

The costs of immunity and the evolution of immunological defense mechanisms

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23.1 Introduction

Why we get sick is a complicated question (Nesse and Williams 1996, Stearns and Koella 2008). Immunologists, pathologists, parasitologists, and other practitioners of what have historically been described as the medical sciences have focused almost exclusively on mechanisms of host immune defense and the virulence mechanisms pathogens use to overcome those defenses. For the evolutionary biologist, the focus on proximate mechanism has been supplanted by broader questions concerning why pathogens may evolve to be more or less virulent, or how susceptibility to infectious disease is maintained in populations over time. In many populations successful defense against parasites and pathogens is an important determinant of fitness, and the selection pressure imposed by pathogens is often very strong. The presence of genetic variation for defense in populations experiencing strong directional selection pressure poses an evolutionary problem that we call the “susceptibility paradox”: despite the ubiquitous selective pressure that would seem to favor improved host defense, why is there persistent susceptibility to diseases that have been encountered by host populations for generations?

Solutions to the susceptibility paradox involve understanding how evolutionary forces contribute to and shape genetic variation for traits affecting the host–pathogen interaction. While inbreeding and mutational processes may certainly play a role in

generating susceptible individuals, the broader maintenance of susceptibility in large outbred populations, where selection for resistance should be efficient, suggests that natural selection also acts to maintain disease susceptibility (Wakelin and Blackwell 1988). One possibility is that susceptibility is maintained as a consequence of balancing selection, due either to overdominant selection or from negative frequency-dependent coevolutionary interactions between host and pathogen (Jaenike 1978, Hamilton 1980, May and Anderson 1990, Frank 1991, Lambrechts *et al.* 2006). While examples of balancing selection have been documented (Lively and Dybdahl 2000, Garrigan and Hedrick 2003, Fumagalli *et al.* 2009), the conditions necessary for maintaining balanced polymorphisms are quite stringent and balancing selection seems unlikely to be the sole factor contributing to the maintenance of susceptibility.

More recently, ecological immunologists have begun to explore more nuanced selective hypotheses, adopting a whole-organism perspective when examining the genetic and environmental factors affecting pathogen defense phenotypes (Rolff and Siva-Jothy 2003, Schmid-Hempel 2003, Siva-Jothy *et al.* 2005, Lazzaro and Little 2009). Explicit in this approach is the recognition that pathogen defense is costly and that further improvements in defense may not be adaptive because they correlate negatively, or “trade off” with other components of fitness. While there are obvious advantages of pathogen defense, resistance to infection is certainly

not the sole determinant of fitness. Organisms must also develop properly and in a timely manner and, as adults, find mates and successfully reproduce. In the absence of genetic correlation among these traits, pathogen defense, rates of development, and reproduction would be predicted to evolve to limits determined solely by physical constraints. Empirical observations showing that populations can respond to artificial selection for resistance (Kraaijeveld and Godfray 1997, Fellowes *et al.* 1998, Ye *et al.* 2009), development time (Nunney 2007), and patterns of reproduction (Richardson and Kojima 1965, Holland and Rice 1999, McKean and Nunney 2008) suggest that organisms are limited not by physical constraints, but rather by the patterns of correlation among these fitness-associated traits.

The assumption that organisms are selected to optimally allocate limited resources among fitness-associated traits is a basic tenet of life

history theory and the presence of trade-offs may act as an important limit to adaptation (Stearns 1992, Roff 2002). Trade-offs involving mechanisms of pathogen defense are referred to as the costs of immunity (Kraaijeveld *et al.* 2002, Rolff and Siva-Jothy 2003, Schmid-Hempel 2003, 2005, Siva-Jothy *et al.* 2005), of which there are three types: maintenance costs, deployment costs, and multiple-fronts costs (see Table 23-1). Maintenance costs are the expense of resource allocation toward developing the infrastructure of an immune system and to constitutively expressed (non-induced) immunological mechanisms. Deployment costs are associated with induction of immune mechanisms. Induced immune mechanisms are initiated through the recognition of potential disease-causing agents and result in the production of factors important in mediating defense. Mechanistically, deployment costs could arise

Table 23-1 The evolutionary costs of immunity. Costs can be measured as negative phenotypic or genetic correlation between traits. Evolutionary costs represent genetic correlation and act as potential limits to adaptation. Shown are methods of measuring the evolutionary costs of immunity and representative examples of the measurement of such costs in the literature.

Type of cost	Measurement	Example
Maintenance cost	Correlated responses to selection on defense in fitness-associated traits measured in the absence of infection	Selection for increased resistance to parasitoid wasps saw a correlated decrease in larval competitive ability (Kraaijeveld and Godfray 1997, Fellowes <i>et al.</i> 1998)
	Negative genetic correlation between defense and other fitness-associated traits (measured in the absence of infection)	A negative genetic correlation between resistance to a bacterial infection and fecundity of uninfected individuals in an environment in which food was limiting (McKean <i>et al.</i> 2008)
Deployment cost	Correlated change in the magnitude of the physiological costs of immune induction following selection for increased defense	Direct measurement of changes in deployment costs in selection lines have not been measured; however, changes in patterns of gene expression following selection for increased defense to <i>Pseudomonas aeruginosa</i> are suggestive (Ye <i>et al.</i> 2009)
	Genotype-by-immune status (induced versus uninduced) interaction for fitness-associated traits	Reductions in starvation and desiccation resistance associated with successful parasitoid defense varied among iso-female lines of <i>Drosophila</i> (Hoang 2001)
Multiple-fronts cost	Selection for improved defense against one pathogen or pathogen strain has a correlated decrease in defense against another	Selection for increased resistance to the parasitoid wasp <i>Leptopilina boulardi</i> saw a correlated increase in resistance to <i>Asobara tabida</i> , a result contrary to the prediction under multiple-fronts costs (Fellowes <i>et al.</i> 1999a); significant local adaptation between pathogens and hosts does indicate that divergence in defense may come at a cost of increased susceptibility to other pathogen strains (Lively <i>et al.</i> 2004)
	Negative genetic correlation in defense against different pathogens or host-genotype-by-pathogen-genotype interaction for defense against an array of pathogens	Host-genotype-by-pathogen-clone interaction for <i>Daphnia magna</i> infected with the bacteria <i>Pasteuria ramosa</i> (Carius <i>et al.</i> 2001)

either as a consequence of the reallocation of resources during the induced response or from immunopathology.

The last category of the costs of immunity, multiple-fronts costs, is relatively little studied (Table 23-1). Multiple-fronts costs are trade-offs between the efficacy of defense against diverse pathogens or pathogen strains, such that an increase in resistance to pathogen A results in a concomitant decrease in resistance to pathogen B. Thus, multiple-fronts costs are conceptually distinct from defense being pleiotropically linked to fitness traits, such as reproduction, that are not directly involved in defense. Multiple-fronts costs are required for negative frequency-dependent coevolution between pathogen and host. However, even in the absence of negative frequency-dependent coevolutionary interactions, multiple-fronts costs could act to maintain susceptibility if host populations encounter a heterogeneous microbial community containing species or strains to which mechanisms of defense show such antagonistic effects.

The presence of the costs of immunity ensures that high-fitness genotypes are not necessarily those possessing the greatest pathogen defense, but instead are those making the best compromise between the competing needs for whole-organism lifetime reproductive success. The evidence of such costs, especially those associated with immunological maintenance and deployment, has been thoroughly reviewed elsewhere (Kraaijeveld *et al.* 2002, Rolff and Siva-Jothy 2003, Schmid-Hempel 2003, 2005, Siva-Jothy *et al.* 2005). It is not our goal to simply restate this evidence. Instead we will focus on the growing understanding of the molecular mechanisms mediating such costs.

While much is being learned of costs of immunity in birds and mammals, including the molecular mechanisms mediating these costs (see, for example, Martin *et al.* 2008), we emphasize here research carried out in insects, especially the *D. melanogaster* model system. Our focus on *D. melanogaster* is not merely one of convenience. In the past 30 years, *Drosophila* has emerged as a model for studies of both the mechanisms and evolution of immune function and pathogen defense (Brennan and Anderson 2004, Royet and Dziarski 2007, Ferrandon *et al.* 2007, Lemaitre and Hoffmann 2007, Sackton

et al. 2007, Dionne and Schneider 2008, Lazzaro 2008, Imler and Eleftherianos 2009) as well as for the study of life history evolution (see the many examples cited in Roff 2002).

In this chapter we assess our current understanding of the underlying mechanisms mediating the various costs of immunity. First, we evaluate evidence of trade-offs between reproduction and immunity, and the potential mechanisms mediating the allocation of energy and resources between these competing needs. Next we examine costs associated with the induction of an immune response, and how mechanisms of immune regulation have likely evolved to limit the costs of immunological deployment. Lastly we examine evidence for trade-offs between different components of defense, including trade-offs between resistance and tolerance as well as potential trade-offs in defense against different pathogens. We conclude by offering our view on the future of efforts to elucidate the molecular mechanisms of the costs of immunity.

23.2 Innate immune defense in *Drosophila*

Mechanisms of defense act to limit pathogen-associated fitness costs through two separate but interconnected mechanisms: “resistance” to pathogen establishment and proliferation and “tolerance” of established infections. Operationally, resistance is measured as the inverse of the pathogen load and has been the traditional focus in studies of pathogen defense in animals (Schneider and Ayres 2008). Tolerance limits the fitness impact of a given pathogen load, and is measured as the slope of the reaction norm describing the relationship between variation in pathogen load and fitness, or “health” (Boots 2008, Råberg *et al.* 2009, Schneider and Ayres 2008). In other words, genotypes that suffer greater health consequences of a given pathogen load are less tolerant than genotypes suffering less from a similar load. The importance of tolerance mechanisms has long been understood in the plant pathology literature (reviewed in Råberg *et al.* 2009), but only recently have animal pathologists begun to experimentally examine the importance of tolerance as a mechanism of host defense (Råberg *et al.*

2007, 2009, Ayres and Schneider 2008, Schneider and Ayres 2008).

Both tolerance and resistance mechanisms will act to reduce the fitness impacts of infections capable of successful colonization. However, resistance mechanisms reducing the per-contact rate of pathogenic infection are also vital components of overall defense. In the septic environment inhabited by *Drosophila* there is likely a constant interaction between the host and a host-associated microbial community of natural pathogens, opportunistic pathogens, commensals, and mutualists. Indeed, the first line of defense, acting to limit the per-contact rate of infection, may be niche occupation by native gut microbiota acting to prevent colonization of potential pathogens (Dillon and Dillon 2004). Barrier epithelial tissues are a second line of defense limiting the per-contact rate of infection. These barrier defense mechanisms include physical and physiological mechanisms as well as immune mechanisms constitutively expressed in various epithelial tissues. For example, the production of lysozyme, antimicrobial peptides (AMPs), and reactive oxygen species in the *Drosophila* gut creates a hostile environment that is not conducive for the survival of many microbes (Daffre *et al.* 1994, Hultmark 1996, Ryu *et al.* 2006, 2008). There is both constitutive and induced expression of AMPs in epithelial tissues, including the salivary glands, gut, and male and female reproductive tissues (Ferrandon *et al.* 1998, Tzou *et al.* 2000). The expression of immune mechanisms at barrier epithelia may interact with the native microbiota in providing defense. For example, dysregulation of antimicrobial peptide expression in the *Drosophila* gut can cause changes in the microbiome, resulting in pathology (Ryu *et al.* 2008).

Various active defense mechanisms form the next line of defense against an incidental or pathological breach of barrier defenses. The mechanisms of immunological defense include encapsulation, melanization, phagocytosis, coagulation, the inducible production of antimicrobial peptides, RNAi, and nutrient sequestration, such as the production of iron-chelating transferrin that may act to limit microbial growth. These defense mechanisms have been reviewed elsewhere (Yoshiga *et al.* 1999, Brennan and Anderson 2004, Dunkov and Georgieva

2006, Ferrandon *et al.* 2007, Lemaitre and Hoffmann 2007, Royet and Dziarski 2007, Dionne and Schneider 2008, Stuart and Ezekowitz 2008, Imler and Eleftherianos 2009). To date, research has focused almost exclusively on resistance-promoting defense mechanisms; only recently have researchers begun to examine defense mechanisms mediating tolerance (Boots 2008, Schneider and Ayres 2008, Råberg *et al.* 2009). Perhaps even less appreciated is the role native microbial symbionts may play in defense to more systemic infections. For example, the secondary symbionts *Hamiltonella defensa* and *Serratia symbiotica* aid in resistance of pea aphids to the parasitoid *Aphidius ervi* (Ferrari *et al.* 2004, Oliver *et al.* 2003, 2005) and another, *Regiella insecticola*, provides increased resistance to the fungus *Pandora neoaphidis* (Scarborough *et al.* 2005).

Innate immune mechanisms are phylogenetically ancient and highly effective in their defense against a broad array of viruses, bacteria, fungi, trypanosomes, nematodes, and parasitoids, indicative of a long evolutionary history of interaction with potential pathogens (Danilova 2006). Furthermore, evolutionary genetic analysis has revealed genes involved in immune function to be some of the most rapidly adaptively genes in the genomes of insects and vertebrates alike (Schlenke and Begun 2003, Nielsen *et al.* 2005, Evans *et al.* 2006, Sackton *et al.* 2007, Waterhouse *et al.* 2007, Lazzaro 2008). Yet genetic variation for disease susceptibility within populations remains, presumably due to costs of immunity that act to slow or prevent the evolution of even greater defense (reviewed in Kraaijeveld *et al.* 2002, Zuk and Stoehr 2002, Schmid-Hempel 2003, 2005, Siva-Jothy *et al.* 2005). We now turn our attention to recent research examining the potential mechanisms mediating such costs and how the costs of immunity have likely played an important role in the evolution of immune system function.

23.3 Trade-offs between reproduction and immunity

Perhaps the trade-off most critically important to host fitness is that between immunity and reproduction. It has become increasingly well established, particularly in insect systems, that mating and reproduction negatively impact pathogen defense

through a variety of mechanisms. The mechanisms and costs may vary between sexes, due to differences in mating activity, physiological construction, and interactions with progeny.

Male *D. melanogaster* suffer reduced ability to clear an infection of non-pathogenic *Escherichia coli* after engaging in extensive courting of and copulation with females (McKean and Nunney 2001). This effect can be attributed to energetic expenditure and a simple decrease in the amount of time spent feeding relative to less vigorously reproductive males (McKean and Nunney 2001, 2005). Intense energetic expenditure has also been shown to transiently decrease immune capacity in crickets and other insects (Adamo and Parsons 2006), as well as in humans (Nieman 1999).

Reproduction and immunity also trade-off in female *D. melanogaster*, although through different mechanisms. Despite the fact that mating weakly induces expression of some defense genes (Lawniczak and Begun 2004, Mack *et al.* 2006, McGraw *et al.* 2004, Peng *et al.* 2005, Domanitskaya *et al.* 2007), mated females actually experience a transiently reduced resistance to infection (Fedorka *et al.* 2007, Short and Lazzaro 2010). This post-mating susceptibility does not occur in *D. melanogaster* mutant females that lack germ lines, and depends on the transfer of sperm and seminal fluid proteins by males (Short and Lazzaro 2010). This indicates that the effect is not just due to the act of copulation, but is instead a function of female reproductive physiology and communication with somatic tissue. Similarly, infertile *Caenorhabditis elegans* exhibit an increased resistance to pathogenic bacteria that depends on immunosuppressive signals from the germ line and developing embryos (Miyata *et al.* 2008, Alper *et al.* 2010). Although the current literature is not definitive, there are several lines of evidence supporting the generalized hypothesis that reproductively induced susceptibility to infection is a consequence of the trade-off between energy allocation to reproduction and the need to maintain homeostasis (see Chapter 24 for a broader discussion of metabolically driven trade-offs).

Both immune defense and reproduction are energetically demanding and subject to nutritional availability (see also Chapter 11). In

humans, malnutrition and susceptibility to infection are closely intertwined (Katona and Katona-Apte 2008). Intense athletic activity increases susceptibility to infection in humans, although this effect can be mitigated through carbohydrate ingestion (Nieman 1999, 2008). Energetic expenditure and nutritional deprivation also decreases resistance to infection in *D. melanogaster* and other insects (McKean and Nunney 2001, 2005, Adamo and Parsons 2006), suggesting that energy accumulation and storage are important for resistance. Negative genetic correlation between resistance and fecundity (measured prior to immune challenge) has been observed in *D. melanogaster*, demonstrating the potential for evolutionary costs of immune maintenance. These costs, however, were apparent only in an environment in which adult food availability was limiting. In a nutritionally superior environment the maintenance costs were erased (McKean *et al.* 2008), suggesting that food availability may affect the expression of genetic variation for these traits.

Reciprocally, infection status can impact metabolic state. Severe and chronic infection causes substantial metabolic change in humans (Powanda and Beisel 2003) and insects (Dionne *et al.* 2006, Schilder and Marden 2006). In insects, metabolic phenotypes of infection can include elevation of hemolymph (blood) sugar levels and loss of glycogen and triglyceride stores. This infection-mediated metabolic syndrome is similar to that of mammalian diabetes and is regulated by insulin-like signaling (Dionne *et al.* 2006, Schilder and Marden 2006). In *D. melanogaster*, immune stimulation results in the marked down-regulation of a large number of genes involved in basal metabolism (De Gregorio *et al.* 2001). There is also a complex interaction between immunity and lipid metabolism in vertebrates (Kyriazakis *et al.* 1998, van den Elzen *et al.* 2005) and insects (Mullen *et al.* 2004, Adamo and Parsons 2006). The complete mechanistic basis for the interaction between dietary lipid content and immune performance is not known, but in at least some insects high dietary lipid levels can reduce resistance to infection through depletion of a hemolymph lipid carrier that pleiotropically functions in immune defense (Adamo and Parsons 2006, Adamo *et al.* 2007).

Although the effects of egg production on female metabolic state have not been thoroughly studied in *D. melanogaster*, there is considerable indirect evidence attesting to its substantial energetic requirements. Mating significantly alters expression of metabolic (as well as immune-related) genes in *D. melanogaster* females relative to virgin controls (Innocenti and Morrow 2009). *D. melanogaster* females cease egg production under starvation conditions, and may even apoptose and resorb incompletely developed eggs (Bownes *et al.* 1988, Terashima and Bownes 2004). The fat body, which is the organ primarily responsible both for systemic humoral immunity in response to challenge and for the nutritional provisioning of developing eggs, may be the tissue most acutely involved in mediating the competing demands between reproduction and immunity.

The insulin/insulin-like growth factor (IGF) and juvenile hormone (JH) endocrine signals are prime candidates for mediating a physiological trade-off between immunity in fecundity in insects (see Chapter 13 for further discussion of the role of endocrine signaling in life history trade-offs). As mentioned above, chronic infection in insects can result in an insulin-mediated metabolic syndrome (Dionne *et al.* 2006, Schilder and Marden 2006). IGF signaling also directly influences egg production by regulating JH levels, which are reduced 80% in insulin insensitive mutants (Tatar *et al.* 2001b). JH, which is activated in females following mating by the male seminal protein, sex peptide (Moshitzky *et al.* 1996, Innocenti and Morrow 2009), initiates yolk protein production and vitellogenesis in the fat body (Bownes 1982). Ectopic provision of JH can stimulate yolk protein production and egg maturation under what would otherwise be starvation conditions (Bownes *et al.* 1988). At the same time, JH is itself a strong inhibitor of insect immune systems under standard nutritional conditions (Rolff and Siva-Jothy 2002, Flatt *et al.* 2008a). In an exciting development, the expression of AMP genes was shown to be directly induced by FOXO under starvation conditions and in the absence of infection (Becker *et al.* 2010). This regulation is independent of the Toll and Imd signaling pathways, which regulate canonical inducible AMP expression, and provides one potential mechanism for metabolic modulation of immune activity.

Although it has not been experimentally demonstrated, it is in principle possible that genetic polymorphism in insulin-like signaling or reproductive endocrinology could mediate evolutionary trade-offs between immunity and reproduction. *D. melanogaster* artificially selected for longevity and late-life fecundity show correlated responses of decreased metabolism and increased energy storage through fat accumulation (Djawdan *et al.* 1998), very similar to the phenotype observed in mutant flies with decreased insulin signaling (Broughton *et al.* 2005, Giannakou *et al.* 2007). Common genetic variation in pleiotropic regulators of immunity and other fitness traits, including reproduction and metabolism, could provide an evolutionary basis for life history trade-offs involving immune defense.

23.4 Deployment costs, tolerance, and the evolution of immune regulation

The very fact that some defense mechanisms are inducible suggests that their constitutive expression would be costly (Harvell 1990, Frost 1999). A number of studies have now demonstrated significant costs associated with the induction of immune defense mechanisms in both vertebrate and invertebrate systems (reviewed in: Kraaijeveld *et al.* 2002, Zuk and Stoehr 2002, Schmid-Hempel 2003, 2005, Siva-Jothy *et al.* 2005). In this section we discuss two important issues concerning the evolution of the costs of immunological deployment and the mechanisms mediating those costs. First, we argue that the evolution of mechanisms for actively down-regulating immune responses has come about as a consequence of natural selection favoring genotypes with reduced deployment costs. Therefore, understanding the mechanism of immune regulation provides insight into the mechanisms specifically evolved to mitigate the costs of immunological deployment. Second, we discuss the need to demonstrate that populations exhibit genetic variation in the physiological cost of immunological deployment in order to understand whether such costs may affect the evolution of defense.

For many of the same reasons that immune responses have evolved to be inducible as opposed to constitutive, we predict that selection will favor

the eventual termination of the induced state. The null hypothesis, which does not require the action of selection favoring termination, is that there is a passive diminution of the induced state arising simply as a consequence of the gradual elimination of immune-inducing agents. Alternatively, the diminution of the induced state could arise as a consequence of active down-regulation (Schneider 2007). We predict active down-regulation will evolve if:

- future encounters with the pathogen are variable and unpredictable
- the continued expression of the defense is costly
- more rapid termination of the response, compared to passive diminution, reduces deployment costs without drastically affecting the efficacy of defense.

There is now abundant evidence that active negative regulation of immune responses have evolved in both vertebrates and invertebrates (Schneider 2007, Serhan and Savill 2005). Negative regulators bring about the resolution of induction of both the Toll and Imd pathways (Aggarwal and Silverman 2008). For example, *wntD* is a gene in the Wnt gene family that has been found to inhibit the translocation of the NF- κ B transcription factor, Dorsal, into the nucleus (Gordon *et al.* 2005). Knockout mutants for *wntD* show dramatically increased constitutive and induced expression of the antimicrobial peptide, diptericin. Paradoxically, while these mutants show increased antimicrobial peptide expression they appear more susceptible to infection by both *Micorococcus luteus* and *Listeria monocytogenes* (Gordon *et al.* 2005, 2008). The *wntD* mutants also show increased expression of the immune-induced gene, *Edin*, a gene of unknown function but whose expression is required for resistance to *L. monocytogenes* infections. Interestingly, over-expression of *Edin* using the UAS/Gal4 system also results in reduced survival following infection, suggesting that this gene is at least partially responsible for the observed cost of immune-induced pathology (Gordon *et al.* 2008). The precise cause of the observed pathology, due either to disruption of energy reallocation during the immune response or perhaps the immune defense attacking host tissues, is unknown.

The transcription factors AP-1 and STAT appear to be inhibitors of the Imd-pathway NF- κ B transcription factor Relish, acting to form complexes that replace Relish at promoter regions and preventing further transcription (Kim *et al.* 2005, 2007). Mutation in these genes results in increased expression of antimicrobial peptide genes such as Attacin A. Similar to *wntD* mutants, the over-expression of Relish target genes resulted in an increased rate of clearance of *E. coli* but a more rapid death of flies following infection (Kim *et al.* 2007). Again, whether this immune-induced pathology results from the disruption of changes in energy balance during the immune response or due to immunopathology is not known. Whether mutations in these negative regulators of induced immune responses affect deployment costs in other fitness-associated traits, such as fecundity, has to date not been investigated.

The discovery of these and other negative regulators of induced immunity suggest that a significant portion of the evolution of immune systems and immune responses may be toward the mitigation of costs associated with the activation and deployment of the mechanisms of defense. This would include not only the active regulation of the transcriptional response discussed here but also in the localized containment of inflammation to limit tissue damage (e.g., Sadd and Siva-Jothy 2006), and perhaps even the evolution of the various mechanisms of immunological memory, which would act to reduce deployment costs upon encountering the same pathogen.

Our view of the importance of deployment costs in shaping the evolution of immune function has important implications for discussion of the mechanisms mediating tolerance to infection in *Drosophila* and other organisms. Schneider and Ayres (2008) have defined three classes of tolerance mechanisms based on the effect the tolerance mechanism has on resistance. Class I mechanisms are typified by effector molecules causing immunopathology. The constitutive or induced expression of such molecules may act to increase resistance, but will decrease tolerance compared to molecules better able to target non-self entities without collateral damage to self. Class II mechanisms are typified by regulators with pleiotropic effects on both resistance and tolerance.

Such regulators enhance resistance by increasing the strength or duration of an immune response but may act to decrease tolerance to infection if these immune responses have immunopathologic consequences or greatly disrupt energy balance. The examples we have provided of the negative regulation of immune responses in *Drosophila*, by molecules such as WntD, AP-1, and STAT, all fall into this second category, and indeed research has indicated that mutations in these genes act to increase resistance but negatively affect the fly because of decreased tolerance. In our view, these first two classes of tolerance mechanism simply reflect the costs of immunity.

The third class of tolerance mechanisms described by Schneider and Ayers (2008) are those that can be separated from resistance mechanisms. Examples include detoxifying enzymes that “clean up” toxins produced by the host or pathogen during infection, genes involved in energy reallocation during the immune response, mechanisms preventing physiological damage, and repair mechanisms. Certainly the reallocation of energy as a consequence of immune system induction is at the heart of how we think about the costs of immunological deployment. Other mechanisms promoting tolerance in a resistance-independent manner may contribute to the costs of defense, but these costs are not necessarily a direct consequence of the expression of resistance mechanisms, as is the case for class I and class II tolerance mechanisms.

Our hypothesis that active down-regulation of immune responses is adaptive assumes that ancestral populations possessed genetic variation in immunological cost of deployment upon which natural selection could act. Whether contemporary populations possess such variation is a little-studied question, but one of vital importance if we are to understand the potential for future evolutionary change in deployment costs and the contribution of such costs to the maintenance of disease susceptibility. The evolutionary costs of immunological deployment may be evaluated in two ways. First, using standard quantitative genetic designs, a significant genotype-by-immune status interaction, comparing naïve and immune-induced individuals, would indicate that the population possesses genetic variation in the physiological cost of deployment upon

which selection could act. An alternative would be to evaluate whether there has been evolutionary divergence in the physiological cost of deployment following experimental evolution for increased defense. In both types of experiment, it is necessary to evaluate the physiological cost of deployment using non-infectious immune inducers so that the costs of deployment can be distinguished from those costs caused by the pathogen itself.

Because of the relative ease of experimental induction of the immune system, there are many examples, in both vertebrates and invertebrates, of physiological costs of deployment (reviewed in: Kraaijeveld *et al.* 2002, Zuk and Stoehr 2002, Schmid-Hempel 2003, 2005, Siva-Jothy *et al.* 2005). However, there is a great paucity of studies examining evolutionary costs of deployment, which evaluate whether genotypes vary in the physiological cost experienced. Flies having successfully defended themselves against the parasitoid wasp *Asobara tabida* are smaller and have reduced fecundity, indicating a significant physiological cost of immune deployment (Fellowes *et al.* 1999b). In a study examining whether deployment costs vary among genotypes, successful defense against attack resulted in reduced desiccation and starvation resistance, and the magnitude of this cost varied among iso-female lines (Hoang 2001). It should be noted, however, that in this type of experiment it is impossible to distinguish the costs of deployment from costs arising from the activities of the wasp itself. We recently examined the evolutionary costs of deployment in response to heat-killed bacteria, which would therefore control for confounding costs associated with pathogenicity, and found more equivocal results (McKean *et al.* 2008). None of the cited studies have attempted to elucidate potential underlying genetic mechanisms. Nonetheless, where evolutionary costs of immunological deployment are found, the logical next experimental step will be to evaluate whether polymorphisms in pathways responsible for regulation of immune responses are associated with variation in the physiological costs of deployment experienced by different genotypes.

In addition to active negative regulation of immune responses, there may be coordinated changes in other physiological systems during an immune response that can reveal mechanisms of

deployment costs. The use of microarray technology, allowing researchers to examine genome-wide changes in patterns of gene expression, is likely to be an important tool in understanding the mechanisms underlying deployment costs. This is well illustrated in a recent study conducted by Ye *et al.* (2009).

Ye *et al.* (2009) artificially selected for increased resistance to the bacterial pathogen, *Pseudomonas aeruginosa*. In the three replicate populations, defense increased from ~15% survival after infection to ~70% survival in 10 generations of selection. Correlated decreases in female longevity and egg viability were observed in uninfected flies from the selection lines, compared to controls, indicating evolutionary costs of immunological maintenance. The researchers then examined evolved changes in patterns of gene expression following infection using whole-genome microarrays. The experimental design did not include a comparison of expression patterns in uninfected control and selection lines, which means that it is impossible to determine if the observed differences are due to evolved changes in the induced transcription of genes following the challenge, or if the changes represent evolved changes in the constitutive expression (or elements of both). Nonetheless, a number of interesting patterns do emerge, including the fact that genes in both the Toll and Imd pathways, as well as genes involved in phagocytosis, evolved significantly greater expression in the selection lines (Ye *et al.* 2009).

There are, however, a number of genes that evolved decreased expression in the selection lines. Overall there were 110 genes showing significant reductions in expression in at least two of the selection lines and 67 which evolved reduced expression evolved in all three lines. We obtained this list of genes from the authors in order to determine whether the function of these significantly down-regulated genes may provide clues associated with potential costs of immunity. First, we averaged the p-values of the three comparisons of control and selection lines and rank-ordered the 67 genes showing evolved decreases in expression. The gene showing the most consistent evolved reduction in expression was Chorion protein 15 (average p-value = 8.52×10^{-7}). This gene is important for eggshell

formation and is expressed late during the process of oogenesis (Cavaliere *et al.* 2008). A previous microarray analysis of induced expression following infection with *P. aeruginosa* did not indicate chorion protein 15 was down-regulated following infection (Apidianakis *et al.* 2005), raising the interesting possibility that evolved reductions in the constitutive expression of this gene may contribute to the observed maintenance cost of reduced egg viability in the selected lines.

We also examined whether the 110 genes that had evolved significant reductions in expression could be assigned to specific biological processes based on gene ontology terms that were over-represented (enriched), using the functional annotation clustering tool in the bioinformatic resource DAVID, the database for annotation, visualization, and integrated discovery (Dennis *et al.* 2003, Huang *et al.* 2007, 2009). Using the highest stringency for the DAVID fuzzy clustering, we found genes involved in chitin metabolism to be over-represented in this gene list (enrichment score = 3.5, where scores greater than 1.3 are considered to be “interesting”). We found similar results when the list of 67 genes that had evolved reduced expression in all three selection replicates was submitted to DAVID. The biological significance of decreased chitin metabolism is unknown, as is whether or not the evolutionary change was in the constitutive or induced expression of the genes. Regardless, the combination of experimental evolution and microarray analysis will undoubtedly prove to be a rich source of hypotheses for further research concerning the molecular mechanisms mediating evolutionary trade-offs.

23.5 Multiple-fronts costs of immunity

Multiple-fronts costs of immunity arise when increased defense against one type of pathogen or pathogen strain has a correlated decrease in defense to another. Such costs are very little studied, and in *D. melanogaster* the two studies examining such costs have failed to find supporting evidence. In the first study, selection for increased resistance to the parasitoid wasp *L. boulardi* had a correlated increase in resistance to *A. tabida*, while selection for increased resistance to *A. tabida* saw no change in resistance to

L. bouhardi (Fellowes *et al.* 1999a; see Table 23-1). In the other, pairwise correlation coefficients for resistance to four different bacterial pathogens (*S. marcescens*, *P. burhodogranaria*, *E. faecalis*, and *L. lactis*) tended to be nonsignificantly positives across a set of 95 inbred lines (Lazzaro *et al.* 2006). There is mechanistic evidence that suggests that multiple-fronts costs may exist in insects, but that these are based in antagonisms between different components of the immune system. For instance, in the Egyptian cotton leafworm *Spodoptera littoralis*, humoral antibiotic activity is slightly negatively correlated with the number of circulating hemocytes, which may be involved in phagocytosis and whose abundance is positively correlated with phenoloxidase activity (Cotter *et al.* 2004). Hemolymph antibacterial activity and phenoloxidase activity have also been negatively correlated in bumblebees (Moret and Schmid-Hempel 2001, Wilfert *et al.* 2007) and the cabbage looper *Trichoplusia ni* (Freitak *et al.* 2007). As different arms of the immune system are differentially important in resistance to distinct pathogens, trade-offs among immune system arms can be taken to suggest that multiple-fronts costs probably exist.

Intriguingly, there are multiple instances of loss-of-function mutations in immune-related genes that have conflicting effects on defense against different microbial pathogens (Dionne and Schneider 2008). For example, loss-of-function mutation in the TNF family ligand, *eiger*, increases *D. melanogaster* defense against *S. typhimurium* and *M. marinum* but results in reduced defense against *S. aureus*, *E. faecalis*, *S. pneumoniae*, *B. bassiana*, and *B. cepacia* (Brandt *et al.* 2004, Schneider *et al.* 2007). Similarly, inactivation of insulin signaling in chico mutants increases *D. melanogaster* defense against *E. faecalis* and *P. aeruginosa* (Libert *et al.* 2008), but such inactivation reduces defensive capabilities in infections with *M. marinum* (Dionne *et al.* 2006). Lastly, loss-of-function mutation in serine protease 7 (CG3066) has complex effects on the defense of *D. melanogaster* against a panel of pathogens, where the mutation increases resistance to *S. pneumoniae*, decreases resistance to *L. monocytogenes* and *S. typhimurium*, increases tolerance but decreases resistance to *E. faecalis*, decreases tolerance but increases resistance to *B. cepacia*, and lastly had no effect on resistance or tol-

erance to infection with *E. coli* (Ayres and Schneider 2008). The examination of pathogenic outcomes across a broad array of pathogens and genetic mutants demonstrates the complexity of innate immune function and indicates potential molecular mechanisms mediating trade-offs in defense against different pathogens. It remains untested but fully expected that naturally occurring genetic variation has similar pleiotropic effects on the outcome of infections with these different pathogens.

23.6 Future directions

Studies of life history evolution, including the costs of immunity, have proceeded largely without understanding of the physiological and genetic mechanisms mediating trait variation and trade-offs (Roff 2007b). Indeed, our understanding of the costs of immunological maintenance and deployment has advanced almost exclusively without reference to underlying mechanisms. This stands in stark contrast to our functional understanding of immunological defense, where an incredible amount is known concerning mechanism (Brennan and Anderson 2004, Ferrandon *et al.* 2007, Royet and Dziarski 2007, Dionne and Schneider 2008, Imler and Eleftherianos 2009). The detailed understanding of the molecular mechanisms of immunological defense is a testament to the power of the reductionist research paradigm of the biomedical sciences, but this reductionist approach has itself come at a cost, neglecting the whole-organism perspective that can provide insight into how the competing demands of development, reproduction, and pathogen defense may contribute to the maintenance of disease susceptibility. Recognizing the importance of the costs of immunity in determining patterns of immune function and the pathogenic outcomes of infection requires a reappraisal of what is meant by effective defense and an evaluation of the heuristic value of exclusively reductionistic approaches (Little *et al.* 2008).

We have identified a number of potential molecular mediators of the various costs of immunity, including hormonal mechanisms, insulin signaling, negative regulators of immune induction, changes in global patterns of gene expression, and genes showing antagonistic pleiotropic effects on patterns

of defense against different pathogens. What is missing is an explicit test of the hypothesis that polymorphism in these various mechanisms promotes the observation of evolutionary trade-offs (i.e., negative genetic correlation) that could act to slow the adaptive evolution of greater immune defense. In addition to analysis of how polymorphism in these particular mechanisms affects the observation of the costs of immunity, we suggest three areas of research that we feel will be important as the field moves forward.

First, it is becoming clear that genotype-by-environment interactions may affect the magnitude or even appearance of the costs of immunity. For example, the maintenance cost of reduced larval competitive ability associated with selection for resistance to parasitoid wasps was only observed in a high-density larval environment (Kraaijeveld and Godfray 1997, Fellowes *et al.* 1998). Likewise, an evolutionary trade-off between fecundity and resistance to a bacterial pathogen was only observed in an environment in which food was limiting (McKean *et al.* 2008). Even host-genotype-by-pathogen-genotype interactions may vary in different environments, although such three-way interactions have been little studied (Vale and Little 2009). Such environmental heterogeneity may itself act to maintain disease susceptibility (Lazzaro and Little 2009). Moving life history analysis forward, it seems that researchers should be very aware of the environmental conditions under which they are carrying out their experiments and report them, including the density, temperature, sex of the study organism, whether individuals were kept in same-sex or mixed sex conditions, the time of day immune challenges were carried out, the infective dose of immune challenge, and the food availability. Ideally, the impact of variation in these and other environmental variables on the costs of immunity and the pathogen-host interaction will continue to be investigated. One sobering lesson is that the strong effect of environmental variation on the observation of the costs of immunity may make it difficult to infer the importance of such costs in nature from experiments carried out in a laboratory setting.

Second, we know very little of the totality of interactions between hosts and their associated microbial community. As already mentioned, this

community is composed of natural pathogens, opportunistic pathogens, commensals, and mutualists, each of which poses unique problems influencing the evolution of immune function and potential costs associated with that evolution. For example, if the vast majority of interactions between hosts and the microbial community are not with natural pathogens capable of causing disease, then we may expect immune responses to be tightly regulated so that potential threats are dealt with quickly, reducing potential deployment costs. Furthermore, the presence of microbial mutualists promoting defense through either niche occupation or other means likely pose a significant problem to immune defense and its evolution. It is conceivable that evolutionary increases in the expression of immune defense mechanisms against various natural pathogens may come at a cost of adversely affecting the community of mutualists and commensals that themselves provide some protection. Indeed, under normal conditions there appears to be a delicate balance between NF- κ B mediated transcription of antimicrobial peptides and the repression of expression by the homeobox transcription factor Caudal. Knocking down Caudal expression by RNAi in *D. melanogaster* in increased antimicrobial peptide production and a pronounced change in the community of bacteria found in the gut, causing pathology in the flies (Ryu *et al.* 2008). In other words, the costs of immunity could be manifest in part through the effect of evolutionary changes in patterns of defense on the community of mutualists and commensals associated with the host.

Lastly, the analysis of the molecular mechanisms mediating the costs of immunity have for the most part ignored developmental changes that could lead to the observation of trade-offs. It seems highly likely that, especially for maintenance costs, decisions concerning the allocation of resources toward the competing needs of developing an immune system and the development of other structures that affect fitness may be made early on. For example, the increased resistance to the parasitoid wasp *Asobara tabida* appears to be due to a two-fold increase in the number of circulating hemocytes in the larvae (Kraaijeveld *et al.* 2001). Kraaijeveld *et al.* (2001) have hypothesized that the mechanism promoting the observed cost of reduced larval competitive ability in the selected lines was due to an evolutionary change

in the allocation of resources toward hemocytes versus toward jaw muscles, an allocation decision that would have affected developmental trajectories very early in development. The developmental signals mediating these allocation decisions, and therefore leading to the observation of maintenance costs, are completely unexplored.

23.7 Summary

1. Given the presumed benefits of improved pathogen defense, the continued maintenance of disease susceptibility poses an evolutionary problem that we call the "susceptibility paradox."
2. The costs of immunity are manifest as trade-offs between defense and other components of fitness and include maintenance costs, deployment costs, and multiple-fronts costs (Table 23-1). The presence of such costs may impose limits on immune defense evolution and thus act to maintain disease susceptibility and provide a solution to the susceptibility paradox.
3. Trade-offs between defense and reproduction may result from the dependence of both processes on nutritional and metabolic stores. This suggests that metabolic genes or metabolism-related endocrine signals may pleiotropically link reproduction and immunity, and that variation in these genes may underlie observed trade-offs.

4. Deployment costs may arise from energy reallocation or immunopathology. We argue that such costs are intimately associated with mechanisms of immune regulation and that negative regulators of immunity have evolved specifically to reduce deployment costs.

5. Very little is known of the potential evolutionary costs of deployment. Should, however, genotypes vary in the physiological cost of deployment experienced, then polymorphism in negative regulators of immune induction become obvious candidates mediating these evolutionary trade-offs.

6. Multiple-fronts costs are manifest as trade-offs in defense against different pathogens and have been little examined. Some studies have found negative genetic correlation between different components of the immune system, suggestive of such costs. Recent genetic studies have identified loss-of-function mutations with antagonistic pleiotropic effects on defense. It is unknown if naturally occurring genetic variation is similarly shaped by such antagonistic effects.

7. The field of ecological immunology and the study of trade-offs associated with the costs of immunity is a relatively recent development in evolutionary ecology. There is still a tremendous amount to be learned concerning the molecular mechanisms mediating the costs of immunity and how such costs affect the evolution of immune defense.

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