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SYMPOSIUM

Condition-Dependent Ornaments, Life Histories, and the Evolving Architecture of Resource-Use

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Synopsis Over the past 20 years, researchers have emphasized condition-dependency as a core feature of many sexually selected ornaments. This empirical focus has been motivated by the assumption that condition-dependent ornaments should function as honest indicators of other fitness-related traits. However, evidence remains mixed regarding whether condition-dependent ornaments are consistently correlated with the expression of other key traits such as immunocompetence. I argue that the diversity of the observed relationships between condition-dependent ornaments and other fitness-related traits can be understood, and even predicted, based on attention to the structure of organisms' life histories. More specifically, these relationships are influenced by the relative variation between individuals within a population in their acquisition of resources versus the allocation of those resources to various physiological functions. However, characterizing these two core attributes of life histories requires that researchers quantify condition, a persistently challenging concept to measure empirically. In this review, I first highlight key concepts related to condition-dependency and life history theory. I then outline why measuring the acquisition and allocation of relevant resources is critical for advancing our understanding of sexually selected ornaments. As attempts to tackle these issues have been hampered in the past by empirical challenges, I offer a number of suggestions that aim to identify more tractable approaches to measuring condition, as well as its acquisition and allocation. I conclude by pointing to the broader value of pursuing these concepts empirically as well as to exciting new directions opened by this perspective.

Introduction

Over the past 20 years, research on condition-dependency has expanded dramatically, particularly for traits thought to have evolved under sexual selection (Cotton et al. 2004a, 2006; Lailvaux and Irschick 2006; Bonduriansky 2007; Johnstone et al. 2009). This boost in emphasis on condition-dependency has been motivated in part by the inclusion of this form of phenotypic plasticity as a core feature in the evolution of sexual traits as honest indicators of individual genetic and/or phenotypic quality (Johnstone 1995; Rowe and Houle 1996; Lorch et al. 2003; Cotton et al. 2004a; Kokko et al. 2006; Kokko and Heubel 2008; Johnstone et al. 2009). The assumption of both the theoretical models and the researchers attempting to empirically verify them has been that condition is the property of the individual that determines their breeding value across a wide range of circumstances, including, but not limited to, their health, ability to contribute to the state of their sexual partners and/or offspring, and prospects for longevity (Rowe and Houle 1996; Houle and Kondrashov 2001; Cotton et al. 2004a). In other words, individuals with higher levels of condition are expected to be on average of higher fitness. The logical extension of this reasoning is that sexual traits or signals that rely heavily on condition for their expression should be excellent indicators of individual fitness.

Compelled by this intuitive concept, researchers have sought to establish condition-dependency in putative sexual ornaments (Cotton et al. 2004a). However, this active area of study has been handicapped by the challenge of empirically realizing the concept of condition. In addition, given that condition is likely to drive expression of many

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fitness-enhancing traits in addition to sexual ornaments, many research groups have also evaluated relationships between ornaments and other key life-history traits such as immune function, parental care, or longevity. However, the assumption that individuals of higher condition are likely to be "good at everything" is not always reasonable, and in fact, often predicted to be false on the basis of life-history theory. Indeed, the diversity of experimental outcomes in this field bears this out. I argue that more careful attention to the structure of life histories will help in predicting when ornaments and other fitness-enhancing traits are likely to tradeoff or correlate positively with each other. In particular, I suggest that the field must begin quantifying the acquisition of condition, independent of its allocation to fitness-related traits. Although this latter point is an ambitious undertaking, I posit that it is accessible immediately within the right biological systems, and that given specific empirical compromises, it can be enacted across a wide range of organisms and traits of interest.

In the text below, I first discuss both the concept of condition and its relationship to the expression of traits via the property of condition-dependency. I then describe how life-history theory proposes that condition-dependency should be structured within natural populations. Interestingly, this life-history perspective appears in a number of theoretical models of the evolution of sexual traits, although some of its implications have not been fully appreciated by empiricists. I therefore connect these bodies of literature to highlight how acquisition and allocation of resources play key, independent roles, both in life history and in the evolution of condition-dependency of sexual traits. Given the latter theoretical emphasis on the acquisition of resources and their allocation to fitness-related traits, I proceed to discuss how these properties of resource-economics can be feasibly measured in natural systems, including recent evidence suggesting that this can and should be done. Finally, I discuss how adopting the perspective outlined in this aticle should move the field forward by enabling more specific predictions of how sexual traits might correlate with other traits of interest to prospective mates.

Condition and condition-dependency

Condition is typically defined as the pool of acquired resources that are available for allocation to fitness-related traits (Rowe and Houle 1996). Although this definition has often been interpreted to imply material currencies such as nutritional resources (e.g., Nur and Hasson 1984; Rowe et al. 1994), other less tangible resources also qualify, including time or social capital. However, it is worth noting that nutritional resources, unlike time or social capital, must be both acquired and assimilated by organisms (Raubenheimer and Simpson 1998; Olijnyk and Nelson 2013). For simplicity, I will refer to the accrual of resources, whether material or not, as resource-acquisition, but this will implicitly include assimilation when applied to nutritional currencies.

Condition-dependent traits are those whose expression relies on the size of an individual's acquired pool of resources, with the assumption typically being that this relationship is a positive one (Fig. 1A). Although the clearest way to establish condition-dependency would be to directly measure both the trait of interest and an individual's pool of resources, researchers have long disagreed about the best way to measure relevant resources (and therefore underlying condition) across individuals (Jakob et al. 1996; Kotiaho 1999; Gosler and Harper 2000; Green 2001; Blanckenhorn and Hosken 2003; Moya-Laraño et al. 2008; Ketola and Kotiaho 2009; Peig and Green 2010). This stems in part from the vagueness of theoretical formulations of condition, as well as issues associated with correctly parsing high-condition individuals from those exhibiting imbalances of resources associated with maladaptive phenotypes (e.g., morbidly obese individuals). As a result, researchers often have focused on estimating condition indirectly by imposing stressors on focal animals that are expected to induce shifts in individual condition (Fig. 1B); such stressors have included food restriction, immune challenges, and experimentally augmented demands from activities such as parental care (e.g., via manipulation of brood size) (Johnstone 1995; Cotton et al. 2004a). Thus, most claims of condition-dependency are derived from negative relationships between trait expression and induced stress. This approach suffers from a number of issues, not the least of which is that responses to stress are themselves likely to be dependent upon condition, and therefore individual ability to buffer the effects of stress on other processes is unlikely to be uniform within any given population.

Despite the caveats above, it seems almost necessarily true that traits should scale with the resources available to fund their expression. Thus, the issue of condition-dependency, as Cotton et al. (2004a) correctly observed, is not one of existence but of degree. Are some traits more dependent on condition than others, or more specifically, do sexually selected traits often exhibit heightened dependence on condition?

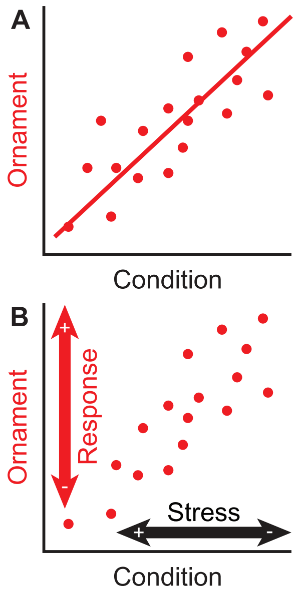

Fig. 1 Phenotypic traits such as sexual ornaments are often thought to scale positively with individual condition, a property called condition-dependency. Although this form of phenotypic plasticity is typically represented as a linear relationship (**A**), this relationship can take other forms such as exponential, quadratic, or cubic curves. Researchers interested in establishing condition-dependency in focal ornamental traits often have chosen to evaluate the effect of stress on ornament-expression (**B**) rather than measuring condition directly. The assumption here is that increasing stress reduces individual condition. Thus, reductions in the expression of ornaments in response to increasing stress often are interpreted as evidence for underlying condition-dependency.

If so, the argument follows that these traits are likely to offer a useful source of information regarding an individual's condition and therefore breeding value across a wide range of other contexts. This is because other traits of potential interest are also likely to be dependent on condition to some degree, and may thus be positively related to the condition-dependent ornament (Fig. 2, "indicator trait"). However, this need not be the case. Traits that are responsive to condition-related stressors when considered alone may actually tradeoff against each other when considered simultaneously, particularly when resources are limiting (Fig. 2, "trait tradeoff"). Alternatively, pairs of traits in which both members of the pair are dependent on condition may be unrelated to each other in expression when measured together in natural populations.

As the relationship between sexually selected ornaments and other fitness-enhancing traits lies at the fundament of these ornaments' value as indicators of individual quality, it is essential for those studying condition-dependency to develop and evaluate clear

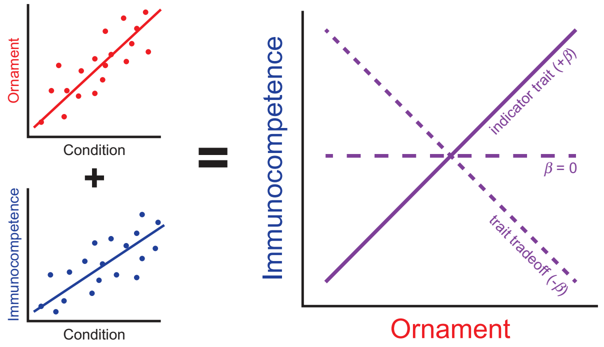

Fig. 2 Individual condition is likely to be linked to the expression of a wide variety of traits, including sexual ornamentation, reproductive output, social dominance, and immunocompetence. As a result, researchers often have assumed that condition-dependent ornaments should serve as honest signals of a number of other characters related to fitness. More explicitly, these ornaments are expected to function as "indicator traits," exhibiting positive correlations ($+\beta$) with other traits of potential interest to the opposite sex. However, empirical efforts often have revealed non-significant ($\beta = 0$) or negative ($-\beta$) relationships between ornaments and other critical traits. The latter often are interpreted as "trait tradeoffs," particularly when animals are exposed to limited resources.

a priori predictions regarding the direction and strength of these relationships in natural populations. However, researchers often have resorted to *a posteriori* explanations for the patterns found in their studies. Although these explanations (e.g., that ornament expression experiences tradeoffs with other traits under certain experimental regimes) may actually be based in biological reality, I argue that such patterns can, and should, be anticipated in advance by attending to predictions from life-history theory regarding how the relationships between traits are structured. As outlined below, this requires separate quantification of the acquisition and allocation of resources.

Life history and the architecture of trait relationships

Life-history theory has grappled for a long time with issues surrounding the acquisition and allocation of resources to fitness (Reznick et al. 2000; Roff 2002). In fact, one of the longstanding goals of research on life history has been to understand how organisms cope with basic resource tradeoffs between fitness-related traits such as somatic maintenance and reproduction (Williams 1966; Reznick 1985; Roff 2000; Roff and Fairbairn 2007). As ornamental traits are themselves life-history traits, this literature is directly relevant to our understanding of condition-dependency and the signaling value of condition-dependent ornaments. The widely held expectation is that organisms cannot be good at everything (i.e., the biological implausibility of the "superflea" or the "Darwinian demon", Law 1979; Reznick et al. 2000) because resources are limited, whether they be nutrition, time, or suitable habitat. Thus, costly traits should typically exhibit tradeoffs as individuals make decisions about how to invest their limited resources. However, van Noordwijk and de Jong (1986) pointed out that such tradeoffs are not always observed in the study of the life histories of natural populations. Rather, researchers often report that traits expected to exhibit negative correlations are found to correlate positively in the field.

Van Noordwijk and de Jong (1986) astutely observed that although tradeoffs between traits are a necessary consequence of balancing costs when individuals are constrained to the same levels of resources, individuals in natural populations are rarely equal in the resources at their disposal. Instead, individuals in wild (and even laboratory) populations are likely to differ both in the amount of resources they have as well as their strategies for investing said resources. van Noordwijk and de Jong (1986) posited that one could make clear predictions regarding the sign of the relationship between traits of interest given knowledge of the relative amount of variation among individuals attributable to differences in acquisition versus allocation of resources (Fig. 3). More specifically, in populations in which individuals largely differ in the amount of resources they have acquired rather than how they have allocated those resources (Fig. 3B), pairs of traits often should be positively correlated with each other when they are considered across members of the population. This is because resource-rich individuals in these populations will have more to spend on all traits, whereas depauperate individuals will have less to invest across the board. In contrast, in ecological scenarios in which individuals are able to acquire similar amounts of resources but differ in how they invest them (Fig. 3C), traits often should exhibit negative tradeoffs. It is important to note that in both of these scenarios (Fig. 3B and C), traits should still tradeoff against each other "within" individual resource-budgets. That is, an individual's investment of more resources in Trait X should still result in fewer resources available for Trait Y. Nevertheless, at the population level, these tradeoffs only are revealed when the ratio of variance in acquisition to variance in allocation is <1 [i.e., $\mathrm{Var(AQ)} < \mathrm{Var(AL)}$, Fig. 3C; also see "trait tradeoff" line in Fig. 2]. If this ratio is >1 [i.e., $\mathrm{Var(AQ)} > \mathrm{Var(AL)}$, Fig. 3B], positive correlations should be observed (e.g., "indicator trait" in Fig. 2). Interestingly, as this ratio approaches unity [$\mathrm{Var(AQ)} \approx \mathrm{Var(AL)}$], traits should show no relationship whatsoever to each other (e.g., $\beta = 0$ in Fig. 2).

Integrating life history and condition-dependency

This life-history perspective on resource economics applies directly to the study of condition-dependency in a number of ways (Fig. 4). First, and perhaps most critically, the van Noordwijk and de Jong model highlights both how and why condition-dependent ornaments might interact with other traits of interest (van Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992). If individuals within a study population differ predominantly in their ability to acquire resources, then the expression of condition-dependent ornaments is likely to correlate positively with a number of other fitness-related traits such as immunity, longevity, and dominance (Fig. 4B). However, if all individuals within a population achieve similar levels of resources (whether high or low), but differ substantially in how they allocate those resources, then condition-dependent ornaments may actually tradeoff against other critical life-history traits (Fig. 4C). This would potentially erode their value as signals of individual quality, or relegate them to indicators of reproductive strategy (i.e., highly ornamented individuals might signal their investment in attractiveness over other components of reproduction such as parental care). Alternatively, these traits could function as visible tallies of costly past experiences, such as prior immune challenges that redirected resources from the development of ornamentation.

Second, this perspective highlights the critical empirical need to separately quantify acquisition and allocation of resources when studying condition-dependent ornaments. Satisfying this requirement promises to substantially deepen our understanding of the architecture of condition-dependency, while at the same time providing *a priori* predictions regarding how condition-dependent traits should function as signals. It also requires us to think carefully about how variation in acquisition and allocation is structured (Fig. 4A), including the role of genotype (G), environment (E) and gene-by-environment interactions ($G \times E$). Our current understanding is notably shallow regarding the role of these components of variation in extant patterns of resource-use (Olijnyk

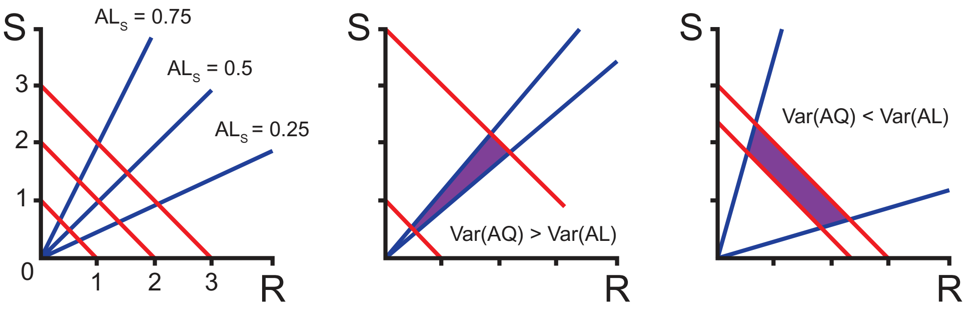

Fig. 3 The van Noordwijk and de Jong (1986) model, which illustrates the critical need to evaluate variation in the acquisition and allocation of resources separately when considering how two life-history traits (such as reproduction, R, and somatic maintenance, S) might be correlated within natural populations. In this graphical model, the acquisition of resources is represented as distance from the origin (labeled at three arbitrary levels on the left panel) and strategies of resource-allocation are illustrated as lines of differing slope radiating from the origin. In the panel on the left, these strategies are labeled in relation to the amount allocated to S (e.g., 75% of resources to S for $AL_S = 0.75$, 50% for $AL_S = 0.5$). In populations in which individuals differ dramatically in the amount of resources they can acquire, but do not differ as much in how they invest those resources [Var(AQ) > Var(AL)], S and R should be positively correlated within the population (center panel) because individuals either will have ample resources both for S and for R or have very few resources to invest. Conversely, if individuals predominantly differ in how they invest their resources rather than in the amount of resources they are able to acquire [Var(AQ) < Var(AL)], S and R should be negatively correlated within the population (right panel) because the salient difference between individuals will be in how they invested roughly equivalent amounts of resource.

and Nelson 2013). However, better information on this front should help us to understand how life histories accommodate condition-dependent ornaments, and how the underlying relationships are likely to evolve over time.

This integration of condition-dependency into the broader perspective of the architecture of life history is by no means new. In fact, one of the most compelling solutions of the "lek paradox" (Borgia 1979), Rowe and Houle's (1996) "genic capture" model, was built on this very same life-history perspective. Rowe and Houle (1996) argued that as ornamental traits exaggerate, they should increasingly rely on an individual's pool of resources, and during this process of increasing dependency on condition, these ornaments should "capture" genetic variance from the large pool of genetic variance underlying resource-acquisition itself. This model was presented as a solution to the "lek paradox" because it offered an explanation for why sexually selected traits might exhibit persistently high genetic variance despite facing strong directional selection. However, one interesting feature of Rowe's and Houle's model is that it does in fact predict the loss of genetic variance, just not from the focal ornamental trait. Rather, the "genic capture" model predicts that genetic variance should be disproportionally shed from resource-allocation over resource-acquisition. That is, during the evolution of increasing condition-dependency, "genic capture" occurs because the ornament's expression becomes tied to genetic variation in underlying condition via the "loss" of intervening genetic variance in resource-allocation.

From the perspective outlined above, this disproportionate loss of genetic variance from resource-allocation is a critical point because it suggests that "genic capture" should lead to a consistent inequality between Var(AQ) and Var(AL). If genetic variance is a strong driver of phenotypic variance in the acquisition and allocation of resources, then "genic capture" should lead to the specific case in which Var(AQ) > Var(AL) (i.e., Fig. 4B) and therefore condition-dependent ornaments that arise via this process should be positively correlated with a wide range of life-history traits. Unfortunately, evidence to evaluate this assertion is lacking at the moment. However, a recent study of genetic variance in resource-use found that in the cricket *Gryllus firmus*, phenotypic variance in life-history traits was overwhelmingly driven by underlying genetic variance in the acquisition of resources rather than their allocation (Robinson and Beckerman 2013). More studies are clearly needed to evaluate whether this pattern is broadly generalizable.

Measuring acquisition and allocation

Although the above arguments are deceptively simple to illustrate in theoretical form (e.g., Figs. 3 and 4), pursuing this empirically requires that researchers revisit the challenge of actually measuring condition itself. That is because condition lies at the nexus of the acquisition and allocation of resources (Fig. 4). Without a measure for it, we are unable to quantify acquisition and allocation separately. Similarly, environmental stressors are still useful in evaluating the

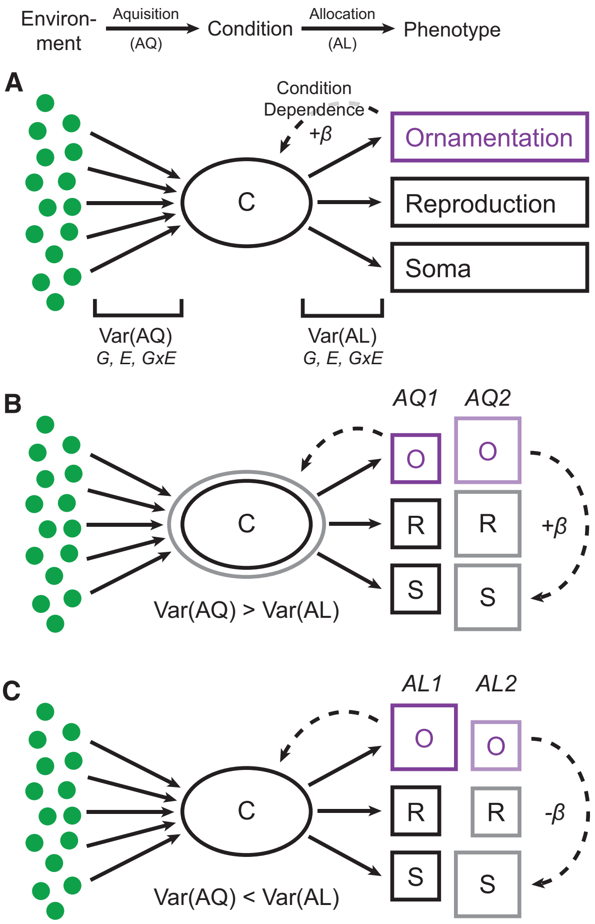

Fig. 4 Life-history framework for considering how the processes of acquisition and allocation of resources contribute to the signaling value of condition-dependent ornaments. The general architecture of these relationships is illustrated in Panel A (top). Moving from left to right, individuals acquire (AQ) resources from the environment, accruing them into a pool of resources termed condition (C). These resources are then allocated (AL) to various aspects of individual phenotype, including ornamentation (O), reproduction (R), and somatic growth and maintenance (S). Variation in acquisition [Var(AQ)] and allocation [Var(AL)] can be decomposed into the effects of the organism's environment (*E*), genotype (*G*), and any gene-by-environment interactions ($G \times E$). Condition-dependency is represented in this schematic as a positive correlation between ornamentation (or any other trait) and underlying condition (i.e., $+\beta$ and dashed line between Ornamentation and C). Panels B and C represent specific scenarios in which the variance in resource-acquisition [Var(AQ)] is either greater than (Panel B) or less than (Panel C) variance in allocation [Var(AL)]. In populations in which individual variance in acquisition is greater than variance in allocation [Panel B; Var(AQ) > Var(AL)], we expect condition-dependent traits to be positively correlated with each other (i.e., $+\beta$ and dashed line between O and S). This is because resource-poor individuals will have less to invest in their phenotype across the board (AQ1, smaller oval for C) when compared with resource-rich individuals (AQ2, larger oval for C). The scenario in Panel B thus leads to sexual ornaments functioning as "indicator traits" for a wide range of fitness-related characters. In contrast, in populations in which individual variance in acquisition is less than the variance in

Fig. 4 Continued
allocation [Panel C; Var(AQ) < Var(AL)], individuals predominantly differ in how they choose to invest a fixed amount of resources (AL1 versus AL2), leading to negative correlations between ornaments and other phenotypic traits (i.e., $-\beta$ and dashed line between O and S).

"*E*" component of variance in acquisition and allocation, but the shortcut of simply measuring the resulting effects of a stressor on phenotype is not valuable in this context because it conflates the relative contributions of acquisition and allocation.

So how, then, might we best measure condition in a way that allows us to also quantify its acquisition and allocation? Clearly, given condition's broad definition and necessarily context-dependent nature, empirical surrogates will require non-trivial compromises. Nevertheless, I argue that one tractable strategy for measuring condition is to quantify the resource, or resources, in the highest demand and shortest supply. Such resources are likely to be important to a wide range of fitness-related traits and should therefore have strong leverage in determining condition. However, care must be taken in identifying these resources, because they should have a shared stake in the production both of ornament/sexual traits and of other traits under consideration. The empirical program would be to first identify a candidate currency, verify that it is indeed limiting to the focal organism and required by a number of key traits, including the ornament of interest, and then quantify at the individual level both its acquisition and its allocation to specific traits.

Although this economic view need not be restricted to material resources, a number of basic nutritional currencies have been identified that satisfy these criteria, at least in certain ecological scenarios. For example, nitrogen (or more explicitly, protein and amino acids) has been implicated as a persistently limiting nutrient for many herbivores (Scriber and Slansky 1981; White 1993; Elser et al. 2000; Schoonhoven et al. 2005; Morehouse et al. 2010; Simpson and Raubenheimer 2012). Nitrogen is also required by nearly all morphological and physiological traits in animals (Fagan et al. 2002; Sterner and Elser 2002; Simpson and Raubenheimer 2012), including many ornaments (Morehouse et al. 2010). Thus, tracking the acquisition and allocation of nitrogen may offer an empirical shortcut to understanding the key relationships described above. Similarly, phosphorous is essential for many processes involved in growth and development, and appears limiting in many environments, particularly aquatic ecosystems (Elser et al. 2000; Sterner and Elser 2002). A number of micronutrients, including salts (Kaspari et al. 2008), can also impose strong limitations on organisms, although their role in many sexually selected traits remains underdeveloped.

There are a number of challenges with this approach, two of which I will address here. First, contemporary work in nutritional ecology has shown that organisms do not simply seek to acquire large quantities of their most limiting resource, but rather must balance the costs and benefits of over-acquiring or under-acquiring multiple nutritional currencies (Simpson and Raubenheimer 2012). Thus, the strategy of quantifying a single ''limiting'' currency oversimplifies the relationship between organisms and their food resources. One solution to this criticism would be to explicitly incorporate nutritional balancing, using an approach such as the Geometric Framework to ask what ratio of key nutrients particular organisms are trying to achieve (Simpson and Raubenheimer 2012). In this multivariate view of the acquisition of resources, an individual's condition could be measured as the Euclidean distance from an established nutritional optimum in multivariate nutritional space.

One of the benefits to this multivariate approach is that it is more likely to identify maladaptive nutritional states that might otherwise be categorized as high condition (e.g., large but morbidly obese individuals would be identified as high in protein, but also disproportionately high in lipids/carbohydrates). However, this multivariate perspective presents empirical challenges for measuring allocation because focal traits are likely to require allocation of different nutritional ratios. This divergence in the nutritional ratios makes comparing patterns of allocation between individuals more challenging. Perhaps more importantly, though, this multivariate view makes comparison of relative variation in acquisition and allocation substantially more complex. One compromise would be to evaluate the nutritional requirements of individuals using a multivariate approach, followed by considering acquisition and allocation of a subset of key currencies individually. An interesting possibility arising from this more demanding approach is that ornaments may engage both in positive and negative correlations with other traits, based on the relative variance in the acquisition and allocation of the resources that they share. For example, suppose there is an ornament that requires large amounts both of proteins and of lipids, and that individuals vary substantially in the amount of protein they can acquire but all individuals acquire the same amount of dietary lipid. It might, therefore, be possible that the ornament could act as an honest indicator of protein-based traits, whereas simultaneously experiencing tradeoffs with lipid-based traits. Whether the additional work required by this more robust multivariate approach is justified will depend on the particulars of the specific focal system, but it would certainly bridge the gap between experimental expediency and nutritional realism with which many simpler studies struggle.

The other major empirical challenge to this life-history approach is the extent to which acquisition and allocation are independent phenomena that can be quantified separately. In many organisms, particularly those with continuous or indeterminate growth, allocation occurs alongside acquisition and the two may be inextricably intertwined. For example, individuals that allocate more resources to traits associated with resource-acquisition may be more likely to acquire more resources later. Although this is not necessarily an insurmountable challenge (e.g., see de Jong 1993), in the first instance I suggest that capital breeders and/or organisms with separate life phases dedicated to the acquisition and allocation of resources (e.g., holometabolous insects) are the most promising groups to investigate. The key feature of these groups is the temporal separation of acquisition and allocation for focal pools of resources. However, even in income breeders, some resource-currencies may still exhibit this temporal structure (e.g., the acquisition and subsequent allocation of carotenoid pigments during molt in songbirds with carotenoid-based ornamentation; Hill et al. 2002). Thus, by the selection of tractable resource-currencies, even more complex systems may be amenable to exploration from this perspective.

In summary, given the fundamental importance of separating the acquisition and allocation of resources when characterizing condition-dependency, researchers must begin focusing again on more direct measurements of condition. A single-currency approach based on identifying key limiting nutrients offers one tractable solution, although this strategy has drawbacks for fully capturing nutritional realism. Other multivariate paradigms such as the Geometric Framework should provide more robust answers regarding the dynamics of resource-acquisition, but come at the cost of higher empirical complexity. Researchers should also consider how easily they can separate acquisition from allocation in their focal species and/or resource-currencies. I suggest that, given the shallowness of current knowledge on this topic, we should take a simple, but practical, approach at the outset. In my view, a single-currency strategy in a capital breeding animal or a holometabolous insect should provide the most rapid progress in the near term.

Conclusions and future directions

Researchers studying sexual selection have embraced condition-dependency as an important feature of many sexual ornaments and armaments, because this form of phenotypic plasticity is thought to impart signaling value to these traits (Cotton et al. 2004a). However, evidence that ornaments dependent on condition serve as indicators of other key fitness-related traits remains mixed (Cotton et al. 2004a, 2004b; Johnstone et al. 2009). I argue that better understanding of how condition-dependent ornaments interact with other traits can be achieved by attending to the structure of organisms' life histories. However, this requires that the field move beyond empirical approaches that conflate the acquisition and allocation of resources to those that parse between these two critical processes.

As I have outlined above, there are a number of advantages to adopting this perspective. First, it promises to contribute greater predictive power for identifying *a priori* the sign and strength of relationships between ornaments and other facets of organisms' phenotypes. Second, this approach should help to uncover which types of ornament are most likely to participate in life-history architectures that lead to positive correlations between ornaments and a broad range of fitness-related traits (i.e., are broadly valuable "indicator traits"). For example, traits that are connected to pervasively important resource-currencies should be more likely to function as summary indicator traits, particularly when individuals differ in the amount of these resources they can acquire. Third, although we know that many sexual traits exhibit condition-dependency (Cotton et al. 2004a), we know considerably less about how this dependency is accommodated by the genetic architecture of individual life histories. Are the changing demands on resources that individuals experience during evolutionary exaggeration of condition-dependent ornaments funded by changes in allocation or in acquisition of resources, or both? With more information about the relative genetic variance in these life-history processes, we can begin to identify plausible trajectories that individual life histories may have taken (or would continue to take) during the evolution of ornaments. Finally, at the most basic level, much remains to be understood regarding the genetic and environmental determinants of organisms' life histories. Thus, while the research program above is likely to be motivated by interest in the evolution of sexually-selected ornaments, it should provide us with much needed information on the structure of life-history architecture that should be even more broadly relevant in evolutionary biology.

In addition to these general considerations, I would also point to several more specific empirical opportunities. First, I suggest that holometabolous insects provide a compelling initial arena for testing these ideas. Many holometabolous insects devote their larval stage to acquiring resources and the pupal and adult stages to allocating them, allowing for clear separation and characterization of these processes. Many such insects also are amenable to large-scale laboratory rearing, which should enable estimation of genetic variances and co-variances for the acquisition and allocation of resources. An empirical emphasis on these groups should therefore provide the most rapid advances in this area in the short term. Second, while it may seem likely that acquisition will be more variable than allocation for many organisms (and this is certainly the assumption of the "genic capture" model), this need not always be the case. One scenario in which individual differences in allocation may be more dominant than differences in acquisition is in species that exhibit persistent variation in behavioral traits, including species with strong behavioral syndromes and those with alternative reproductive strategies. Behavioral syndromes have become increasingly linked with individual differences in life-history strategies and associated patterns of resource-use (Sih et al. 2004; Sih and Bell 2008). The role that such variation in the allocation of resources might play in the evolution of condition-dependent sexual signals remains an open and exciting question. Third, the arguments above have dealt heavily with details or examples related to material resource-use. However, other currencies such as time, lifespan, or social capital might also be considered from this viewpoint. For temporal currencies, one might consider traits that extend lifespan as participating in the acquisition of condition, whereas the allocation of condition would be realized through patterns of time-budgeting between different tasks (e.g., mate-choice, courtship, feeding, and avoiding predators). Do individuals within a population largely differ in how long they live or how they allocate their time? Finally, anthropogenic influxes of once limiting resources (e.g., nitrogen and phosphorous via use of synthetic fertilizers, sodium via road salt, Snell-Rood et al. 2014) are now changing the resource landscape for many organisms in ways that may impact the development and outcomes of condition-dependency. These disturbances of resources present a critical opportunity to study both the short-term and long-term consequences of reducing environmental variation in the availability of resources at local scales (but potentially enhancing it at regional scales). Work that targets the evolution of life histories in the face of human-induced rapid environmental change is therefore likely to provide fresh insights into some of these more persistent questions in evolutionary biology and sexual selection.

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