable to trade-off. Research on trade-offs should be increasingly directed toward understanding the underlying mechanism of the negative association between traits.

TRADE-OFF ARCHITECTURE AND EFFECT OF NUTRIENT ACQUSITION

Y Model and Variable Nutrient Input

During the past decade, the properties of trade-offs have been studied using quantitative-genetic and optimization models. Most of these models are more complex versions of the standard "Y" model of allocation discussed previously. An important result of these studies is that, for a variety of reasons, a positive correlation can exist between traits that are linked in a functional trade-off. For example, once more than two traits are involved in a trade-off (see Figure 1H), positive correlations can occur between subsets of those traits (Charlesworth 1990, Houle 1991, Roff 1992). Furthermore, if variability in nutrient input among individuals, due to either genetic variation in loci that control nutrient acquisition or to environmental variation in available resources, is greater than variability in nutrient allocation, positive correlations between traits that comprise a functional trade-off can occur (Figure 1F–G; van Noordwijk & de Jong 1986, de Laguerie et al. 1991, Houle 1991, de Jong & van Noordwijk 1992, de Jong 1993). de Laguerie et al. (1991) and de Jong (1993) developed allocation tree models of trade-offs, involving successive dichotomous branches (trade offs) in a tree with nutrient input as the trunk (See Figure 1H). Both the position of a branch point on an allocation tree and the extent of resource transformations strongly affect whether positive or negative correlations exist between traits that trade off.

Theoretical studies of trade-offs clearly show that the sign of a correlation between two traits cannot be used as an unambiguous indicator of whether those traits interact functionally in a negative manner (i.e., whether they trade-off). This important result underscores that functional trade-offs can be validated only by direct physiological studies rather than by purely phenotypic or genetic approaches. Theoretical studies also illustrate the importance of controlling or quantifying nutrient input in functional studies of nutrient-based internal trade-offs (Figure 1). Quantifying nutrient input has long been regarded as an essential aspect of energy budget studies (Congdon et al. 1982, Nagy 1983, Withers 1992), but has been neglected in many recent energetics studies of trade-offs. This omission is a likely cause of unexpected results obtained in some trade-off studies, such as the failure to observe increased metabolic costs when reproduction is increased (Rose &

Bradley 1998; see also Zera et al. 1998, Reznick et al. 2000). Trade-off models discussed above also provide an explanation for the common observation that traits that are expected to trade-off, and hence exhibit negative correlations, are often positively correlated (Mole & Zera 1993, Reznick et al. 2000). Although these trade-off models are more complex versions of the original "Y" model of allocation (van Noordwijk & de Jong 1986), they are still rudimentary descriptors of the physiology of internal resource allocation.

Trade-Off Plasticity and Priority Rules

Trade-offs are influenced not only by variation among individuals in nutrient input, but also by the absolute amount of nutrient input. Reduced nutrient availability can substantially magnify, while increased nutrient availability can diminish or obviate an apparent trade-off (Figure 1) (Kaitala 1987, Chippindale et al. 1993, Simmons & Bradley 1997, Nijhout & Emlen 1998, Zera et al. 1998, Zera & Brink 2000; see clutch size studies in "Birds" section). These plastic responses of a trade-off are determined by priority rules, which govern relative allocation to organismal processes as a function of nutrient input. Recent experiments have only begun to identify the broad outlines of these rules at the whole-organism level. For example, in laboratory and field experiments on bivalves, cladocerans, insects, and mammals, allocation to maintenance or storage was found to take precedence over allocation to reproduction under nutrient-poor or stressful conditions (Rogowitz 1996, Perrin et al. 1990, Boggs & Ross 1993, Jokela & Mutikainen 1995, Zera et al. 1998). Priority rules are shaped by ecological factors. A more thorough understanding of the evolution of priority rules requires a deeper synthesis among physiological studies of allocation, ecological studies of nutrient acquisition (e.g., foraging), and life history studies in the field (Boggs 1992, 1997).

Timing of Nutrient Input and Trade-Off Dynamics

Another important aspect of nutrient acquisition on a trade-off is the relative timing of these two processes. The most extensively studied aspect of this topic concerns capital versus income breeding. In income breeding, resources used for reproduction are acquired during the reproductive period, while in capital breeding, resources are derived from stores acquired during an earlier period (Drent & Daan 1980, Jonsson 1997, Bonnet et al. 1998). The relative advantage of capitol versus income breeding, and the relative demographic and energetic costs and benefits of energy storage are a matter of debate (e.g., Jonsson 1997, Bonnet et al. 1998). Capital breeding can give rise to trade-offs between different stages of the life cycle, nearly all physiological aspects of which are not well understood. Recent experiments have documented the use of nutrients in reproduction that were acquired during earlier stages; in some cases, unexpectedly long time lags (e.g., >12 months in lizards) between resource acquisition and expenditure on reproduction were noted (e.g., Reznick & Yang 1993, Boggs 1997, Doughty & Shine 1998).

Especially noteworthy are the feeding and radiotracer studies by Boggs and colleagues (Boggs 1997). These studies investigated the relative use of larval and adult-acquired nutrients in reproduction in butterflies as a function of life history and foraging. The relationship between the timing of nutrient acquisition and use of energy stores for reproduction also has important implications for the identification of the ecological causes of trade-offs. For example, a long time lag between resource input and use for reproduction will tend to obscure the influence of specific aspects of resource availability in the field on reproductive output (Doughty & Shine 1997, 1998).

Trade-offs are not static; they can change during development and can evolve (Leroi et al. 1994b). Many life history models have explored dynamical aspects of resource allocation (Perrin & Sibly 1993, Noonburg et al. 1998, Heino & Kaitala 1999). For example, such models predict that the ratio (P/m), where $P =$ productivity (growth and reproduction), and where $m =$ mortality becomes more sensitive to mortality as a function of age. Assuming a trade-off between mortality and productivity, organisms should initially invest in productivity, then later in survival. This might explain why growth rate decreases with age (Perrin & Sibly 1993). One problem with these and a broad class of related models is that their empirical validity is not well established owing to the paucity of direct mechanistic information on putative resource allocation trade-offs.

MEASURING PHYSIOLOGICAL TRADE-OFFS

Three main empirical approaches have been used to investigate life history trade-offs and their physiological causes: (*a*) measurement of phenotypic correlations on unmanipulated individuals, (*b*) genetic analyses, and (*c*) experimental manipulation of phenotypes. The relative merits of these approaches have been extensively debated (e. g., Reznick 1985, 1992, Bell & Koufopanou 1986, Partridge & Sibly 1991, Partridge 1992, Sinervo & Basolo 1996, Rose & Bradley 1998, Harshman & Schmid 1998, Zera et al. 1998). Phenotypic correlations measured on unmanipulated individuals in the field or lab are important in that they can suggest physiological causes of trade-offs. However, there is broad agreement that phenotypic correlations, by themselves, can provide only limited information on the physiological mechanisms that underlie trade-offs. The main problem is that uncontrolled variables can reduce the magnitude of a trade-off or can lead to spurious correlations. For example, as mentioned above, variable nutrient intake can cause two traits involved in a trade-off to be positively correlated (van Noordwijk & de Jong 1986, de Jong 1993), a problem that is expected to be particularly acute in field studies (Haukioja & Hakala 1986, Tuomi et al. 1983). Simple changes in experimental design can sometimes obviate the masking effect of uncontrolled variables on trade-offs. For example, a negative correlation between somatic lipid reserves and reproductive effort in a lizard species was identified by quantifying lipid levels before and after reproduction in the same individuals using a non-invasive method (Doughty & Shine 1997). Individual variation in lipid levels had previously obscured this negative association.

One school of thought is that genetically based covariation should be a focus of attention in trade-off studies because only genetically based traits can evolve (Reznick 1985, Bell & Koufopanou 1986, Partridge & Sibly 1991, Rose et al. 1996). Physiological-genetic studies of life history trade-offs represent one of the most important advances in functional studies of trade-offs during the past decade. Nevertheless, genetic approaches also have important drawbacks (Bell & Koufopanou 1986, Partridge & Sibly 1991). Most notably, in the process of measuring the genetic basis of a trade-off (e.g., via artificial selection), the trade-off itself and its relationship to its physiological causes can be altered (Moller et al. 1989, Partridge & Sibly 1991, Rose & Bradley 1998). Furthermore, genetic studies are limited by standing genetic variation and only indicate how traits may evolve in the short-term; they can only be performed on a subset of organisms, and require much more time and resources than do phenotypic studies (Partridge & Sibly 1991).

The most controversial empirical approach in life history studies is environmental manipulation (sometimes called phenotypic manipulation) (Reznick 1985, 1992, Partridge & Sibly 1991, Sinervo & Basolo 1996, Chippindale et al. 1997). This approach essentially involves altering an environmental variable (e.g., nutrient level) to generate a phenotypic trade-off whose properties can then be studied. The main advantages of this approach are that a great range of character values can be produced, and trade-offs between genetically invariant traits can be investigated. The most serious disadvantage is the typical lack of specificity of the manipulation. Traits can be modified independently of the mechanisms that link them in a trade-off, thus giving rise to altered trade-off functions (Moller et al. 1989, Partridge & Sibly 1991, Sinervo & Basolo 1996). Some of the problems with environmental manipulation can be circumvented by using more targeted surgical or endocrine manipulations (i.e., physiological manipulations or phenotypic engineering (Sinervo & McEdward 1988, Marler & Moore 1988, 1991, Ketterson & Nolan 1992, 1999, Landwer 1994, Sinervo & Basolo 1996, Zera et al. 1998, Zera & Cisper 2001). These manipulations represent a powerful approach to the study of functional aspects of life history trade-offs. They not only shed light on the specific physiological mechanisms that underlie trade-offs, but they can also be used to produce phenotypes to test various trade-off hypotheses (phenotypic engineering) (Ketterson & Nolan 1992, 1999, Zera et al. 1998, Sinervo 1999).

Like other approaches, physiological manipulation has its limitations. For example, surgical removal of an organ does not necessarily abolish the energetic cost of producing or maintaining the function performed by that organ. Removal of ovaries does not abolish physiological costs of reproduction since yolk proteins are still synthesized in other organs, sometimes in enormous quantities (Chinzei & Wyatt 1985). Applied hormones can have pharmacological effects or can alter trade-offs in unsuspected ways by inducing the production of unknown regulators

(Zera et al. 1998). Thus, in the absence of direct measures of endocrine traits (e.g., in vivo hormone titers), only limited conclusions can be drawn from hormone manipulation experiments concerning specific endocrine mechanisms that underlie trade-offs (e.g., Zera et al. 1998, Zera & Cisper 2001). A developing consensus is that each empirical approach has its strengths and weaknesses, and that the use of multiple complementary approaches is essential for a thorough investigation of the physiological causes of life history trade-offs (Moller et al. 1989, Partridge & Sibly 1991, Sinervo & Basolo 1996, Rose & Bradley 1998; Zera et al. 1998; Zera and Cisper 2001).

MODEL SYSTEMS

Wing-Polymorphic Crickets

For over four decades, wing polymorphism has been viewed as a classic example of a life history trade-off that results from the differential allocation of internal reserves to ovarian growth versus somatic growth, maintenance, or storage (i.e., growth and maintenance of fight muscles, accumulation of flight fuels, Johnson 1969, Bell & Koufopanou 1986, Zera & Denno 1997). During the past decade, detailed energetic, endocrine, and genetic studies in wing polymorphic crickets have provided strong support for this notion (Mole & Zera 1993, Tanaka 1993, Zera et al. 1994, 1997, 1998, Zera & Denno 1997, Roff et al. 1997, Zera & Brink 2000, Zera & Cisper 2001). Wing polymorphism is now one of the life history trade-off models most thoroughly studied from a physiological perspective.

Wing polymorphic species consist of a flight-capable morph that has large functional flight muscles and large quantities of lipid flight-fuel, and of flightless morphs that have small, nonfunctional flight muscles and much reduced lipid stores. Early fecundity is negatively associated with flight capability (Roff 1986, Zera & Denno 1997, Zera et al. 1998). Differences between morphs in these dispersal and reproductive traits are often large, making wing polymorphism an exceptional experimental model for investigating trade-off physiology. For example, at the end of the first week of adulthood, flight muscles are typically reduced by 40%, ovaries are enlarged by 200%–400%, and whole-body triglyceride reserves are reduced by 30% in flightless versus flight-capable morphs of *Gryllus* (crickets) (Mole & Zera 1993, Zera et al. 1994, 1998, Zera & Larsen 2001).

Feeding studies of *Gryllus* species have provided some of the best documented examples of the relative importance of nutrient acquisition versus nutrient allocation in a life history trade-off. Naturally occurring or hormonally engineered flightless morphs of two *Gryllus* species consumed and assimilated the same amount of nutrients as the flight-capable morph (Mole & Zera 1993, Zera et al. 1998). Thus, the increased ovarian growth of the flightless morph in these species must have resulted, at least in part, from the greater allocation of absorbed nutrients, rather than from increased food consumption or assimilation by the flightless morph. In a third species, *G. firmus*, increased ovarian growth in the flightless morph was due to both increased nutrient allocation and greater food intake (Zera et al. 1998, Zera & Brink 2000, A.J. Zera & T. Rooneem, unpublished data).

Only by quantifying nutrient consumption and assimilation by the morphs could increased allocation of nutrients (internal trade-off) as opposed to increased acquisition of nutrients (no internal trade-off) have been identified as a potential cause of the difference in ovarian growth between morphs (Mole & Zera 1993, Zera & Denno 1997, Zera et al. 1998). The study of *G. firmus* is the only case in which genetically based differences in total nutrient consumption, assimilation, and allocation have been documented between phenotypes that differ in life histories (Zera & Brink 2000, Zera & Rooneem, unpublished data). One limitation of these investigations in *Gryllus* is that indices of nutrient allocation and acquisition were measured in units of mass rather than in units of energy (Zera et al. 1998, Zera & Brink 2000). However, more recent studies indicate that morphs differ to similar degree in these indices measured in units of energy (A.J. Zera & T. Rooneem, unpublished data). Although nutrient input is an integral component of energy budgets (Congdon et al. 1982, Withers 1992), many recent energetic studies of intraspecific life history trade-offs have not measured nutrient consumption or assimilation.

Some of the most detailed information on specific physiological causes of life history trade-offs has come from studies of *Gryllus*. Biosynthesis of triglyceride flight fuel may be an especially important physiological cost of flight capability that results in reduced ovarian growth (Zera & Larsen 2001). As mentioned above, whole-body triglyceride content was 30%–40% higher in flight-capable versus flightless morphs of two *Gryllus* species on a variety of diets (Zera & Denno 1997, Zera et al. 1994, 1998, Zera & Brink 2000, Zera & Larsen 2001). In *G. firmus*, a genetically based elevation in triglyceride stores in the flight-capable morph (*a*) was produced during a period of reduced ovarian growth in the flight-capable morph, (*b*) did not result from increased lipid intake from the diet, and (*c*) paralleled increased activities of enzymes of lipid biosynthesis and rate of lipid biosynthesis in the flight-capable morph (Zera & Brink 2000, Zera & Larsen 2001, Zhao & Zera 2001). The extent to which the negative association between lipid biosynthesis and ovarian growth results from an energetic trade-off (differential allocation of limited internal reserves to these two organismal traits) is unknown. Other possibilities include a regulatory trade-off in which antagonistic aspects of the control of lipid versus protein biosynthesis preclude the accumulation of elevated amounts of both of these compounds (Zhao & Zera 2001). Finally, the trade-off between lipid accumulation and ovarian growth could result from limited space within the abdomen.

Increased maintenance of flight muscles, but not flight muscle growth, has also been implicated as a potentially important energetic cost of flight capability. The large flight muscles of the flight-capable morph exhibited a 300%–350% greater respiration rate in vitro compared with the reduced flight muscles of the flightless morphs, and may contribute to the higher whole-body respiration rate of the flight-capable morph (Zera et al. 1997, 1998, Zera & Brink 2000). By contrast, on high nutrient diets, flight muscle growth, as indicated by increased mass or rate of muscle protein biosynthesis, is restricted to the first 2 to 3 days of adulthood in *Gryllus* species, before significant ovarian growth commences (Gomi et al. 1995, Zera et al. 1998, A.J. Zera & T. Rooneem, unpublished data). Thus, flight muscle growth does not appear to directly trade-off with ovarian growth. Finally, some potentially important contributors to the energetic cost of flight capability, such as increased activity of the flight-capable morph in the absence of flight, have yet to be assessed for any case of wing polymorphism (Zera et al. 1998).

Feeding studies in *Gryllus* also have provided information on the physiological mechanisms by which trade-offs may be exacerbated when nutrient input is decreased (Figure 1). In both *G. assimilis* and *G. firmus*, ovarian growth in the flight-capable versus the flightless morph was reduced to a greater degree on a low-nutrient diet compared with a high-nutrient diet. Whole-organism respiration was proportionally higher in the flight-capable morph compared with the flightless morph when on a low-nutrient diet compared with a high-nutrient diet (Zera et al. 1998, Zera & Brink 2000, A.J. Zera & T. Rooneem, unpublished data). These data suggest that some aspect of maintenance metabolism of the flight-capable morph, possibly flight-muscle maintenance, consumes a greater proportion of the reduced energy budget on the low-nutrient diet. This would reduce nutrients available for ovarian growth in the flight-capable versus the flightless morph to a greater degree on the low-nutrient diet, compared with the high-nutrient diet. The Colorado potato beetle histolyzes its flight muscles prior to overwintering, suggesting that maintenance metabolism of flight muscles may be a significant energy drain under prolonged low-nutrient conditions (El-Ibrashy 1965, Zera & Denno 1997). Alternatively, other factors such as increased activity of the flight-capable morph of *Gryllus* species may account for its increased respiratory metabolism, relative to the flight-capable morph, under low-nutrient conditions.

Because hormones regulate many key components of life histories (e.g., egg production, growth, metabolism), variation in endocrine regulation has long been suspected to be a primary physiological cause of life history trade-offs (Stearns 1989, Ketterson & Nolan 1992, 1999). Yet detailed studies of the mechanisms by which hormones regulate life history trade-offs have only begun during the past decade. Wing polymorphism in *Gryllus* is currently the most intensively studied life history trade-off with respect to endocrine regulation and is one of the only cases where genetic information is available on this topic (Zera & Tiebel 1989, Zera & Denno 1997, Roff et al. 1997, Zera & Huang 1999, Zera & Cisper 2001, Zera & Bottsford 2001). Thus far, hormonal studies have focused almost exclusively on the regulation of growth and degeneration of the key organs involved in the trade-off between flight capability and fecundity: ovaries and flight muscles. An elevated hemolymph titer of juvenile hormone (JH), a major gonadotropin in insects, has long been suspected to cause the elevated ovarian growth during early adulthood in the flightless morph of wing polymorphic species (Nijhout 1994, 1999, Zera & Denno 1997). This notion is supported by the strong positive effect of a JH mimic on ovarian growth in several *Gryllus* species (Zera et al. 1998, Zera &

Cisper 2001). Recent direct measures of the in vivo JH titer in *G. firmus* indicate that the hormonal regulation of morph-specific ovarian growth is more complex than previously suspected. The hemolymph JH titer is, in fact, lower in the flight-capable morph relative to the flightless morph in the morning. However, the level of this hormone rises dramatically (10- to 100-fold) during the day in the flight-capable morph, but not in the flightless morph, which leads to a higher JH titer in the flight-capable versus flightless morphs in the evening (Zera & Cisper 2001). The short-term elevation in the JH titer possibly regulates nocturnal flight in the long-winged morph of *G. firmus*. Although JH is likely involved in the increased ovarian growth of the flightless morph, it clearly cannot be the only factor involved and may not be the primary factor (Zera & Cisper 2001). This level of complexity in the endocrine regulation of a life history trade-off could only have been identified by direct measurement of in vivo hormone levels.

Discontinuous variation in the size of flight muscles, the other key organ participating in the trade-off between flight capability and ovarian growth, is produced by two different mechanisms. Differences in muscle growth between morphs can occur during the juvenile stage. Variation in the titers of JH and 20-hydroxy ecdysone, which are important developmental as well as reproductive hormones in insects, may regulate differences in muscle growth. Extensive endocrine-genetic studies suggest that the catabolic enzyme, juvenile hormone esterase, which is thought to regulate the JH titer in many insects, may modulate the JH titer in nascent *Gryllus* morphs, leading to variation in the development of flight muscles and wings (Zera & Tiebel, 1989, Zera & Denno 1997, Roff et al. 1997, Zera & Huang 1999, Zera 1999). Studies of Zera & Tiebel (1989) and Roff et al. (1997) are among the few investigations in which genetic covariance has been documented between an important component of a life history trait (i.e., wing and flight muscle phenotype) and a putative endocrine regulator of that trait.

Discontinuous variation in flight muscle mass in *Gryllus* and many other insects also results from histolysis (degeneration) of fully developed muscles during adulthood. Flight muscle degeneration occurs coincident with ovarian growth, which leads to a strong negative correlation between the size of these two organs (Pener 1985, Zera & Denno 1997). Hormonal manipulation in *G. firmus* and other insects strongly points to JH as the regulator of this trade-off (Pener 1985, Zera & Denno 1997, Zera & Cisper 2001). However, as mentioned above, an assessment of the exact mechanisms by which JH regulates the trade-off between ovaries and flight muscles is complicated by the large diurnal change in the JH titer in the flight-capable morph (Zera & Cisper 2001). Endocrine factors other than JH may also be involved in regulating this trade-off. To summarize, energetic and endocrine aspects of life history trade-offs have been extensively studied in species of *Gryllus*. However, the relative contribution of differential allocation of limited internal reserves, antagonistic aspects of hormonal regulation, or other factors, such as limited space within the organism, to the negative association between components of flight capability and ovarian growth is unclear and remains a major challenge to future research.

Drosophila

The distinguishing feature of studies using Drosophila is the range and power of genetic approaches that have been used to investigate life history trade-offs. As one example, artificial or natural selection in the laboratory is especially useful for studying life history evolution and mechanisms underlying apparent trade-offs (Rose et al. 1990, Huey & Kingsolver 1993, Rose et al. 1996, Gibbs 1999, Harshman & Hoffmann 2000a). Selected and control lines are often markedly divergent and can be useful for physiological studies of life history trade-offs, while indirect responses to selection can identify genetically based trade-offs (Rose et al. 1990).

A range of life history trade-offs have been implicated using *Drosophila* selection experiments. For example, selection for a relatively short larval period is correlated with reduced larval viability, diminished adult size, and reduced fecundity (Nunney 1996, Chippindale et al. 1997). Relative to selected lines (i.e., in control lines), an extended period of larval development was correlated with an accumulation of lipid and increased dry weight, as well as increased conservation of larval reserves in young adults (Chippindale et al. 1996, 1997).

The trade-off between extended longevity and early age reproduction has been a focus of numerous physiological-genetic studies. Selection for longevity and late life reproduction consistently produces lines characterized by longer-lived flies with decreased early age fecundity (Rose 1984, Luckinbill et al. 1984, Partridge et al. 1999). Sgro & Partridge (1999) sterilized females using irradiation or by crossing to a dominant sterile mutation, and in both cases they circumvented the age-specific mortality cost of reproduction. They concluded that aging was a function of the damaging effects of earlier reproduction. Underlying delayed early reproduction in one set of selected lines was a decreased rate of early age vitellogenic oocyte maturation (Carlson et al. 1998, Carlson & Harshman 1999). Moreover, there is preliminary evidence for an early age diminution in whole-body ecdysteroid titers in one set of lines selected for longevity and late life reproduction (Harshman 1999).

Differential respiration does not appear to play a role in the trade-off between longevity and early age reproduction. Variable results on respiration rates were obtained using one set of lines selected for longevity (summarized in Rose & Bradley 1998). When respiration was measured in small chambers, Service (1987) found relatively higher respiration rates at young ages in the control (unselected) lines, but not at later ages. However, Djawdan et al. (1996) found no difference between selected and control lines when respiration was measured in cages. When adults from both lines were provided with supplementary yeast, the control line females exhibited a slightly higher metabolic rate than selected line females (Simmons & Bradley 1997). Djawdan et al. (1997) found no difference in respiration rate when the mass of selected and control flies was adjusted by removing the weight of water, lipid, and carbohydrate.

The accumulation of energy storage compounds in flies selected for greater longevity suggests that there could be an energetic basis underlying the trade-off between fecundity and longevity (Service 1987, Djawdan et al. 1996). Djawdan et al. (1996) and Simmons & Bradley (1997) have determined that the selected (long-lived) females store more energy in the body and that the control line females, which are more fecund early in life, allocate much more energy to reproduction. However, energy might not be limiting in the laboratory environment because flies may consume as much food as needed for a given level of reproduction (Rose & Bradley 1998).

Stress resistance has been documented as a correlated response to selection for extended longevity and late-life reproduction. One set of lines selected for extended longevity exhibited desiccation resistance and increased glycogen content, as well as starvation resistance and increased lipid content (Rose 1984, Service et al. 1985). Another set of lines selected for extended longevity did not have substantially increased starvation resistance or desiccation resistance but was clearly resistant to oxidative stress (Luckinbill et al. 1984, Force et al. 1995). Increased oxidative stress resistance might be a consistent response to selection for extended longevity (Harshman & Haberer 2000). An association between longevity and starvation resistance is supported by extensively replicated selection experiments, on each of the traits (Service et al. 1985, Rose et al. 1992). Moreover, selection for reduced longevity was correlated with decreased lipid levels (Zwann et al. 1995). However, selection for extended longevity did not result in significant increased starvation resistance in two selection experiments (Zwann et al. 1995, Force et al. 1995). Selection on the basis of differential adult mortality did not affect starvation resistance as an indirect response to selection, but the response to selection did indicate trade-offs between early fecundity, late fecundity, and starvation resistance that were mediated by lipid allocation (Gasser et al. 2000). Selection for female starvation resistance was conducted using a wild-type stock maintained in the laboratory for approximately 35 generations prior to selection and using relatively large numbers of replicate-selected and control lines (Harshman & Schmid 1998). Selection for female starvation resistance resulted in multiple stress resistance as an indirect response to selection, but increased longevity was not a correlated response (Harshman & Schmid 1998, Harshman et al. 1999).

Relevant selection experiments identify a prospective trade-off between fecundity and adult stress resistance. Selection for increased desiccation resistance using *D. melanogaster* resulted in reduced early age fecundity in one study (Hoffmann & Parsons 1989), but not in another study (Chippindale et al. 1993). Selection for cold resistance in *D. melanogaster* and *D. simulans* was correlated with decreased early age fecundity (Watson & Hoffmann 1996). Selection for female starvation resistance resulted in reduced early age fecundity (Wayne et al. 2001). Lines selected for extended longevity and reverse selection also provide evidence for a negative genetic relationship between fecundity and starvation resistance (Service et al. 1985, Service et al. 1988, Leroi et al. 1994a), although this relationship changed in the course of a long-term selection experiment (Leroi et al. 1994b). A negative relationship between fecundity and ethanol or desiccation resistance was not observed in the reverse selection experiment (Service et al. 1988). Sib analysis revealed a negative genetic correlation between fecundity and starvation resistance (Service & Rose 1985). Phenotypic manipulation experiments also provide evidence for a trade-off between fecundity and stress resistance (Chippindale et al. 1993, Salmon et al. 2001, Wang et al. 2001). Perhaps stress susceptibility associated with reproduction contributes to decreased survival as a cost of reproduction.

There are problems associated with selection in the laboratory (Rose et al. 1990, Harshman & Hoffmann 2000a). Supernumerous correlations among selected traits could be the consequence of strong unrelenting directional selection in the laboratory (Harshman & Hoffmann 2000a). Other artifacts may arise from constraints on normal behavioral options in culture containers (Huey et al. 1991) and from copious food availability in the laboratory (Harshman & Hoffmann 2000a). Moreover, there is substantial variation in the quality of different selection experiments, and there are problems associated with experiments conducted on fly stocks recently derived from the field (Service & Rose 1985, Harshman & Hoffmann 2000a,b, Matos et al. 2000). For a variety of reasons, the indirect responses observed in similar selection experiments are often heterogeneous (Tower 1996, Harshman & Hoffmann 2000a). Consistent indirect responses (robust responses) are most informative with respect to implicating mechanisms underlying life history trade-offs (Harshman & Hoffmann 2000a, Harshman & Haberer 2000).

Another genetic approach has been to use lines of *D. melanogaster* that have been made homozygous for chromosomes isolated from natural populations for life history and physiological measurements (Clark 1989). In this study, there was a positive correlation between viability and fecundity, as well as associations between these traits and metabolic enzyme activities. A caveat is that inbreeding (inbreeding depression) can generate positive correlations among traits because of the pleiotropic effects of recessive deleterious alleles. As another genetic approach, P element mutagenesis has been used to induce mutational variation in longevity, age-specific reproduction, and metabolic enzyme activities (Clark & Guadalupe 1995, Clark et al. 1995). Finally, mutation analysis of life history characters is potentially informative for the study of the physiology of trade-offs (Lin et al. 1998).

Transgenic Drosophila can play an important role in investigating the physiology of life history trade-offs (Tatar 2000). For example, extra copies of a heat shock protein (Hsp70) gene in transgenic *D. melanogaster* confer heat stress resistance and reduced age specific mortality, but also result in decreased larval growth and survival (Tatar et al. 1997, Krebs & Feder 1997, Feder & Hoffman 1999). Stearns & Kaiser (1993) increased the expression of elongation factor EF-1 alpha by introducing an extra copy of the gene. The effects on a trade-off between reproduction and longevity were marginal and varied depending upon the experimental design. However, when enhanced EF-1 alpha expression increased lifespan, it also decreased fecundity.

Lizards

Studies of lizards have been at the forefront of research on life history physiology for over two decades (e.g., Tinkle & Hadley 1975, Congdon et al. 1982, Schwarzkopf 1994, Marler & Moore 1991, Sinervo 1999). Many lizard species are amenable to experimental manipulation and field studies, thus allowing integrated physiological and ecological investigations of trade-offs (Marler & Moore 1991, Marler et al. 1995, Sinervo 1999). Lizards also grow significantly after sexual maturity and thus are a useful vertebrate model to study trade-offs between adult growth and reproduction. Many lizard species also store fat reserves for long periods of time and thus are useful for investigating trade-offs between reproduction and storage. Lizards were the focus of pioneering studies in which detailed energy budgets were constructed in interspecific investigations of life history evolution (reviewed in Congdon et al. 1982). More recently, studies on lizards were among the first to investigate, and currently provide some of the most important information on endocrine aspects of trade-offs (Marler & Moore 1988, Marler et al. 1995, Sinervo 1999, Sinervo et al. 2000).

The negative correlation between egg number and egg size is a classic life history trade-off (Stearns 1992, Roff 1992, Schwarzkopf et al. 1999) that has been documented in a variety of lizard species (Sinervo 1990, Schwarzkopf 1994, Doughty & Shine 1997). However, correlations were derived mainly from uncontrolled and unmanipulated field studies and thus provide little information on underlying physiological mechanisms. In a breakthrough series of studies, Sinervo and colleagues (reviewed in Sinervo 1999) used experimental manipulations to study the proximate mechanisms controlling the trade-off between egg size and egg number in the side-blotched lizard, *Uta stansburiana*. Application of the gonadotrophin, FSH (follicle-stimulating hormone), increased egg number but decreased egg size, whereas ablation of a proportion of the egg follicles resulted in a smaller number of larger eggs. Experimental results were interpreted in terms of competition by the developing eggs for limited yolk or space in the maternal abdomen. These studies were among the first to experimentally investigate the endocrine causes of a classic life history trade-off and to suggest that variation in the titer of, or tissue response to, FSH in field populations may be a physiological cause of the trade-off between egg size and egg number. However, these hormone manipulation experiments need to be interpreted with caution since FSH titers or receptors have yet to be directly measured in individuals of this species.

Phenotypic manipulation allowed Sinervo and colleagues to investigate several aspects of the evolution of the trade-off between egg size and egg number (reviewed in Sinervo 1994, 1999). Lizards of different size produced by endocrine or surgical manipulation were returned to field sites, and their survivorship to adult maturity was monitored. Results showed that the trade-off between egg size and egg number was influenced by natural selection. A morphological constraint on egg size in *Uta* was also identified. Unusually large eggs became lodged in the oviduct or burst upon oviposition in the laboratory (Sinervo & Licht 1991).

Behaviors that enhance current reproduction but that decrease future reproduction are important components of the cost of reproduction. Marler and colleagues (Marler & Moore 1988, 1991, Marler et al. 1995) investigated the endocrine regulation of this type of behavior-based trade-off in the field using the lizard *Sceloporus* *jarrovi*. In this species, testosterone is elevated during the nonbreeding season and functions to elicit behaviors involved in territorial defense (Moore 1986). A comprehensive set of field experiments involving measurement of energy consumption using doubly labeled water, supplemental feeding, and measurement of time-energy budgets showed that lizards with experimentally elevated testosterone (but within physiological levels) had increased activity and reduced survivorship. This increased activity resulted from an increased number of territorial displays and movements, with consequent decreased time spent feeding (Marler et al. 1995). Increased testosterone level was also associated with a higher parasite load (C.A. Marler, personal communication). These and other studies (e.g., Sinervo et al. 2000, Veiga et al. 1998) are important because they identify potential direct negative effects of the hormonal regulation of reproduction and behavior.

Lizard studies were at the forefront of interspecific investigations of life history energetics during the 1970s and early 1980s (reviewed in Congdon et al. 1982). More recent studies have focused on the effect of variation in the thermal environment on seasonal or interpopulational variation in life histories (Dunham et al. 1989, Adoph & Porter 1993, Niewiarowski 2001). However, there have been surprisingly few detailed studies of the energetic correlates of life history variation within populations of lizards. A few studies have focused on variation in energy reserves, growth, and metabolism within populations, especially in the context of the cost of reproduction. For example, metabolic rates measured in the field were higher in reproductive versus nonreproductive females of several species (Nagy 1983, Anderson & Karasov 1988). A number of correlational and experimental studies indicate that a common effect of current reproduction may be the reduction of internal reserves, which impacts future reproduction either by reducing survivorship or by reducing nutrients required for future reproduction (Landwer 1994, Schwarzkopf 1994, Doughty & Shine 1997, 1998, Wilson & Booth 1998). The trade-off between reproductive effort and energy storage in many purely correlational studies may have been underestimated or missed entirely because of the masking effect of variation in storage reserves (Doughty & Shine 1997).

The physiological cost of current reproduction on future reproduction could be mitigated if nutrient reserves are replenished before or during future reproduction. However, field studies indicate that up to 90% of the energy used for egg production comes from fat stores rather than recently consumed food (Karasov & Anderson 1998). Doughty & Shine (1998) also showed that variation in nutrient input affected variation in lipid stores and reproductive output during the next year. Thus, long time lags can occur between variation in nutrient acquisition and variation in reproduction, further complicating physiological studies of trade-offs in the field.

On average, about 30% of growth in lizards occurs after sexual maturity, and fecundity in lizards is correlated with body size (Schwarzkopf 1994). Hence, current reproduction can reduce future reproduction by diverting nutrients away from current growth. Such a trade-off between current reproduction and growth is suggested by increased growth during years in which reproduction does not occur in some lizard species (Schwarzkopf 1993). Landwer (1994) found that *Urosaurus* *ornatus*, in which egg production was experimentally reduced, showed greater growth in the field compared with unmanipulated controls.

Ecological factors such as age-dependent survivorship can have a strong influence on physiological aspects of trade-offs, such as the prioritization of nutrient allocation. For example, short-lived mainland anoles allocated a greater amount of supplemental food to current reproduction, compared with long-lived island anoles which converted supplemental food mainly into fat reserves (Guyer 1988, Schwarzkopf 1994). Tail breakage is an important adaptation for escape from predation in lizards (Dial & Fitzpatrick 1981, Wilson & Booth 1998). Allocation of energy to tail regeneration versus current reproduction in lizards depends upon whether the species is short- or long-lived (Dial & Fitzpatrick 1981, Wilson & Booth 1998). The relative importance of ecological factors such as predation, and physiological factors such as allocation, in the evolution of life history traits such as age-specific fecundity is the subject of debate in lizard studies. Results of various mathematical models have led workers to support either physiological or ecological factors as being of primary importance (Shine & Schwarzkopf 1992, Niewiarowski & Dunham 1994, Shine et al. 1996).

Finally, studies of skinks indicate how lineage-specific attributes can magnify an apparent life history trade-off. In lizards, tail loss allows escape from predators but reduces future reproduction because the tail is an important lipid storage organ. Certain lineages of skinks lack abdominal fat bodies and store nearly 100% of body lipid reserves in the tail. The impact of tail loss is especially pronounced in skinks that lack abdominal fat bodies, reducing clutch sizes 50% to 100% (Wilson & Booth 1998).

Birds

Three ornithologists were the intellectual predecessors of modern life history thinking: Lack, Skutch, and Moreau (Ricklefs 2000a). Lack's insight (Lack 1947, 1954), that clutch size evolves to maximize individual reproductive success, became a cornerstone of life history theory and motivated physiological studies on life histories. Continuing to the present, extensive knowledge about bird demography and intensive field studies provide an important context for physiological studies of life history trade-offs. However, it has been argued that our knowledge of avian life histories is still rudimentary, and thus basic studies of biochemistry and physiology of life history traits and the controlling endocrine mechanisms are badly needed (Ricklefs 2000b). Because of space constraints, this section focuses on two topics: energetics, especially in relation to the cost of reproduction, and immunocompetence, a topic of relatively intense recent study on birds.

Birds have the highest core body temperature of any endotherm (Nagy 1987) and flying birds have size constraints that presumably limit the amount of energy storage (Calder 1984). Thus, it would appear that energetics must play an important role in shaping bird life histories (Walsberg 1983, Paladino 1989, McNab 1997). Birds expend relatively high levels of energy during reproduction and thermoregulation

(Weiner 1992). Energy constraints, which can arise from the competing costs of reproduction, thermoregulation, growth, energy assimilation, and energy assimilation capacity (Karasov 1986, Weiner 1992, Konarzewski 1995, Jackson & Diamond 1996), could be integral to life history evolution. As an alternative, the cost of foraging and the energetic demands of other external activities could be limiting, and various aspects of physiology might simply adjust to meet energetic requirements at any particular point in the life history (Ricklefs 1991, 1996). From another perspective, predation appears to be a major factor in shaping bird life histories (Conway & Martin 2000, Ghalambor & Martin 2000). In general, it is not clear to what degree life histories are defined by endogenous trade-offs and physiological constraints.

Either from observational data or by experimental clutch manipulation, there is evidence for a cost of reproduction in birds (Linden & Moller 1989, Dijkstra et al. 1990, Styrsky et al. 1999). This cost can be manifest in terms of parental survival, future reproduction and/or offspring condition-fitness. The cost of reproduction is often observed as an effect on offspring (Linden & Moller 1989). Egg mass representing the energetic investment of reproduction has an effect on initial offspring growth and development of passerines, but the effect of egg mass often does not extend to older offspring (Styrsky et al. 2000). Other factors that are positively correlated with egg mass could have an extended effect on offspring (Styrsky et al. 2000). In lesser black-backed gulls (*Larus fuscus*), the order of egg laying was correlated with abundance of antioxidants (carotenoid and vitamin E), arachidonic acid, and cholesterol ester fractions in the eggs (Royle et al. 1999). Fat storage could partially underlie the trade-off between reproduction and parental survival, especially in passerines where energy storage reserves tend to be quite limited. Increased fat storage could support reproduction, but there can be a survival cost (Lima 1986, Witter & Cuthill 1993). Specifically, stored fat might incur acquisition and maintenance costs (Houston et al. 1997) as well as flight energetics or agility costs (Rogers & Smith 1993, Gosler et al. 1995).

Overall, metabolism and energy budgets have been the focus of physiological work on the cost of reproduction. Historically, evidence accumulated for an energetic cost of bird reproduction (King 1973, Ricklefs 1974, Drent & Daan 1980). For many species, the preponderance of this cost is due to parental care rather than egg production (Trillmich 1986, Ward 1996). The ecology of some birds can make this cost acute. For example, the low foraging efficiency of two diving petrels (*Pelecanoides urinatrix* and *P. georgicus*) and an auklet (*Aethia pusilla*) results in relatively high daily energy expenditure during the breeding season (Roby & Ricklefs 1986). Parental weight loss is common at the time of brood provisioning, and this loss can reflect energy demands on the parents (Martin 1987). When clutch sizes were experimentally increased during incubation, there was an increase in parental energy expenditure in eight of nine studies, but diminished adult body condition was observed in only two of five studies (Thompson et al. 1998). In the glaucous-winged gull (*Larus glaucescens*), experimental brood enlargement resulted in increased parental reproductive effort, increased loss of weight during the breeding season, and reduced winter survival (Reid 1987). Is the cost of reproduction mediated by energetics? In general, it is conceptually and empirically difficult to demonstrate that an energy budget deficit is directly responsible for the costs of reproduction.

A decline in immunocompetence and potential damage from microbes and parasites could be a physiological cost of reproduction. In general, there is considerable current interest in avian immune function in relation to physiological trade-offs and life histories (Sheldon & Verhulst 1996, Horak et al. 1999, Owens & Wilson 1999). In the collared flycatcher (*Ficedula albicollins*) and other bird species, there tends to be a negative relationship between brood size and immune system indicators (Gustafsson et al. 1994). The allocation of endogenous energy might play an important role in a trade-off between reproduction and immune system function (Apanius 1998). However, immunocompetence can be measured in numerous ways, and it is important to be aware of the assumptions, limitations, and consequences of various methods (Norris & Evans 2000). Moreover, studies relating immunocompetence to fitness and disease resistance or resource limitation in the field are rare (Owens & Wilson 1999, Norris & Evans 2000). One prospect for the future is to directly manipulate immunocompetence (Sheldon & Verhulst 1996) in relation to the cost of reproduction or other life history trade-offs.

Is immune function costly? When a passerine (*Parus caeruleus*) was subjected to cold stress, the increase in daily energy expenditure was associated with decreased antibody responses (Svensson et al. 1998). The energetic cost of the antibody response was estimated to be 8% to 13% of the basal metabolic rate. Although there is direct and indirect support for the hypothesis of a costly immune response (Sheldon & Verhulst 1996), a number of studies have failed to find a significant relationship between energetics and the immune response (Owens & Wilson 1999). Moreover, it has been argued that the energetic cost of immune system function might be relatively low (Hillgarth & Wingfield 1997, Owens & Wilson 1999).

The relative cost of life history traits is relevant to a prospective trade-off with the immune system. Hoglund & Sheldon (1998) argue that allocation to sexual display, which is apparently costly, should be considered in the same manner as allocation to a classic life history trait. A relatively high level of cost for sexual ornamentation could trade-off with immune function (Sheldon & Verhulst 1996, Norris & Evans 2000). Hamilton & Zuk (1982) formulated the idea that the intensity of secondary sexual ornamentation would signal resistance to parasites. There is evidence for positive correlations between sexual ornamentation and resistance to parasites and pathogens (reviewed in Moller 1990, Hamilton & Poulin 1997, Lindstrom & Lundstrom 2000). However, there also is countervailing evidence for a negative relationship, perhaps a trade-off, between sexual ornamentation and infection (Moller 1997, Norris et al. 1994, Richner et al. 1995, Dale 1996, Sheldon & Verhulst 1996). Hormones could play a role in such a trade-off by intensifying sexual display with a concomitant decrease in immune function (Folstad & Karter 1992). Zuk et al. (1995) have shown that testosterone level is negatively associated with leukocyte counts in the red jungle fowl (*Gallus gallus*), but no such relationship was detected in the barn swallow (*Hirundo rustica*) by Saino et al. (1995). However, Saino et al. (1995) found reduced antibody production when testosterone was administered to the barn swallows in the field. No suppression of the avian immune system was observed in a laboratory study of the effects of testosterone on red-winged blackbirds (*Agelaius phoeniceus*) (Hasselquist et al. 1999), nor was there a correlation between elevated testosterone titers and parasite abundance in the same species (Weatherhead et al. 1993). Similarly, Ros et al. (1997) did not find a negative correlation between testosterone titer and antibody production in black-headed gulls (*Larus ridibundus*). In a study on the house sparrow (*Passer domesticus*), testosterone administration appeared to decrease antibody production (Evans et al. 2000). In this study, the suppressive effect of decreased corticosterone was taken into account, and consequently the net effect of testosterone was to stimulate antibody production hypothetically by "dominance influencing access to resources" (Evans et al. 2000). Testosterone administration to captive and field dark-eyed juncos (*Junco hyemalis*) resulted in decreased antibody production and increased corticosterone abundance (Castro et al. 2001). Testosterone could affect immune function indirectly via corticosteroids (Evans et al. 2000, Castro et al. 2001). Corticosteroids have been associated with increased parasite loads (Hillgarth & Wingfield 1997). Gonadal hormones, including testosterone and metabolites, can play a role in controlling adult plumage (Hillgarth & Wingfield 1997). The components of an endocrine mediated trade-off between the immune system and sexual ornamentation have been documented in some studies, and differential resource allocation could play a role in this prospective trade-off.

Avian endocrinology studies have identified mechanisms whereby life history traits are linked. Bird corticosteroids can increase gluconeogenesis and survival under stress conditions, but suppress reproduction and the immune system (Wingfield 1988, Wingfield et al. 1998). Testosterone administered to dark-eyed junco (*Junco hyemalis*) males resulted in physiological changes including accelerated loss of mass, reduced subcutaneous fat, and a delay in the molt (Ketterson et al. 1991, Nolan et al. 1992). Studies on the dark-eyed junco and a diversity of other bird species indicate that testosterone can stimulate mating effort, suppress parental effort, and could be associated with a diminished life span (Ketterson & Nolan 1999). As mentioned previously in this review, hormones often regulate multiple antagonistic processes, and thus are notable candidate mediators of life history trade-offs (Ketterson & Nolan 1992, 1999, Finch & Rose 1995).

SUMMARY AND FUTURE DIRECTIONS

The past decade has seen significant advances in physiological studies of life history trade-offs. With respect to the topic of energetics, the most important advances have been (*a*) the first genetic analyses of energetic components of trade-offs, (*b*) the integration of investigations of nutrient input and allocation, (*c*) development of more sophisticated models of resource acquisition and allocation, and (*d*) more detailed investigations of specific physiological costs associated with life history traits. Advances have largely come about owing to a shift to more focused, comprehensive, and integrated studies.

Although hormones have long been suspected to be key regulators of life history trade-offs (Stearns 1989, Ketterson & Nolan 1992, 1999), only during the past decade have the first detailed endocrine studies of trade-offs been undertaken. These investigations also constitute one of the most significant recent advances in functional studies of life history trade-offs. Thus far endocrine investigations have involved manipulation or quantification of the titers of hormones or the activities of enzymes that regulate hormones, that potentially control life history trade-offs. This approach will almost certainly become more common in the future. Endocrine studies will also likely expand to other important topics, such as investigations of the endocrine regulation of trade-offs at the level of hormone receptors, and ultimately the hormonal control of gene expression.

A central unresolved issue in trade-off physiology is the relative importance of energetic, regulatory, and other (e.g., space) constraints as causes of life history trade-offs. Although energetics has been the primary focus of functional studies of trade-offs, in no case is it certain that the differential allocation of limiting internal resources is the primary cause of a life history trade-off. There is an increasing appreciation that the physiological mechanisms that underlie life history trade-offs are complex and that their elucidation will require a much deeper understanding of basic energetic, regulatory, and structural aspects of organismal function and how these aspects interact.

Molecular genetic and genomic studies of organismal trade-offs, typically in model species, have just begun. It is now possible to study gene regulation in terms of transcription factors and regulatory DNA elements to some degree in any organism. Genomic and cDNA library sequences, microarrays, general transformation procedures, and bioinformatics are “democratizing the genome.” Thus, extension of molecular genetic studies beyond a few model species to many species with life histories of interest will likely constitute an important future development relevant to functional studies of trade-offs.

A potentially important avenue of research includes traits and processes that have not traditionally been investigated in a life history context. For example, oxidative damage may be one of the universal challenges of life on earth and oxidative stress resistance may trade-off with life history characters (Salmon et al. 2001). The cost of acclimation (Hoffmann 1995, Huey & Berrigan 1996) and development (Ricklefs 1979, Lindstrom 1999) are additional examples of topics that could be important in life history studies, but which have received scant attention.

This is an exciting time in evolutionary biology, in which the confluence of methodological and conceptual advances in molecular genetics, development, and physiology will result in an increasingly mechanistic understanding of evolution in model systems and in the diversity of living organisms. In particular, delineation of mechanisms underlying life history trade-offs will allow us to understand how organisms do and can evolve.

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