

# Plasticity as panacea? Nerves, hormones, and the currencies of trade-offs

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**Abstract** Phenotypic plasticity is nearly universal among organisms, and evidence indicates that plasticity can exhibit additive genetic variation and respond to selection. These findings have important implications for our understanding of how plasticity may be constrained and how its mechanistic structure may affect its evolution. Many life history trade-offs may be conceptualized as plastic traits, with individuals varying in their position along trade-off axes due to genetic differences, developmental plasticity, or short-term plasticity occurring throughout an individual's lifetime. Behavioral plasticity is key to understanding when organisms are likely to encounter trade-offs, whether those trade-offs can be mitigated, and how the trade-offs affect the ecology and evolution of populations. In this review, we discuss hormonal and neural mechanisms that may influence how plastic behavioral traits are expressed and evolve. We also outline a classification of life history trade-offs and their mechanistic bases and discuss the currencies most likely to mediate each category of trade-off and how they are tied to the mechanisms by which animals express their behaviors [*Current Zoology* 61 (2): 251–264, 2015].

**Keywords** Phenotypic plasticity, Life history trade-offs, Hormones, Neural tissue

## 1 Introduction

Nearly all traits exhibit plasticity, in that their expression depends both on an individual's genotype at one or more loci and on the environment in which the individual lives (West-Eberhard, 2003; Németh et al., 2013). In some cases, more plastic genotypes may allow individuals to better adjust to changing or unpredictable environments than genotypes producing narrower ranges of trait values. In these cases, plasticity is adaptive (Pfennig, 1990; Pigliucci, 2005; Charmantier et al., 2008). Previous research suggests that the capacity for plasticity and the phenotypic variation generated by plasticity can contribute to the ecological success of populations (Forsman, 2014).

The study of the costs of and limits to plasticity seeks to explain why, given these benefits, animals are not infinitely changeable in response to external and internal cues (DeWitt et al., 1998; Auld et al., 2010). Costs and limits often arise from the mechanisms through which plasticity is expressed and may explain why we sometimes do not observe the pattern of plasticity we might expect (Ghalambor et al., 2007). Similarly, the study of life history trade-offs seeks to explain why we do not observe some trait combinations that would seem to maximize individual fitness. A trade-off exists when,

all else being equal, a change in one trait that increases fitness implies a change in one or more other traits that decreases fitness (Stearns, 1989). Reasons may include negative genetic correlations among traits, limited resource pools, limiting nutrients, or constraints imposed by time, risk, or decision accuracy (Stearns, 1989; Sinervo and Svensson, 1998; Stearns, 2000; Zera and Harshman, 2001; Janz, 2003; Roff, 2011).

A vast literature exists on trade-offs and their consequences, much of it focused on genetic trade-offs, in which a negative genetic correlation exists between the traits involved, such that artificial selection for an increased value of one trait drives a corresponding decrease in the value(s) of the other(s) (Roff, 2011). So-called "phenotypic" trade-offs, in contrast, are sometimes considered of limited relevance to life history evolution, because a trait for which no additive genetic variation exists will not respond to selection (Roff and Fairbairn, 2007; Roff, 2011). However, work on the evolution of phenotypic plasticity may indicate a reconsideration of this approach is warranted.

Mechanistic studies have revealed that plasticity itself varies among individuals, populations, and species; and that considerable additive genetic variation often underlies this variation (Pigliucci, 2005; Nussey et al., 2005; Forsman, 2014). Like other forms of plasticity,

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Received Dec. 1, 2014; accepted Feb. 7, 2015.

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phenotypic trade-offs may result from genetic variation in reaction norms, allowing them to respond to selection and shape the evolution of populations (Bolnick et al., 2003; Sgrò and Hoffmann, 2004; Wolf et al., 2007). The fact that many phenotypic trade-offs manifest through behavior (Barnard and Brown, 1985; Sheldon, 2000; McNamara and Houston, 2008; Mathot et al., 2014) suggests a better understanding of behavioral mechanisms may benefit researchers into life history evolution who seek to integrate phenotypic trade-offs into the framework developed for trade-offs resulting from negative genetic correlations between canalized traits.

Here, we develop a classification scheme (Table 1) combining a previous classification of trade-offs (Angilletta Jr. et al., 2003) with categories describing the mechanisms that may underlie inter-individual behavioral variation. We point out commonalities between the related but sometimes poorly integrated literatures on phenotypic plasticity and life history trade-offs. Both fields have benefited from research on the mechanisms underlying the phenomena on which they focus (Zera and Harshman, 2001; Auld et al., 2010; Németh et al., 2013; Lailvaux and Husak., 2014). We describe how behavioral ecologists interested in how behavioral plasticity in life history traits arises, when we might expect to observe it, and what its ecological and evolutionary consequences are may also benefit from these mechanistic insights. Finally, we describe recent findings re-

garding hormonal and neural mechanisms that influence how and whether trade-offs manifest through behavioral plasticity and how likely it is that the associations between traits involved in a trade-off can be weakened.

## 2 Life History Trade-offs and Behavioral Plasticity

When two or more traits exhibit a trade-off, there may be no single best trait combination, or the trait combination generating highest fitness may vary temporally or spatially. When individuals within a population express trait combinations occurring at different points along a fitness isocline, this variation may result from different genotypes, developmental plasticity leading to fixed phenotypes later in life, or short-term (often behavioral) plasticity that may manifest at any time during the individual's lifespan (Stearns, 1989; Sinervo and Svensson, 1998; Stearns, 2000; Zera and Harshman, 2001). In the first two instances, physiological or morphological differences among types may restrict the behaviors an individual can perform (Rowland and Emlen, 2009; Paull et al., 2012). In the third case, behavior itself often mediates trade-off expression, and the mechanism underlying the behavior is crucial to understanding when the trade-off may be important and what implications it has for the evolutionary trajectory of a population (Mathot et al., 2014).

Even when they do not manifest through behavioral

**Table 1** A classification scheme for life history trade-offs and their underlying mechanisms, based on Angilletta et al (2003)

|                                |  | Trade-off category   |   |  |
|--------------------------------|--|--|---|--|
|                                |  | Allocation   | Acquisition   | Specialist-generalist  |
| Mechanism underlying variation | Genetic polymorphism                     | Genotypes differ in how they allocate resources among competing functions or structures<br><i>e.g.</i> Offspring size/number trade-off differs among female lizard throat color morphs (Sinervo et al., 2000)  | Genotypes differ in how they balance resource acquisition vs. risk of mortality<br><i>e.g.</i> Shy-bold behavioral syndromes underlain by genetic variation (reviewed in Sih et al., 2004)  | Genotypes differ in whether they use a variety of resources with moderate efficiency or a few resources with high efficiency<br><i>e.g.</i> Individual butterflies vary in how strictly they discriminate ancestral from novel host plants (Wee and Singer, 2007)    |
|                                | Developmental plasticity                 | Conditions early in development predict what allocation strategy will maximize individual fitness (often "threshold traits")<br><i>e.g.</i> Major, minor, and hornless morphs in dung beetles (Rowland and Emlen, 2009)                                  | Conditions early in development influence how individuals balance resource acquisition vs. mortality risk<br><i>e.g.</i> Song exposure as juveniles affects satellite vs. calling behavior in male crickets (Bailey et al., 2008)                           | Conditions early in development affect whether individuals use a variety of resources with moderate efficiency or a few resources with high efficiency<br><i>e.g.</i> Early diet affects whether toad larvae develop as omnivore or carnivore morphs (Pfennig, 1990) |
|                                | Short-term (often behavioral) plasticity | Individuals shift resource allocation among competing needs over short time scales, in response to internal or external cues.<br><i>e.g.</i> Differential allocation of reproductive investment based on mate attractiveness (reviewed by Sheldon, 2000) | Individuals shift between high/low risk/reward behavioral strategies over short time-scales, in response to internal or external cues<br><i>e.g.</i> Shrews with greater food requirements engaged in riskier foraging strategies (Barnard and Brown, 1985) | Individuals exploit a variety of resources with moderate efficiency under some conditions and a few resources with high efficiency under other conditions<br><i>e.g.</i> Grasshoppers grow faster but pause more on mixed diets (Bernays and Bright, 2001)           |

plasticity, many life history trade-offs are linked to behavior because behavior is involved in the expression of the traits comprising them. Examples include the trade-off between foraging and predation risk (Mathot et al., 2014) or between survival and reproduction (Lancaster et al., 2008). In these cases, describing the mechanisms producing those behaviors is crucial to understanding how the trade-offs impact the ecology and evolution of the organisms in which they occur.

Under a classification scheme proposed by Angilletta et al. (2003), trade-offs can be assigned to three fundamental types: 1) allocation trade-offs, in which a limiting resource must be divided between competing functions or structures, 2) acquisition trade-offs, in which an individual who spends more time or energy seeking out resources (e.g., food or mates) exposes itself to greater risk of mortality or reproductive failure, and 3) specialist-generalist trade-offs, in which individuals better able to use a small range of resources or environments are less able to use resources or environments outside that range. These three fundamental forms of trade-offs have historically been dealt with by different subfields of evolutionary biology and behavioral ecology (Angilletta et al., 2003), and they may differ in the mechanisms most likely to mediate them and their implications for the evolution of populations.

Some phenotypic traits may be involved in trade-offs in more than one category. For example, the male beetle morphs described below differ in their allocation of resources to horn growth and also in how they balance the risk of death during combat vs. the risk of failure to mate (Rowland and Emlen, 2009). However, assigning an observed or hypothesized trade-off to one of these categories can help predict the currency through which the trade-off is likely to be expressed and how morphological, physiological, and behavioral mechanisms may affect the trade-off's expression and evolution within and between populations or species. Early in the study of trade-offs, the currency underlying negative correlations between traits was often nonspecifically identified as "energy" or "resources" (van Noordwijk and de Jong, 1986). It is clearly true, at a fundamental level, that trade-offs result from the fact that organisms do not have access to unlimited energy. However, the energy an individual invests in the branches of a traditional Y-model is not simply poured out among functions as if from a cup (Zera and Harshman, 2001; Harshman and Zera, 2007). The mechanistic details of how energy is stored, transported, and used within an organism are crucial to predicting when a particular trade-off is most

relevant (e.g., under most circumstances, during overall dietary restriction, or only when a particular nutrient is lacking) (Stahlschmidt et al., 2013; Lailvaux and Husak, 2014).

Cox et al. (2014) provide a recent example of how assuming that energy exists in a pool from which it can be pulled at will may lead to incorrect predictions regarding how trade-offs shape behavior. They manipulated the allocation trade-off between survival and reproduction in free-living, wild brown anoles by removing females' fat bodies, ovaries, both, or neither in a full factorial design. Ovariectomized females had greater growth and survival, as predicted by the hypothesis that reproduction and survival are alternative "sinks" for energy allocation. However, females whose fat bodies were removed did not have lower post-breeding survival, which may indicate the trade-off is not a simple binary and/or the fat bodies are not the only source from which energy for survival and reproduction can be drawn.

This study is consistent with another suggestion from recent literature on energy storage and allocation: many studies of the reproduction-survival trade-off focus exclusively on the breeding season, but energy reserve variation throughout the year or throughout an individual's lifespan may affect whether trade-offs manifest, by influencing what structures are formed, what resources are acquired, and how those resources are allocated. McNamara and Houston (2008) describe how, in birds, energy reserves throughout the year are an important determinant of feather quality, which in turn affects thermoregulatory efficiency, which loops back to affect energy reserves. In general, the message from detailed mechanistic studies of allocation trade-offs is that we still lack a thorough understanding of what "resources" and "energy" literally are in many contexts, or of how they are stored, transferred, and used within an organism.

The importance of mechanism to understanding how behavior mediates life history trade-offs becomes particularly clear in the case of acquisition and specialist-generalist trade-offs, whose currencies may not be as intuitively expressed in terms of energy as the currencies of allocation trade-offs. Acquisition trade-offs may be better conceptualized as trade-offs between risks, such as the risk of mortality due to predation vs. the risk of mortality due to starvation; or the risk of mortality due to predation vs. the risk of failure to reproduce (Kokko et al., 2002). Depending on the developmental mechanisms by which specialization and generalization

are achieved, specialist-generalist trade-offs may manifest through currencies of risk (e.g. failure to adapt to a changing environment vs. increased success in a stable environment, Moran, 1992); energy (e.g., the cost of maintaining the metabolic machinery necessary for a generalist vs. increased intake from multiple resources, Sol et al., 2008); accuracy of decision making, or handling time for resource consumption (Janz, 2003).

In the following section and Table 1, we expand Angilletta et al.'s (2003) classification of trade-offs by discussing examples in which variation in trade-offs of each of the three types results from genetic polymorphism, developmental plasticity, or short-term behavioral plasticity. We explore how understanding the mechanisms behind the trade-offs influenced the authors' interpretation of their data or predictions regarding how the trade-off might affect the ecology or evolution of the population under study.

### 3 Mechanisms of Behavioral Variation and the Currencies of Trade-offs

#### 3.1 Allocation trade-offs

Trade-offs in resource allocation are perhaps the most widely studied and intuitive category of life history trade-offs (Saeki et al., 2014; Lailvaux and Husak, 2014). Their intuitive nature, however, can mask the multiple interacting phenotypes and environments that influence whether a particular population faces a particular trade-off and, if so, how the trade-off is resolved. When an allocation trade-off is genetically based, such that genotypes differ in how they allocate resources among competing structures or functions, alternative strategies may cycle under frequency- or density-dependent selection. Female throat color morphs in the side-blotched lizard *Uta stansburiana* are an example in relation to the offspring size vs. number trade-off: orange-throated females have larger clutches of smaller offspring, whereas yellow-throated females have smaller clutches of larger offspring. These populations experience density cycles, and orange-throated females do better under conditions of low population density, whereas yellow-throated females have higher fitness when population density is high (Sinervo et al., 2000; Sinervo, 2001). In this case, the form of selection on a genetically-based trade-off has important consequences for the maintenance of alternative behavioral strategies with regard to another allocation trade-off, that of current vs. future reproduction. In response to crowding, corticosterone is elevated in all females (Comendant et al.,

2003). This change increased likelihood of reproduction and decreased survival probability in orange-throated females but had the opposite effect in yellow-throated females, indicating that genotypes in the population differed in how they prioritized trade-offs in offspring quality vs. quantity and current vs. future reproduction (Lancaster et al., 2008).

Allocation trade-offs resulting from developmental plasticity may arise when conditions early in development predict the allocation strategy that will maximize fitness. Often, alternative phenotypes represent a "threshold trait" where a developmental switch is thrown based on how quickly an individual is growing or maturing. Alternative phenotypes may have equal fitnesses, or one or more of the types may be a "best of a bad job" strategy (Moran, 1992). For example, males of many beetle species may develop as one of three facultative morphs: major horned males, minor horned males, and hornless males (Rowland and Emlen, 2009). Depending on nutrition during larval development, males either allocate structural and metabolic resources to develop a costly weapon and defensive behaviors, develop a reduced weapon and behave as sneakers, or abandon weapon development entirely (Emlen et al., 2006; Emlen et al., 2007; Rowland and Emlen, 2009).

When allocation trade-offs manifest through short-term plasticity, however, individuals may reallocate resources among competing needs throughout their lives, often by altering behaviors. For example, individuals in several taxa alter parental behavior and reproductive investment depending on their mates' attractiveness (Burley, 1988; Sheldon, 2000). What precisely is reallocated may be costly behavior itself, as in convict cichlids that adjust defensive display frequency depending on the desirability of their partners (Robart, 2012). In other cases, nutrients (Uller et al., 2005), and/or hormones (Gil et al., 1999) may be shifted among competing structures or uses depending on the attractiveness of an individual's mate and thus the likelihood of reproductive success through current vs future offspring.

#### 3.2 Acquisition trade-offs

Acquisition trade-offs occur when individuals accept risk to acquire resources, including food, territory, or reproductive opportunities. One well-studied, genetically based acquisition trade-off is the shy-bold continuum of behavioral syndromes (Sih et al., 2004). In numerous species, individuals with certain genotypes express either active and aggressive or passive and less aggressive behaviors across multiple contexts (Wolf et al., 2007; Bell et al., 2009; Dingemanse et al., 2010).

Bold individuals exhibit active and exploratory behavior that may allow them to acquire more resources but increase their risk of mortality due to extrinsic factors. In contrast, shy individuals are less likely to exploit novel resources but less likely to encounter novel threats (Sih et al., 2004; Dingemanse et al., 2010). These personality traits appear heritable in many taxa (Bell et al., 2009). A recent study (Mathot et al., 2014) found that great tits with higher basal metabolic rates (which are heritable and imply greater nutritional demands) took greater risks while foraging, but only in high-predation environments. Despite revealing the challenges of quantifying risk, reward, and the trade-off between them, this and similar studies may help identify the loci involved in genetic variation in how acquisition trade-offs are resolved.

In some cases, conditions early in development may influence how individuals later resolve the trade-off between mortality risk and resource acquisition. In many species, individuals vary in whether they perform showy sexual displays, increasing their probability of mating and their risk of predation; or engage in a lower-risk, lower-reward strategy like satellite or sneaker behavior (Rowland and Emlen, 2009; Bailey et al., 2010). Conditions early in development often mediate which strategy an adult adopts. For example, male Pacific field crickets *Teleogryllus oceanicus* who are reared in silence, suggesting a low-density population, are likelier to engage in a satellite mating strategy than to call (Bailey et al., 2010). In the same system, females face a trade-off between the risk of remaining unmated and the risk of responding too quickly to a male and producing low-quality offspring. Females reared in silence become more responsive to mating calls, as predicted if the risk of remaining unmated outweighs the risk of mating with less desirable males when mates are rare (Bailey and Zuk, 2008).

Finally, individuals sometimes shift between high and low risk/reward behavioral strategies over short time scales, in response to internal or external cues. One classic example includes condition-sensitive foraging, where individuals at greater caloric deficits (i.e., increased risk of starvation), incur additional risk in pursuit of greater rewards by visiting high-variance food resources (Barnard and Brown, 1985). Recent work on the Pacific field cricket has revealed that female mate choice behavior, while influenced by juvenile conditions as described above, also remains plastic into adulthood. When an adult female experiences changes in the acoustic environment that signal changes in population

density, she adjusts her responsiveness to mating calls accordingly, becoming less responsive if she experiences silence followed by song and more responsive if she experiences song followed by silence (Swanger and Zuk, in prep).

### 3.3 Specialist-generalist trade-offs

Specialist-generalist trade-offs occur when a “jack of all trades is master of none,” that is, when exploiting a wide range of resources prevents an individual from exploiting a more restricted range of resources with greater efficiency (Angilletta et al., 2003). In general, they are less studied from a life history perspective than allocation or acquisition trade-offs, although the coexistence of specialists and generalists is an important focus of research in community ecology (McPeck, 1996; Egas et al., 2004).

Genetically-based variation along the specialist-generalist axis has been documented at interspecific (Joshi and Thompson, 1995; Janz et al., 2001; Nosil, 2002), intraspecific but interpopulation (Janz, 2003), and intrapopulation (Wee and Singer, 2007) levels. However, the currency of the presumed trade-off between the strategies, and their relative benefits, are often unclear from empirical work. Decision time and accuracy are currencies often proposed for specialist-generalist trade-offs, under the assumption that generalists will identify appropriate resources faster than specialists, but specialists will make fewer mistakes than generalists (Dall and Cuthill, 1997; Janz, 2003). Generalists also may persist in more microhabitats or in habitats with sparse but diverse resources (Futuyma and Moreno, 1988; Kelley and Farrell, 1998). At least in taxa where specialist-generalist variation is genetically based, however, support for these hypotheses is equivocal. For example, Janz (2003) found that butterflies from a generalist population were both slower and less accurate in identifying oviposition sites than individuals from a specialist population.

This and similar studies have led some researchers to propose neural constraints as the primary mechanism for the specialist-generalist trade-off in phytophagous insects: the benefits of a broader dietary range in generalists may be counterbalanced by the time and cognitive complexity required to choose among a greater number of resources than specialists must consider (Dall and Cuthill, 1997; Bernays, 1998; Janz, 2003). This hypothesis is consistent with the costliness of developing and maintaining neural tissue (Aiello and Wheeler, 1995; Attwell and Laughlin, 2001). It is supported empirically by the finding that gravid females

from specialist species (or specialist populations within trophically variable species) could better distinguish high and low quality examples of their primary host plant than generalist females ovipositing on the same species (Janz and Nylin, 1997). However, Wee and Singer (2007) tested a population of butterflies in which individuals vary in their propensity to accept a novel oviposition host in addition to their ancestral host. They found no difference between specialists and generalists in time taken to identify the ancestral host or to successfully oviposit. Because this study was carried out at a different level than previous research, its results may not be entirely comparable, but it raises intriguing questions about the basis for and consequences of variation along the specialist-generalist axis among individuals, populations, and species.

In the theoretical realm, Tosh et al (2009) used a genetic algorithm to train artificial neural networks as either resource specialists or generalists. Specialists had higher decision accuracy than generalists when choosing non-hosts had a neutral or slightly positive (although less positive than choosing hosts) effect on fitness. In contrast, generalists made more accurate decisions than specialists when choosing non-hosts negatively affected fitness. This somewhat counterintuitive result was later partially supported by an empirical study (Tosh et al., 2011) where human subjects learned to distinguish “host” from “non-host” letters during a computer game similar to the training regimen used for the neural networks in Tosh et al (2009). Among humans, specialists outperformed generalists when non-hosts were somewhat valuable, but there was no difference between specialists and generalists when errors were severely punished. However, neither of these studies differentiated between the cost of incorrectly choosing a non-host and the cost of incorrectly rejecting a host, because hosts and non-hosts were presented simultaneously. The authors suggest that an internal trade-off between these two kinds of accuracy might help explain their results, (Tosh et al., 2009; Tosh et al., 2011), so experiments measuring these two types of errors separately could be a profitable direction for future work.

When the prevalence of a particular resource early in an individual’s development predicts whether a specialist or generalist phenotype will generate higher reproductive success, an individual’s position on the specialist-generalist continuum may be determined by developmental plasticity. One well-studied example is the larva of the spadefoot toad, which usually develops

slowly and eats a variety of plant detritus and zooplankton. When the ephemeral pools in which tadpoles live have abundant brine shrimp, however, individuals develop as specialist carnivore morphs with keratinized beaks, reduced guts, and shorter development time (Pfennig, 1990). Specialist carnivores are likelier than generalist omnivores to develop quickly enough to survive faster-drying pools, which typically have more brine shrimp than longer-lasting pools, so this plasticity appears to be adaptive, but they face increased competition because their morphological adaptations to consuming brine shrimp reduce their efficiency at consuming other food sources (Paull et al., 2012). However, reduced competition among omnivores may itself result from individual omnivores specializing on particular resources within the broad range of foods their morph consumes (Paull et al., 2012).

Clear examples of short-term plasticity in generalist vs. specialist strategies are lacking, although work on individual foraging strategies has documented that adults vary in their resource use, and that specialization on one resource may compromise an individual’s ability to feed on resources that were previously within its repertoire. For example, grasshoppers from the generalist species *Schistocerca americana* grew faster but fed less efficiently (that is, with more pauses during feeding) when given a mixture of plant species than when given either plant species alone (Bernays and Bright, 2001). However, this study did not change individuals’ diets from generalist to specialist during adulthood, so the timescale of plasticity in behavior is not clear.

A trend towards individual specialization even among species, populations, or morphs categorized as generalists appears to be widespread (Kohda, 1994; Bolnick et al., 2003), raising the possibility that the relevant trade-off may not be between specialists and “jacks of all trades” but rather between specialists on alternative resources within a range of possibilities. In general, greater work on variation in specialization over an individual’s lifetime would be helpful, in addition to studies addressing whether individuals become less specialized over time or in response to changing environments.

At a broader scale, plasticity itself may be seen as a generalist strategy, whereas canalization is a specialized strategy. Populations where individuals vary in plasticity, therefore, represent cases of variation along a specialist-generalist axis (Wennersten and Forsman, 2012). Theoretical research indicates that trade-offs between current and future reproduction may favor the evolution of behavioral personalities, an example of a genetically-

based acquisition trade-off (Sih et al., 2004; Wolf et al., 2007). In this case, all three categories of trade-off we have discussed here (Table 1, Angilletta et al., 2003), mutually influence each other's expression and evolution. Such interactions are likely common in natural populations, and a better understanding of how they unfold could be a profitable area for future research.

## 4 Mechanisms of Plasticity and the Currency of Trade-offs

Below, we discuss hormonally and neurally mediated behavioral plasticity that is associated with (primarily) phenotypic trade-offs. Hormonal mechanisms of plasticity are frequently associated with trade-offs because hormones are multifunctional, and changes in hormone titer can influence multiple target tissues (Ketterson and Nolan, 1999; Flatt et al., 2005; Hau, 2007). Neurally mediated plasticity is associated with energetic trade-offs due to the high cost of maintaining neural tissue (Laughlin et al., 1998; Isler and van Schaik, 2009). By fitting the physiological and molecular mechanisms of plasticity into the framework proposed by Angilletta et al. (2003) and expanded here, we offer insight into how the mechanisms of phenotypic trade-offs affect their evolution.

### 4.1 Hormones: Plasticity with complex evolutionary consequences

Hormones are signaling molecules that function at multiple scales: within and between cells, and within and between tissues (Newman, 2007), and often mediate adaptive plasticity. However, the factors allowing hormones to coordinate well-integrated plastic phenotypes can also constrain the evolution of plastic traits:

*Hormones operate on multiple timescales.* Hormonally mediated plasticity may be activational, when a shift in hormone titer produces a physiological or behavioral change that persists only while the hormone persists at that level, or organizational, in which a change in hormone titer produces a developmental shift. Selection on phenotypic plasticity may influence both activational and organizational aspects of hormone function (Adkins-Regan, 2012).

*Hormones are transmitted systemically to influence multiple tissues.* Any tissue with receptors for a hormone can respond to an elevation in that hormone's titer. Selection on phenotype may influence circulating hormone titer, tissue sensitivity to hormones, or both. These outcomes have distinct evolutionary implications: changes in circulating titers should have more systemic

effects, while the effects of changes in receptor density or sensitivity should be more local (Ketterson and Nolan, 1999).

The multifunctionality of hormones' effects on physiology and behavior means that selection on hormone-mediated traits is likely associated with shifts in other traits. Many of the hypotheses and predictions about the evolution of hormonally mediated trade-offs stem from studies on the vertebrate hormone testosterone (Ketterson and Nolan, 1999; Hau, 2007). Here, we focus on the insect hormone juvenile hormone (JH), one of the most versatile hormones. JH plays a key role nearly all aspects of insect development, life history, and behavior (Flatt and Kawecki, 2007; Flatt et al., 2005; Tibbetts and Crocker, 2014). Including this particularly multifunctional hormone in the discussion of hormones and constraints should yield insight into aspects of life history trade-offs that are widely applicable across taxa and thus have more universal evolutionary implications.

### 4.2 Juvenile hormone, hormonal pleiotropy, and phenotypic integration

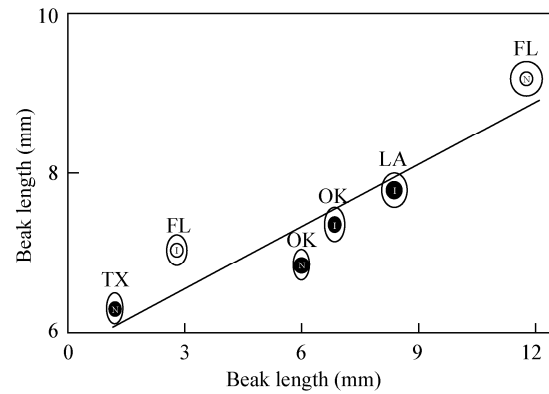
In many ways, JH exemplifies key features of hormones. JH influences traits that are diverse in type and timescale, including development, reproductive physiology and behavior, and multiple life history traits (Dingle, 1972; Dingle and Winchell, 1997; Flatt et al., 2005; Tibbetts and Crocker, 2014).

JH's many functions often result in hormonal pleiotropy: an adaptive change in one trait is associated with a non-adaptive or maladaptive change in another (Ketterson and Nolan, 1999). Many cricket species are wing polymorphic, with both long-winged, flight-capable individuals (LW) and short-winged, non-flying individuals (SW) (Nijhout, 1994; Dingle and Winchell, 1997; Roff et al., 1997; Roff et al., 1999; Zera and Harshman, 2001). Wing morph is associated with shifts in reproductive investment, with SW individuals investing more in reproduction (Roff, 1990; Dingle and Winchell, 1997; Saglam et al., 2008) and wing morph and reproductive investment are influenced by JH titer during the penultimate development stage (Dingle and Winchell, 1997). The adaptive value of wing morph plasticity arises from habitat persistence: temporary habitats favor migratory, flight-capable morphs, and habitat permanence favors non-migratory, short-winged individuals (Dingle and Winchell, 1997). However, the association between migratory capability and reduced fecundity appears fixed, so while migration may be adaptive, long-winged individuals pay a reproductive penalty.

JH's pleiotropic effects do not only result in constraint: plastic traits do not function independently but as one component of an overall phenotype that must be integrated (Snell-Rood, 2013). In the horned flour beetle *Gnathocerus cornutus*, application of the JH analogue methoprene before prepupal development results in exaggeration of weapons used in male-male competition and the body parts that support these weapons (Okada et al., 2012). This suggests JH's role in development is not only to determine the relative values of fitness-related traits, but also to integrate these traits with the phenotype as a whole.

Phenotypic integration may have facilitated the rapid local adaptation of races of soapberry bugs *Jadera haematoloma* in the southern United States. *Jadera haematoloma* is native to the Florida Keys but has radiated to central and eastern Florida and rapidly adapted to novel ecology, including differences in the size and timing of food availability. Derived populations of *J. haematoloma* that feed on the seeds of smaller fruits have evolved smaller beaks, consistent with adaptive evolution of beak size (Carroll and Boyd, 1992; Carroll et al., 1998; Carroll et al., 2005). A selection experiment for beak size in *J. haematoloma* revealed significant genetic variation in beak size (Dingle et al., 2009). Several characteristics exhibited correlated evolution with beak size: lines selected for short beaks also increased their proportions of short-winged, non-migratory individuals (Dingle et al., 2009). This is likely an adaptive combination: the hosts derived populations of *J. haematoloma* feed on are synchronous breeders, which should favor non-migratory behavior (Dingle and Winchell, 1997; Carroll et al., 1998; Dingle et al., 2009) (Fig. 1). While JH's role in facilitating the life history changes correlated with beak length has not been investigated, it is reasonable to suppose that JH has a role because it is a critical regulator of insect life histories (Dingle and Winchell, 1997; Zera and Harshman, 2001; Flatt and Kawecki, 2007). In an ecological context, adaptive correlated changes between beak length and wing morph suggest further research on JH as a phenotypic integrator is merited.

The above discussion highlights potential tension in our understanding of the role of hormones in evolution: are hormones a source of constraint or are they phenotypic integrators? It is critical to remember that hormone systems are also evolved traits: when trade-offs are stable over time, single molecules that mediate negative correlations between relevant traits may be efficient mechanism for dealing with those trade-offs (Hau,



**Fig. 1 The relationship between beak length and host plant fruit radius appears to be the result of local adaptation in *J. haematoloma* populations**

Populations associated with larger fruits also have larger beaks (Carroll et al., 1992). These local hosts also vary in the timing of fruit availability, with smaller fruits produced synchronously and seasonally. The observed correlation between beak length and fruit size prompted a selection experiment to understand the genetic basis of beak length; this work found that selection for shorter beaks resulted in a decrease in frequency of migratory morphs, predicted to be adaptive on synchronously available resources (Dingle et al., 2009). The finding that direct selection on beak length influences ecologically relevant life history traits suggests an opportunity to study the role of hormones in the production of adaptive suites of traits. Figure redrawn from Carroll et al., 1992.

2007; Lessells, 2008). Whether a hormone system serves as a phenotypic integrator or a constraint depends on the context in which selection acts: in the case of *Jadera haematoloma*, phenotypic correlations appear adaptive; however, a migration-reproduction trade-off is clearly a constraint.

### 4.3 Can evolution decouple suites of hormonally mediated traits?

The evolution of hormonally mediated plastic traits is complex, because selection acts only indirectly on the mechanisms producing the trait. Two non-mutually exclusive hypotheses have been proposed for the evolution of hormonally mediated traits. The circulating titer of the hormone may shift, producing a change in the phenotype under selection, but also influencing tissues that have receptors for that hormone; or individual tissue sensitivity to the hormone may evolve, allowing the hormone-mediated trait to evolve relatively independently (Ketterson and Nolan, 1999; Hau, 2007).

Selection experiments often reveal tight linkage between aspects of phenotype regulated by JH. In the honeybee *Apis mellifera* "pollen-hoarding syndrome," pollen-hoarding behavior is associated with changes in physiology and other behaviors: fewer eggs, lower vitellogenin, lower locomotor activity in young adults, and later-life initiation of foraging (Amdam and Page,



2010). A bidirectional selection experiment for high and low pollen-hoarding behavior revealed that these differences are associated with changes in JH titer in larvae, pupae, and early adults. These changes were associated with changes in developmental pacing and their linkages with adult physiology and behavior (Amdam et al., 2010). A change in JH titer, resulting in a suite of phenotypic changes, following selection on a single ecologically relevant trait is consistent with the finding that novel ecological selection for behavior and/or morphology (i.e., a simulated host shift) is commonly linked to life history changes that do not themselves appear to be adaptations to ecology (Prowell Pashley, 1988; Messina and Karren, 2003; Messina, 2004; Dingle et al., 2009; Fox et al., 2011).

What insight do selection experiments yield into the decoupling of correlated traits linked by hormones? A study on a polyphenic laboratory strain of the tobacco hornworm *Manduca sexta* in which the titer of JH during development resulted in either large, green pupae or small, black pupae attempted to break the size-color linkage. Selection for both black coloration and large size was applied to a line previously selected to be monophenic black and small, but the change in pupal size was not significant. A change in size was only achieved when selection on coloration was relaxed (Suzuki and Nijhout, 2008). The tight linkage of color and pupal size suggests that suites of traits mediated by JH may be difficult to separate even under strong selection. However, Flatt and Kawecki (2007) simulated elevated JH titer that could occur due to selection on other JH-mediated traits. They artificially selected lines of *Drosophila melanogaster* by rearing them in media containing methoprene (a JH analogue, or JHa) for 19 generations and found a mosaic response to exogenous JHa. When flies from control lines were reared in JHa-supplemented medium, they took longer to develop, developed into smaller larvae, and had higher early-life fecundity, and shorter lifespan than flies reared on medium without JHa. Unlike the control flies, when reared in JHa, JHa-selected flies' early-life fecundity was similar to control flies in the absence of JHa, and their lifespans were longer (Flatt and Kawecki, 2007). Taken together, these two studies suggest insects can evolve reduced sensitivity to JH in some fitness-related traits and eliminate some life history trade-offs but not others. If ecological selection on life history traits is more variable than ecological selection on color (Mousseau and Roff, 1987), there may exist more genetic variation in the mechanistic link between JH and life history, allowing selection to act relatively quickly on sensitivity to the

hormone.

#### 4.4 The high cost of neural tissue and the expensive tissue hypothesis

Neural tissue is one of the most energetically demanding tissues in the animal body. Neurons must maintain an ion gradient across their membranes, which requires a large, steady supply of ATP, and this cost is likely consistently high over time. While the cost of signaling is high and scales with neuronal firing rate, maintaining an ion gradient is expensive even at rest (Attwell and Laughlin 2001). Consistent with the idea that the energetic demands of neural tissue are high while the costs of other tissues are often context-dependent, in Weddell seals *Leptonychotes weddellii* engaging in simulated diving, blood flow to the brain remains relatively constant while blood flow to other tissues shifts substantially (Zapol et al., 1979).

Aiello and Wheeler (1995) proposed the expensive tissue hypothesis (ETH) as a unifying explanation of primate brain size. According to the ETH, because neural tissue is energetically demanding, increasing brain size is compensated by a decrease in the length of the gut, another metabolically costly tissue. The ETH is often studied narrowly, considering only the brain-gut trade-off; however, tests of the ETH often reveal that brain size trades off not necessarily with gut size, but with other expensive tissues or activities.

#### 4.5 Inter- and intraspecific evidence for the expensive tissue hypothesis

The high costs of neural tissue must be defrayed: animals might increase their overall metabolic rate, or they might shift the relative metabolic demands from one costly tissue to another. Few studies find that animals with large relative brain masses have higher metabolic rates, and those that do find that brain size has a relatively small effect on basal metabolic rate (McNab and Eisenberg, 1989; Martin, 1996; Isler and van Schaik, 2006b; Finarelli, 2010). More patterns are consistent with the expensive tissue hypothesis.

At the phylogenetic level, evidence favoring the expensive tissue hypothesis grows when considering trade-offs between brain size and other expensive tissues or activities. In three species of highly encephalized fish, relative brain size is negatively correlated with gut size (Kaufman et al., 2003). Also, a selection experiment on guppies *Poecilia reticulata* found males in lines artificially selected for large brains grew shorter intestines, suggesting a brain-gut trade-off (Kotrschal et al., 2013). Across birds, brain size is inversely correlated with the size of the pectoral muscle, which suggests that the energetic demands of neural tissues are paid for with a

reduction in costly flying (Isler and van Schaik, 2006a). Fruit flies under selection by nutritional stress for 17–18 generations exhibited reduced capacity to learn to avoid an electric shock in a T-maze (Kolss and Kawecki, 2008). Whether the ETH is interpreted narrowly (brain-gut trade-off) or broadly (a trade-off between brain size and an expensive tissue or activity), there is substantial support for the notion that expensive neural tissue is paid for not in an increase in metabolic rate, but by shifting energy allocation.

There is also solid evidence that individuals experiencing greater cognitive demands pay a high cost, reproductively or otherwise. In cabbage white butterflies *Pieris rapae*, subjects housed in more complex oviposition environments (which require more learning) had lower lifetime fecundity than butterflies in simpler oviposition environments (Snell-Rood et al., 2011; Snell-Rood et al., 2013). Honeybees *Apis mellifera* given a learning task exhibited reduced survival and decreased measures of energy storage (Jaumann et al., 2013). Overall, there is substantial support for the hypothesis that the energetic demands of learning are enough to generate phenotypic trade-offs at the individual level, and that these costs are also borne out at higher evolutionary scales.

## 5 Evolutionary Implications of Expensive Tissues

What are the life history implications of the expensive tissue hypothesis? One possibility is that large-brained animals forage more effectively, allowing them to increase calorie intake sufficiently to compensate for higher investment in expensive tissues. An observational study on bumblebees *Bombus terrestris* found that colonies that learned more quickly foraged for nectar more effectively (Raine and Chittka, 2008). Multiple studies find links between brain size and invasion success, and though they do not explicitly link brain size to foraging, more effective foraging is thought to be a key determinant of invasion success (Sol et al., 2002; Sol and Lefebvre, 2003; Sol et al., 2008; Amiel et al., 2011; Snell-Rood and Wick, 2013). However, a key question is whether the enhanced foraging success that may be associated with larger brains can compensate for the higher costs of neural tissue. To our knowledge, the critical test of whether animals with larger brains consume *enough* more calories to compensate for the higher cost of a larger brain has not been conducted. Thus, we proceed with the assumption that in some cases, higher foraging success does not fully compensate for a larger brain, and that at least some life history traits

associated with brain size are consequences of costly neural tissue.

In mammals, brain size is often correlated with maternal BMR and/or the duration of gestation or lactation (Martin, 1996; Weisbecker and Goswami, 2010). The large investment required for each offspring is often associated with a “slower” life history, i.e., a life history characterized by longer lifespan, fewer offspring, and parental care for offspring that often experience an extended juvenile phase (Promislow and Harvey, 1990). Consistent with a relationship between maternal investment per offspring, brain size, and lifespan, larger-brained mammals live longer than smaller-brained mammals (González-Lagos et al., 2010). As mentioned above, female *P. rapae* ovipositing in more complex environments exhibit reduced lifetime fecundity. They also invest more in each individual offspring, ultimately influencing the adult size of their offspring (Snell-Rood et al., 2011; Snell-Rood et al., 2013). Taken together, these studies suggest investment in neural tissue not only limits investment in other traits, but drives animals toward a “slower” life history: longer lifespan, and fewer, better-provisioned offspring.

Another proposed evolutionary consequence of greater cognitive capacity conferred by larger brains is the ability to engage in more generalist foraging behaviors. This hypothesis finds some support in birds: large-brained species exhibit more innovative behavior, including tool use (Lefebvre et al., 1997; Emery and Clayton, 2004; Lefebvre, 2011; Jönsson et al., 2012). Consistent with large relative brain size producing successful generalists, large-brained mammals better invade novel habitats than smaller-brained mammals (Sol et al., 2008). However, large brains do not appear *sufficient* for the evolution of generalist foraging behavior: corvids and hawks have relatively large brains for their body size (Isler and van Schaik, 2006a), but only corvids are generalist foragers. One explanation for the fact that large brains do not always confer generalist foraging behaviors is that finely tuned sensory capabilities, characteristic of visual predators, require large amounts of expensive neural tissue (Niven and Laughlin, 2008). Additionally, other factors, such as motor diversity (the ability to manipulate objects in diverse ways) may play a role in innovation without being correlated with brain size (Griffin et al., 2014). Further complicating the proposed brain size-foraging generalist link, a test in North American birds found no relationship between a species’ number of documented behavioral innovations and its propensity to engage in generalist foraging behavior in the wild (Overington et al., 2011). Taken to-

gether, although large brains are associated with high costs (and thus likely adaptive), the relationship between brain size, innovation, and ecological generalism is unclear (Healy and Rowe, 2007).

For several reasons, the evolution of neurally mediated behavioral plasticity may proceed more simply than the evolution of hormonally mediated behavioral plasticity. There are few ways for the costs of a large brain to be reduced (Attwell and Laughlin, 2001). That is, the negative fitness consequences of larger brain size cannot be uncoupled from the positive consequences, so the life history implications of larger brain size (selection for a “slower” life) may be relatively consistent. In the case of hormonally mediated plasticity, there is evidence that selection influences a more diverse suite of traits, for example, life history, morphological, and behavioral (Ketterson et al., 1992; Enstrom et al., 1997; Flatt et al., 2005; Flatt and Kawecki., 2007). There is also more evidence that the costs of a hormonally-mediated plastic trait can sometimes be evolutionarily uncoupled from the benefits (Flatt and Kawecki, 2007; Suzuki and Nijhout, 2008). However, this evolutionary capacity seems limited (Bergeon Burns et al., 2013), so hormonally-mediated plasticity is likely consistently associated with correlated evolution and trade-offs. For all the physiological mechanisms of behavioral plasticity that we have discussed here, adaptive plasticity in one trait is associated with correlated effects in at least one other morphological, physiological, or behavioral trait.

## 6 Conclusions and Future Directions

Conceptualizing behavioral variation as a reaction norm (Dingemans et al., 2010) has helped incorporate phenotypic plasticity into the evolutionary biology framework developed for variation in canalized traits underlain by genetic polymorphisms. We argue that behavioral plasticity is crucial to understanding many life history trade-offs. In some cases, negative genetic correlations among traits or alternative developmental trajectories fixed early in life affect the range of behaviors an individual is capable of expressing (Pfennig, 1990; Emlen et al., 2007; Rowland and Emlen, 2009; Paull et al., 2012). In others, an individual’s behavior itself determines its position along a trade-off axis, and that position may change throughout that individual’s life with changing conditions. Recent research into the physiology of hormones and neural tissues has been crucial to understanding the most likely currencies for each category of trade-off and how easily negative correlations between particular suites of traits may be

eroded over evolutionary time (Ketterson and Nolan, 1999, Attwell and Laughlin, 2001; Bergeon Burns et al., 2013).

McNamara and Houston (2009) argued that better integrating mechanism and function in behavioral ecology would help researchers consider more complicated questions, such as why constraints have evolved, rather than simply what the optimal behavioral strategy is given a particular constraint. We provide a classification scheme (Table 1) to help organize research into how the architecture of behavioral traits involved in life history trade-offs may influence when and how those trade-offs constrain individual behavior or population evolution (Forsman, 2014). We also discuss recent results regarding how and when features of the nervous and endocrine systems of vertebrate and invertebrate animals influence the scale at which behavioral plasticity acts and the likelihood suites of traits involved in trade-offs may change their correlation structure. We hope understanding the timescale over which we might expect plasticity in a behavioral trait to occur, an insight which generally requires information about the neural, hormonal, and physiological mechanisms involved, will help advance research focused on both proximate and ultimate questions in life history evolution.

**Acknowledgments** We thank Marlene Zuk and Susan Balenger for help and advice throughout our work on this manuscript. We also thank James Marshall, Tim Fawcett, and Andrew Higginson for organizing this special issue. Finally, we thank Andrew Higginson, Sören Nylin and two anonymous reviewers for helpful comments on a previous version of this manuscript. EB was supported by a Howard Hughes Medical Institute Teaching Postdoctoral fellowship during her work on this review.

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