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An evolutionary perspective on conflict and compensation in physiological and functional traits

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Abstract Physiological and functional traits, especially those related to behavior and whole-organism performance capacities, are subject to a variety of both parallel and opposing natural and sexual selection pressures. These selection pressures show considerable interspecific variation, shaping contemporary behavioral and functional diversity, but the form and intensity of selection on physiological and functional traits can also vary intraspecifically. The same suites of traits can experience quite different selection pressures, depending on the sex or age of a given individual, as well as the presence and nature of alternative reproductive strategies and tactics. These inter- and intra-locus genetic conflicts have potentially important consequences for the evolutionary trajectories of traits subject to them. Consequently, any intraspecific conflicts which could displace traits from their selective optima in certain classes of individuals relative to others are expected to result in selection for mechanisms to compensate for deviation from those optima. Such conflicts include interlocus sexual conflict, intralocus sexual conflict, and interacting phenotypes, as well as conflict within a sex. In this paper, we consider the evidence for, and implications of, such conflicts for physiological and functional traits in diverse taxa, including both vertebrates and invertebrates, and evaluate the various mechanisms, ranging from behavioral and mechanical to energetic and genetic, enabling compensation. We also discuss how pre- and post-mating conflicts, as well as interacting phenotypes, might affect the evolution of behavior and physiological and functional traits. Investigators that seek to understand the links among behavior, morphology, physiology, and function should consider such conflicts [*Current Zoology* 60 (6): 755–767, 2014].

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The interests of any two interacting individuals are seldom identical. Such interactions therefore harbor the possibility of conflict, even in situations where the individuals involved share much of the same genome and are engaged in apparently mutually beneficial activities, such as reproduction. The study of these evolutionary conflicts can be traced back to the seminal work of Trivers (1972) and Parker (1979), and has subsequently been extended to a variety of different ecological and evolutionary contexts (Arnqvist and Rowe, 2005; Chapman, 2006; Haig, 2010). These conflicts may have important implications for the evolutionary trajectories of traits that are either directly involved in such interactions, or that are indirectly affected by the interaction outcomes. More explicitly, conflicts between the sexes and within a sex create the potential for selection that can drive divergent and complex intraspecific responses to that selection (Hosken et al., 2009). Work on such conflicts has historically been focused on select traits that are closely related to reproduction and fitness (Bonduriansky et al., 2008), but a result of this focus is an arguable neglect of many other aspects of the phenotype that might be subject to or influenced by conflict. Any trait that influences fitness and has genetic (or phenotypic) correlations with other traits, or a genetic correlation between the sexes, has the potential to be influenced by, or create, genomic conflict. Important examples are the many functional and physiological traits that are either themselves the target of conflict or are otherwise linked to traits subject to various kinds of conflict (Sinervo et al., 2000; Sinervo and Calsbeek, 2003; Irschick et al., 2008; Lailvaux et al., 2010; Careau and Garland, 2012). For example, there is intraspecific variation in selection on functional traits (Irschick et al., 2008), as well as ontogenetic changes in selection on a single trait (Irschick and Lailvaux, 2006). Sprint speed, for instance, is neither a determinant of survival in all age classes of collared lizards (Husak, 2006), nor is it equally important to reproductive success in adult males and females (Husak et al., 2006, 2008). The functional traits important for male contest success can also change over ontogeny, as in green anole lizards, where bite-

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force performance replaces jumping performance in importance as males age (Lailvaux et al., 2004). Such intraspecific variation in selection on the same suites of traits results in conflict because of genetic correlations among traits, leading those in conflict (males versus females and/or individuals within a sex) to deviate from fitness optima (Cox and Calsbeek, 2009; Lailvaux et al., 2010). Despite the potential for widespread evolutionary conflict, the majority of the literature on such conflicts has tended to focus primarily on sexual conflict (e.g., Arnqvist and Rowe, 2005; Bonduriansky and Chenoweth, 2009; Cox and Calsbeek, 2009) even though genomic conflicts can occur within a sex and in traits other than those associated with sexual conflict.

Physiological and whole-animal performance traits are important in a number of fitness-related endeavors, including during interactions with other individuals. Such traits are typically the end result of integration of multiple body systems and traits at lower levels of biological organization. Thus, selection on these integrated functional traits shapes not only the functional traits themselves, but also the lower-level traits that underlie them (Bartholomew, 1958; Huey and Stevenson, 1979; Arnold, 1983; Pough, 1989; Bennett and Huey, 1990). Traditionally, such functional traits have been studied relatively independently of “behavior” (Pough, 1989; Garland and Losos, 1994), though this distinction is beginning to decline (Husak et al., 2009; Careau and Garland, 2012). Although “performance” is often characterized as a laboratory measure, our broader use of performance as a measure of accomplishing an ecologically relevant task includes most measures of what behavioral ecologists and physiologists would consider “behavior” (see also Husak et al., 2009; Lailvaux and Husak, 2014). In short, behavior, no matter how defined, is constrained by underlying physiological and functional traits (Arnold, 1988; Garland and Losos, 1994; Careau and Garland, 2012) and thus is susceptible to tradeoffs and conflict just as its underlying morphological and physiological underpinnings are, especially in those cases when lower-level traits are involved in multiple higher-level traits (e.g., aerobic capacity is important to locomotor endurance, foraging ability, and dynamic displaying, among other things; Brandt, 2003). This multiple utility of certain traits can in some cases lead to linked traits evolving due to similar or opposing selection. Phenotypic traits, whether they are behavioral, functional, or physiological, are integrated and thus interact in complicated ways.

In this paper, we review the concepts of genetic and sexual conflicts, and evaluate the literature on intra-specific functional and physiological trade-offs from this perspective. Specifically, we consider how different types of conflict might influence the evolution of physiological and performance traits in the context of inter-individual interactions (Table 1). As this is a selective review, we do not focus on the multitude of inter- and intra-locus sexual conflict studies that have been the focus of several reviews (e.g., Arnqvist and Rowe, 2005; Chapman, 2006; Bonduriansky and Chenoweth, 2009; Cox and Calsbeek, 2009). Instead we focus on inter-sexual conflict involving physiological and functional traits, as well as intrasexual conflict on those same types of traits, and the evolution of compensatory traits. We identify several avenues for future research that could prove fruitful in understanding the evolutionary and behavioral consequences of intra-specific conflict and compensation on whole-animal function.

2 Interlocus Sexual Conflict

The potential for interlocus sexual conflict exists wherever the optimal outcome of a male-female interac-

Table 1 Definitions of key terms discussed in the paper

Term	Definition	Reference
Interlocus sexual conflict	Antagonistic selection on different alleles in each sex, resulting in coevolutionary 'arms races' or displacement of one or both sexes from its phenotypic optimum due to selection on the other sex.	Anrqvist and Rowe, 2005.
Intralocus sexual conflict	Displacement of one or both sexes from its phenotypic optimum due to antagonistic selection on the same alleles in each sex.	Bonduriansky and Chenoweth, 2009.
Indirect genetic effect	A genetic effect of an individual on the phenotypic trait of another individual.	Griffing, 1967; Moore et al., 1997; Bijma 2013.
Interacting phenotype	Phenotype resulting from the interactions between two individuals, as well as the expression of those individuals’ genes.	Moore et al., 1997; Wolf et al. 1999; McGlothlin et al. 2010.
Alternative reproductive tactics	Intraspecific variation in male and female reproductive behavior within a population.	Gross, 1996; Oliveira et al., 2008.
Evolutionary compensation	Phenotypic change to reduce costs of another trait, such as an exaggerated ornament or signal.	Møller, 1996; Husak and Swallow, 2011.

tion is different for the average male and the average female. A hallmark of interlocus conflict is that the outcome of the interaction of interest is determined either by different traits in each sex, or, more generally, by traits associated with different loci in males and females. This frequently results in suites of sexually antagonistic, interacting adaptations to bias the outcome of that interaction in favor of one sex or the other. Indeed, Parker (1979, 1983) predicted the evolution of unresolvable conflict, and eventual coevolutionary "arms races" between males and females. Subsequent work has borne out this prediction in a diversity of taxa (reviewed in Arnqvist and Rowe, 2005).

Interlocus sexual conflict can occur over any number of traits related to reproductive success, such as mating or remating rate, fertilization efficiency, parental investment, or even the decision of whether or not to mate at all (Trivers, 1972; Parker 1979; Rice, 1996; Rice and Chippindale, 2001; Arnqvist and Rowe, 2005; Rice et al., 2006). These conflicts levy costs, usually asymmetrically on one sex relative to the other, in terms of low mate quality, loss of foraging opportunities, and costs of resisting matings, amongst others. The costs of resisting mating are a common feature of animal mating systems, and have led to the characterization of the sex with the higher potential rate of reproduction (usually males) as the "persistent" sex, and that with the lower (usually females) as the "resistant" sex (Arnqvist and Rowe, 2005). The costs of persistence and resistance are especially pertinent from a functional and physiological perspective. Females are frequently reported to vigorously resist costly and unwanted mating attempts, and may suffer serious injury or death whilst doing so. In the dungfly *Sepsis cynipsea*, for example, males attempting to copulate will use their forelimbs to clasp females during mating, and females may resist by attempting to dislodge the males. Internal injuries to females, as well as damage to female wings, are a common outcome of such resistance struggles (Blanckenhorn et al., 2002), and likely have serious consequences for female locomotor performance, at a minimum. In addition to physical injury, struggles while resisting mating can incur significant energetic costs to females of other animal species, particularly during lengthy interactions (Jormalainen, 1998). For instance, female water striders engaged in mating resistance have elevated energetic expenditure (Watson et al., 1998).

A growing literature shows that the outcomes of escalated physical, aggressive interactions are often rooted in measurable functional and physiological traits, especially whole-organism performance capacities such as biting, running, or jumping (Lailvaux et al., 2004; Lappin and Husak, 2005), such that superior performers often prevail over poorer performers, even after accounting for confounding effects of body size (Lailvaux and Irschick, 2006a, 2007; Husak et al., 2006; Hall et al., 2010; Mowles et al., 2010). Given the ubiquity of physical female resistance to unwanted or excessive mating attempts by males, as well as the often intense nature of such interactions, it is possible that similar functional and performance traits may be important to both males and females in this context as well (Jormalainen, 1998). Indeed, performance capacities predict dominance interaction outcomes among female *Cherax dispar* crayfish (Bywater et al., 2008), suggesting that females accrue the same benefits from performance traits during escalated physical interactions as males do. However, no studies to our knowledge have thus far investigated the efficacy of performance traits either in increasing female resistance, or in aiding male persistence during mating attempts. The nature of these interactions suggests that such traits would indeed be important for persistence or resistance, if not both. Furthermore, males are often reported to take advantage of particular situations where females are weakened, immobilized, or otherwise defenseless, so as to circumvent female premating resistance entirely. Male *Drosophila melanogaster* and *Drosophila simulans* fruit flies, for example, have been reported to patrol areas and mate with soft-bodied females just emerged from their pupal stage, and that have also not yet had the opportunity to unfold their wings (Markow, 2000). This preference for females that are unable to resist strongly suggests that female resistance, rooted in the same or similar functional capacities that drive physical fighting ability, is likely to be effective in some cases in preventing unwanted matings or mating attempts. By the same token, variation in certain performance capacities could also conceivably underlie male variation in persistence or manipulative ability, an important driver of male fitness (Bonduriansky, 2014).

Increased energetic expenditure during mating resistance or avoidance can impact other life-history traits that share a common resource pool with traits that are pertinent to female resistance, and which could therefore trade-off against each other under conditions where energetic resources are limiting (Häirdling and Kaitala, 2005). In addition, male persistence and mate guarding likely impose energetic costs on males as well (e.g., Plaistow et al., 2003), and thus male traits may be subject to similar life-history trade-offs as females. From a functional perspective, these trade-offs represent an underexplored, yet potentially crucial source of variation in animal physiological and performance capacities, since whole-organism performance traits in particular are built and expressed in the same way as other key life-history traits, yet are seldom considered or studied as such (Lailvaux and Husak, 2014). If whole-organism performance capacities are indeed involved in persistence, resistance, or other aspects of conflict over mating decisions and mating rates, then selection generated as a result of this conflict could be an important driver of the evolution of both male and female performance capacities, and may even lead to divergent selection on certain performance traits between males and females. Thus, intergenomic sexual conflict should be considered as an agent of selection on performance evolution, in addition to the classically studied forces of natural and sexual selection.

3 Intralocus Sexual Conflict

In addition to conflicts over the outcomes of interactions between individuals from various intraspecific classes, conflicts can also exist when the same traits experience divergent or antagonistic intraspecific selection in each sex. This intralocus conflict has been the focus of much attention, especially with regard to conflict between males and females, because of the potential for traits to be displaced from their selective optima in one sex due to antagonistic selection in the other sex. Depending on the degree and intensity of such selection and on the nature and sign of the intersexual genetic correlation, a certain trait may therefore be expressed more or less optimally in one sex, whereas the expression of that same trait in the other sex is compromised due to the conflicting selecting pressures. For example, pelvic architecture may place a constraint on egg size in some oviparous vertebrate species due to selection on the pelvis for other functions, such as locomotion (Congdon and Gibbons, 1987). If locomotion is strongly selected for in male lizards (Husak and Fox, 2008), for example, then such selection might decrease the width of the pelvic aperture in females through the shared genetic correlation for that trait, resulting in smaller female egg size (Sinervo and Licht, 1991; Sinervo, 1999; but see Oufiero et al., 2007). In another example, male and female great weed warblers *Acrocephalus arundinaceus* experience unresolved intralocus sexual conflict over wing size (Tarka et al., 2014). Shorter wings are favored in females, but longer wings are favored in males, and the intersex genetic correlation leads to females with alleles for long wings having lower fitness. In each of these examples a functional benefit to males results in a fitness cost to females, because the function that selection favors in males is not optimal for females, which experience different selection pressures. Conflicts such as these, and others like them, could underscore important trade-offs between function and reproduction in some animal taxa.

Although potentially widespread, the evolutionary importance of intralocus sexual conflict in particular has nevertheless historically been controversial (Arnqvist and Rowe, 2005; Bonduriansky and Chenoweth, 2009). Despite a long-standing notion that intralocus sexual conflict constrains or biases the evolutionary trajectories of a variety of morphological, functional, and behavioral traits between males and females, the existence and ubiquity of sexual dimorphism for such traits and for the physiological mechanisms underlying them constitutes a strong counterpoint to this idea (Lailvaux, 2007; Stillwell et al., 2010; but see Huey and Pianka, 2007). Indeed, studies have generally failed to find evidence that genetic correlations between the sexes constrain the evolution of sexual size dimorphism (Fedorka et al., 2007; Foerster et al., 2007; but see Jensen et al., 2003; Parker and Garant, 2004). Several potential resolutions to these intralocus sexual conflicts are currently recognized (Van Doorn, 2009), including forms of compensation for the expression of suboptimal phenotypes in one sex relative to the other (Husak et al., 2011; Cameron et al., 2013); gene duplication (Gallach and Betran, 2011); and the evolution of complete sex-limitation, whereby certain traits or alleles are expressed in only one sex, but not both. Also, females may assess genetic compatibility and optimize mating with particular mates to reduce intragenomic conflict, as in stalk-eyed flies where females choose males with long eyestalks to avoid meiotic drive genes (Cotton et al., 2014). Importantly, however, the various mechanisms of conflict resolution have thus far tended to adopt an (arguably necessary) univariate perspective, and have neglected to consider the effects of, for example, sex-limitation on the expression of traits that might be pleiotropically, genetically, or phenotypically linked to those traits experiencing intralocus sexual conflict. For example, Harano et al. (2010) showed that selecting for larger mandible size in male dimorphic *Gnatocerus cornutus* beetles significantly reduced the fitness of females, despite females never developing exaggerated mandibles. Instead, females from populations selected for larger mandibles had smaller abdomens, which influences the number of eggs that can be carried. Thus, development of large mandibles appears to drive changes in genetically correlated characters that likely affect fitness in females (in this case, abdomen size); consequently, while intralocus conflict in mandible size is resolved, intersexual conflict over overall fitness is not.

This unresolved conflict between multivariate suites of traits, as opposed to univariate traits, may affect the evolution of integrated trait complexes that underpin animal function. Indeed, a high degree of phenotypic or genetic covariation among traits biases evolutionary transformations in natural populations due to lack of additive genetic variation for individual traits (Schluter, 2000). Thus, phenotypic integration of the type expressed in functional systems such as snake feeding, which is itself the result of selection for functional coherence among traits (Vincent et al., 2006), could potentially affect or constrain the degree of sexual dimorphism within species that differ markedly in their external phenotype (Delph, 2005; Fedorka et al., 2007). However, compelling evidence for such constraints is currently lacking from the literature, and indeed several studies suggest that selection may in fact act differently between the sexes on suites of functionally integrated traits, resulting in different patterns of integration in each sex for the same set of traits. For example, male *Romalea microptera* grasshoppers show a higher degree of phenotypic integration for head morphology than females (Vincent and Lailvaux, 2008), despite females having larger head sizes and potentially higher bite forces (Vincent, 2006) (though bite force was not measured). However, although existing evidence suggests that functional traits may not be especially constrained by sexual conflict, the ubiquity of sex-differences in functional, physiological, and behavioral traits nonetheless suggests that rejection of intralocus conflict in this context may be premature.

In a recent review, Bonduriansky and Chenoweth (2009) suggest that one of the most ambitious questions remaining to answer about intralocus sexual conflict is the "frequency with which new conflicts arise and the consequences of intralocus sexual conflict for sexual coevolution, adaptation and speciation" (p. 287). This is directly applicable to physiological and functional traits that can be genetically correlated with traits experiencing conflict. Indeed, they use a functional trait (performance in the form of "predator avoidance") that also plays a role in male sexual competition (which is likely common; reviewed in Lailvaux and Irschick, 2006a; Husak and Fox, 2008) as an example of how the measurement of trait optima may be influenced by artificial laboratory conditions. However, such links between functional and sexually dimorphic traits are more than inconveniences; these links may be important players in how and whether intralocus sexual conflict is resolved.

4 Intrasexual Conflict and Alternative Reproductive Tactics

It is probably no exaggeration that much of the diversity in behavior, morphology, and physiology that we see in nature has its seeds in evolutionary conflict (Bonduriansky, 2011). This is true both inter- and intra-specifically. Indeed, conflict may lead to multiple phenotypic possibilities within a species depending on the form and strength of selection on traits, as well as the genetic architecture of those traits. Selection may strongly favor one trait, for mating success for example, but that same selection, via a genetic correlation, may move another trait (or traits) away from its selective optimum, leading to conflict that may have many possible results. At one extreme there may be unresolved intrasexual conflict, and at another extreme there may be alternative combinations of traits with their own respective fitness optima (i.e., alternative reproductive tactics, see below). In the former case, there are a multitude of possibilities for conflict within a sex. In *Teleogryllus commodus* crickets, males that advertise to females longer have increased mating success but at the expense of longevity (Hunt et al., 2004). Lailvaux et al. (2010) showed that male calling effort and attractiveness, key components of mating success, are negatively genetically correlated with jumping performance, a trait important for survival, along the major axis of genetic variation (g_{max}). Such a tradeoff creates the possibility for multiple male fitness optima that reflect the longevity versus mating effort strategies. However, Lailvaux et al. (2010) also found evidence for two additional significant axes of genetic variation comprising different trait combinations to that of g_{max}, and therefore possibly three different male fitness optima (of likely varying importance) that implicate performance in different ways. Similarly, quantitative genetic analysis and artificial selection of flour beetles *Gnatocerus cornutus* revealed a negative genetic correlation between mandible length, a sexually selected trait, and locomotor performance in males (Fuchikawa and Okada, 2013). These examples illustrate how the genetic architecture underlying traits or suites of traits can dramatically impact the phenotypic trajectory of each and suggest that intrasexual conflict may be common for traits used during intraspecific interactions.

Another striking manifestation of intraspecific variation in selection on traits, often driven by conflict and competition between males, is the variety of alternative reproductive tactics (ARTs) observed in many animal taxa (Oliveira et al., 2008). But while the evolution and expression of ARTs are remarkably well understood, the extent to which ARTs might lead to conflict between the sexes has thus far been underappreciated (Alonzo, 2008). Conflict between the sexes over mating is already a common feature of animal mating systems (see above). Intrasexual variation in strategies involved in matings can add an additional layer of complexity to mating interactions. If males exhibit different mating tactics, and if any of those tactics has a differential effect on female fitness-related traits such as longevity, fecundity, or residual reproductive success, then male and female conflict over the existence of the ART would be expected, along with the evolution of female choice among the ARTs (Alonzo and Warner, 2000; Alonzo, 2008). Given the condition-dependent nature of many ARTs, this scenario has implications for the evolution of any related traits that form part of the expressed tactics. In species harboring territorial and sneaker males, for example, either sneaking or defending territories (or both) may be associated with performance or physiological traits that enable or enhance the success of that tactic. Although not well explored within the context of ARTs, evidence suggests that mating tactics are indeed buttressed by performance traits. For example, color morphs in *Uta stansburiana* have different endurance capacities, with the aggressive orange males that defend territories exhibiting higher endurance (Sinervo et al., 2000; but see Meyers et al., 2006). Similarly, faster-sprinting males *Crotaphytus collaris* lizards not only sire more offspring than slower males (Husak et al., 2006), but they are also better at defending females against mating attempts by sneaker males (Husak et al., 2008). By contrast, being faster does not appear to aid males in sneaking attempts in this species (Husak et al., 2008). *Crotaphytus collaris*, like many lizards, does not appear to exhibit pre-copulatory female choice (Baird et al., 1997), and the prediction of evolution of female preferences against either tactic cannot be evaluated in this species. However, this work hints at an intriguing role for performance traits in ARTs, and consequently for generating additional conflict between the sexes over mating interactions as well.

From a life-history perspective, the expression of ARTs can involve the concomitant expression of elaborate and often costly morphological characters. The dung beetle genus *Onthophagus* contains several species where males exist as either sneakers or guarders, with guarding males often expressing, on the head or thorax, large horns that are reduced or absent in sneakers (Emlen, 1997; Moczek and Emlen, 2000). Expression of these horns is associated with local developmental trade-offs which may vary with the location of the horn, whereby the size of nearby morphological structures is negatively correlated with horn size (Emlen, 2001). Such trade-offs have been noted between horns and structures such as antennae, eyes, and wings (Emlen, 2011). Expression of the thoracic horn in *Onthophagus sagittarius*, for example, is associated with reduction in wing size, which has implications for flight performance (Emlen, 2011; but see McCullough et al., 2012). Depending on the relative importance of locomotion in different habitat types, species in which guarder males find their functional capacities reduced may therefore find those males in conflict with females over wing size. The evolutionary outcomes of such conflict are not immediately apparent, given the threshold model for horn expression by which male type in dung beetles is determined (Emlen and Nijhout, 2000; Moczek et al., 2004). However, Bielak et al. (2014) showed that selection on aggressive fighter males as opposed to non-aggressive scramblers in the bulb mite *Rhizoglyphus robini* resulted in reductions in female fecundity and longevity in the male fighter selected lines, likely via intralocus sexual conflict. These examples show that conflict within a sex (intrasexual conflict) may in turn lead to intralocus, intersexual conflict, affecting the evolution of a multitude of traits.

5 Pre- and Post-mating Conflicts

The evolutionary outcomes of sexual conflict are increasingly well understood. Conflict involving specific traits, especially those involved in reproduction, can affect the opportunity, form, and intensity of selection acting on those traits (Hall et al., 2008), as well as the available genetic variation for such traits (Hall et al., 2010). However, conflicts involving mating can manifest at several points in time before, during, and even after the act of mating itself. Pre-mating conflicts often center on aspects of female choice and/or male persistence, and measures pertaining to this, such as latency to mate, may have different interpretations from the perspectives of either sex, ultimately leading to different evolutionary dynamics for males and females. In many species, for example, mate choice depends on characteristics of both sexes, and any measures thereof are consequently a function not only of female preferences and responsiveness, but also of male attractiveness and coercive ability. These composite measures, which are considered themselves to be traits and are in part determined by the phenotypes of other individuals, are termed *interacting phenotypes* (Moore et al., 1997), and may bias the response to selection in some unexpected ways due to the means by which the additive genetic variance underlying such phenotypes is partitioned between the sexes - in effect, the additive genetic variance for a given individual is itself part of the environmental variance of another, a phenomenon known as *indirect genetic effects* (IGEs). Given that it is the additive genetic variance that selection acts upon to elicit an evolutionary response (Falconer and Mackay, 1996), interacting phenotypes can themselves evolve via IGEs (McGlothlin et al., 2010), and there is reason to believe that they may do so rapidly (Moore et al., 2002). However, the lability of interacting-phenotype evolution is dependent on the nature of the intersexual genetic correlations, as well as on the identity and role of the phenotypes that interact. For example, female laying date in red-billed gulls depends on both male and female genotypes, but the genetic contributions of males and females do not align and are negatively genetically correlated with each, likely contributing to the underlying variation in laying date (Brommer and Rattiste, 2008).

Just as pre-mating conflicts may involve IGEs via interacting phenotypes, post-mating conflicts are also potentially subject to these same correlative mechanisms. The cricket *Teleogryllus commodus*, for example, exhibits both pre-mating conflict in terms of the pre-mating interactions (which can be captured in the measure of latency to mate), and post-mating conflict which manifests as male guarding of females and harassment to prevent females from removing the spermatophore, which the male attaches to the female during mating (Bussière et al., 2006; Hall et al., 2010). Males and females contribute unequal amounts of genetic variation to the three primary stages of reproductive interactions in *T. commodus*. This is despite both sexes actively participating in each of these stages, with genetic variation for latency to mate being limited to males, genetic variation for spermatophore attachment limited to females, and genetic variation for post-copulatory mate guarding intensity to prevent spermatophore attachment being entirely absent (Hall et al., 2013). Consequently, evolution of latency to mate, a measure which encompasses female preferences and resistance in addition to male traits such as persistence and coercive ability, is dependent entirely on the genetic variation exhibited by males. Similarly, the time taken for a male to attach his spermatophore to the female can evolve only through selection on females.

Several questions present themselves with regard to the roles of functional and physiological traits in both pre- and post-mating sexual conflicts. For example, do high-performance males have an advantage in terms of harassing females? Do performance traits aid females in resisting male harassment? Thus far, explicit integration of measures of performance and physiology into components of behavioral mating interactions has been slow. Evidence currently suggests that females do not necessarily prefer males who are good performers (Lailvaux and Irschick, 2006b; Huyghe et al., 2012, 2013), and indeed there is reason to believe that high-performance males are likely to be viewed by females as unattractive (Lailvaux et al., 2010; but see Postma, 2014), and may even be actively discriminated against. For example, Huyghe et al. (2013) suggested that female *Podarcis melliselensis* lizards prefer larger males, but avoid those with higher bite forces for their body size, possibly to evade harassment by stronger males. The use of performance capacities to coerce females into mating with males they would otherwise prefer not to, as discussed above, is a possibility, albeit one that demands rigorous empirical study. By contrast, the use of female performance capacities to resist the unwanted advances of particular males has, to our knowledge, never been studied. Similarly, whether performance aids males in harassing females in post-mating contexts such as preventing spermatophore removal, or whether such traits allow females to overcome post-mating harassment is also unknown.

In addition, the nature of the evolutionary consequences of interacting phenotypes means that an understanding of the role of functional traits during reproductive interactions is crucial for understanding the responses to selection on those traits in males and females. On the one hand, if functional traits do indeed play a role in pre- and post-mating sexual conflicts and thereby influence the expression of interacting phenotypes such as latency to mate, mate guarding, or spermatophore attachment times, then those traits could affect the genetic variance and, potentially, evolutionary trajectories of the interacting phenotypes through their contribution to IGEs. On the other hand, a perhaps less likely possibility is that evolutionary changes in those interacting phenotypes could feed back and affect the evolution of the functional traits determining them as well, and consequently that some proportion of the differences in both male and female functional capacities can be explained by the sex-specific genetic variance in those traits. Examination of the effects of interacting phenotypes and IGEs on the evolution of functional traits represents a novel frontier for physiological and performance traits, and may also have implications for any other correlated behavioral, morphological, or otherwise fitness-related traits. However, the reciprocal effects of interacting phenotypes and indirect genetic effects on functional traits, if any, would be highly dependent on the direction and nature of the intersexual genetic correlations. A valuable first step towards resolving these issues would be to include measurement of relevant functional and physiological traits in considerations of indirect genetic effects when considering pre- and post-mating conflicts.

6 Compensation and Coevolution

In certain scenarios, traits may coevolve in parallel to each other due to parallel selection pressures and/or positive genetic or phenotypic correlations. An example of this is evolutionary compensation for costs associated with signals or exaggerated ornaments (reviewed in Husak and Swallow, 2011). Animal signals used in inter- and intra-sexual interactions, such as behavioral displays and exaggerated ornaments, are typically thought to be necessarily costly for reliability to be maintained (reviewed in Maynard Smith and Harper, 2003; Searcy and Nowicki, 2005; Tibbets, 2014; but see Számadó, 2011). However, such costs have proven difficult to detect (Kotiaho, 2001). One possible reason for the lack of detectable costs of reliable signals is that there has been coevolution of compensatory traits to ameliorate potential or past costs (reviewed in Oufiero and Garland, 2007; Husak and Swallow, 2011). Under this scenario, as ornaments become more exaggerated or signals incur more costs (e.g., due to conspicuousness or energetic expenditure), there is concomitant evolution of physiological and functional traits to reduce those costs. This leads to a positive association between the ornament or signal and the compensatory trait(s).

There are some well-studied examples of compensation, almost wholly in flying species (but see Cameron et al., 2013; Dennenmoser and Christy, 2013). For example, birds with exaggerated tail feathers have lengthened wingspans (e.g., Andersson and Andersson, 1994; Balmford et al., 1994), presumably to offset the aerodynamic costs of the elongated tails (Thomas, 1993). Similarly, male rhinoceros beetles *Trypoxylus dichotomus* have larger wings and flight muscles than females, which lack the large horn used during male-male combat, and males with relatively larger horns also have relatively larger wings (McCullough et al., 2012; McCullough and Emlen, 2013). Stalk-eyed flies have apparently compensated for the aerodynamic costs imposed by having their eyes on the ends of stalks that can exceed their body length, and which are favored in male-male contests and by female choice (Wilkinson and Dodson, 1997). Here, males have evolved larger flight muscles (Swallow et al., 2000), as well as greater wing areas, which should produce more force during flight and enhance maneuverability to offset the altered moment of inertia caused by enlarged eyestalks (Ribak and Swallow, 2007; Ribak et al., 2009; Husak et al., 2011). Interestingly, intersexual genetic correlations (Wilkinson, 1993) result in females having eyestalks as well, even though they are apparently not used as a signal as in males. This likely has generated intralocus sexual conflict, resolved at least partially by the evolution of sexual dimorphism in eyespan and wing area instead of sex-limited expression of eyestalks. However, despite the evolution of compensatory traits, stalk-eyed flies may display conflict and compensation at various stages of resolution. In two species very dimorphic for eyespan (*Teleopsis thaii* and *T. whitei*; Baker and Wilkinson, 2001; Ribak et al., 2009; see Fig. 1), one species (*T. thaii*) has also evolved dimorphism in wing size, whereas the other (*T. whitei*) has not (Husak et al., 2011). Further, in both species, residual wing length is correlated with residual eyespan in females, suggesting that there is also compensation among females of these species for large eye stalks via longer wings (though not with greater area; Fig. 1). Under this scenario, the intersex genetic correlation for eyestalks results in females bearing a ‘burden’ of sexual selection on male eyespan, making enlarged eyestalks also costly for females. This may represent unresolved or partially resolved intralocus sexual conflict, where female eyespan is pulled beyond a biomechanical optimum for flight performance. Female *T. thaii* and *T. whitei* may decrease that ‘burden’ by compensating, as males do, with longer wings. A similar phenomenon was found in barn swallows, where females exhibited stronger compensation, via larger wings, for long tails than did males (Møller et al., 1995; see also Cameron et al., 2013). In another species of stalk-eyed fly, *Diasemopsis meigenii*, there may also be unresolved intralocus sexual conflict. Sexual dimorphism in eyespan is present in this species, but there is not corresponding dimorphism in wing size, and there is no compensation among females for elongated eyestalks. Although it appears intralocus sexual conflict may be closer to resolution for eyespan, this may not be true for wing size, and females may not be at their fitness optimum (see Husak et al., 2011 for alternative explanations). In Asian house geckoes *Hemidactylus frenatus*, the large heads of males, favored for territorial fights, comes at a cost of reduced sprint speed (Cameron et al., 2013). However, females show no such tradeoff, but they do show a positive relationship between size-corrected head size and limb length, presumably compensation for suboptimal head size due to selection on male head size (Cameron et al., 2013). These examples illustrate how an improved locomotor system may compensate for decreases to fitness imposed by the signal. They also show that intralocus sexual conflict may interact with the evolution of compensatory mechanisms to result in complicated patterns of partially resolved or unresolved intralocus sexual conflict, resulting in difficult-to-predict phenotypic outcomes.

Husak and Swallow (2011) suggested that it is possible for a population to be in a state of equilibrium with regard to ornament costs due to coevolution of ornaments and compensatory traits. Here, the cost of the ornament has been balanced by selection for compensatory traits and each trait is at or near its respective fitness optimum in that selective environment. However, no mechanism was proposed to explain how this phenotypic integration could occur, and such an equilibrium may only exist under certain selective environments and with genetic correlations between the traits involved. Weak, positive genetic correlations between an ornament and compensatory trait may impede the speed of reaching optima. Conversely, negative genetic correlations between these two traits may prevent reaching fitness optima for either trait. This would also be true if these two traits have negative genetic correlations with other traits important to fitness. A critical piece missing in the literature on compensation is how signals or weapons and compensatory traits are/become linked. There is little to no work on the quantitative genetics of compensatory traits and how they are genetically correlated with signals or weapons. However, some intriguing work by Emlen et al. (2012) suggests that insulin/insulin-like growth factor signalling may underlie such phenotypic correlations, though the genetic basis of this link is still unclear. Further, since insulin/IGF signalling pathways are present in most tissues of the bodies of many animals, the potential for conflict with other traits exists. To our knowledge this possibility remains unexplored.

Compensatory traits have been found in several taxa, but they are not always detected when expected (e.g., Oufiero et al., 2014a, 2014b). This can be due to a number of reasons, not least of which is that the appropriate traits were not measured or are difficult to meas-

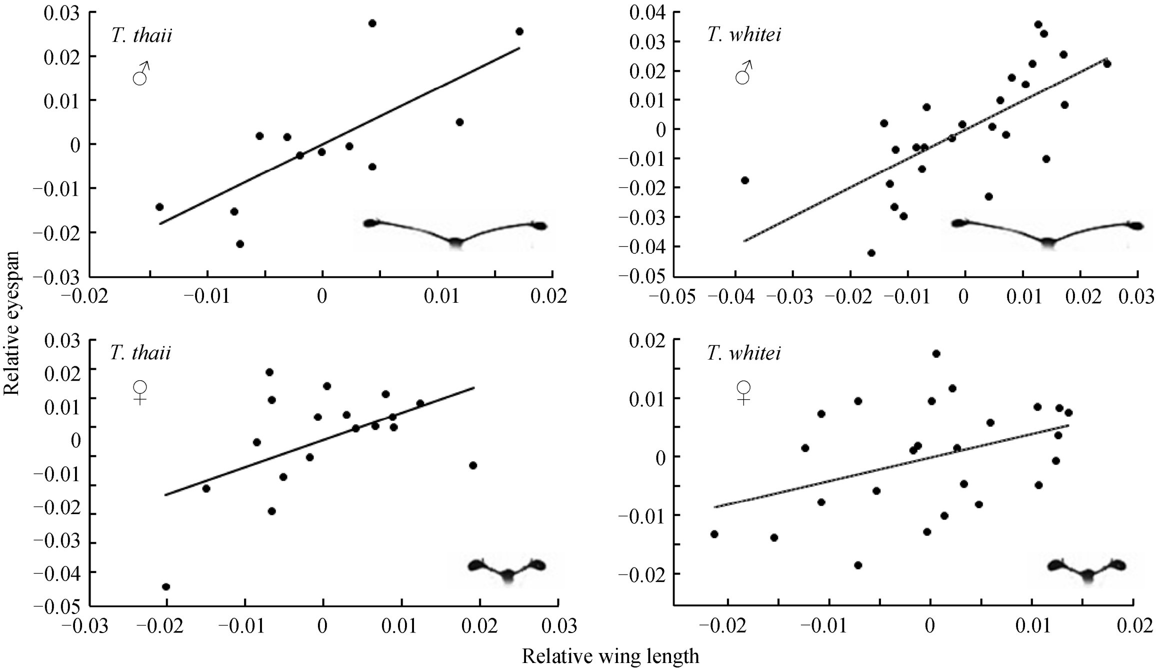

Fig. 1 Compensation for exaggerated eyestalks in males and females of two sexually dimorphic stalk-eyed fly species
Heads of males and females are shown to scale relative to each other in each panel. Data are from Husak et al. (2011).

ure. Thus, there is still a need to understand how common compensation for ornaments and signals is across taxa and types of signals. Most work has been conducted on flying animals and compensation for ornaments or weapons (Husak and Swallow, 2011), so additional work on terrestrial (Dennenmoser and Christy, 2013) and aquatic (see Oufiero et al., 2014a, 2014b) animals, as well as more dynamic signals, is important before drawing generalizations. There is also little theoretical or empirical data on whether and how genetic correlations and opposing selection constrain compensation. The extent to which such potential tradeoffs or constraints can be overcome by evolution of the genetic variance-covariance matrix (the G-matrix) is also unknown. These issues will likely be complicated by the dynamics of the form and intensity of selection on these correlated traits. Finally, it is unclear how commonly compensation evolves in resolving intralocus sexual conflict.

7 Conclusion and Prospectus

In summary, selection on any given trait that is used during intraspecific interactions is subject to conflict or creating conflict in correlated traits. This can have important implications for the evolution of adapted suites of traits, the evolution of sex differences, and the evolution of alternative reproductive strategies. Although a great number of studies have tackled the issues of interlocus and intralocus sexual conflict, there are a number of areas of research that we feel deserve attention. In particular, the failure to explicitly incorporate physiological and functional traits into studies of conflict leaves open a number of important questions about phenotypic evolution. In addition to questions raised in each of the above sections, we feel the following questions may serve as a guide for future research. 1) How are functional and physiological traits genetically correlated with other traits important to reproduction and survival? 2) How common is intersexual conflict in physiological and functional traits? 3) How does compensation or coevolution of functional and physiological traits affect the evolution of other traits that are genetically correlated? 4) How are physiological and functional traits involved in pre- and post-mating conflicts? 5) How common is intrasexual conflict in physiological and functional traits, and what are the evolutionary outcomes? The study of conflicts and how they shape phenotypic evolution at multiple levels of selection is a rapidly growing field of research, as is the study of functional and performance traits. Integrating the two together will undoubtedly move both fields forward to give a better understanding of how the multivariate phenotype evolves.

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