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IDEA AND PERSPECTIVE

Condition-dependent traits as signals of the functionality of vital cellular processes

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Abstract

Condition is a nearly ubiquitous term in the behavioural, physiological and evolutionary ecology literature; however, existing definitions are incomplete or ambiguous. This poor conceptualization has led to confusion regarding what is being signalled by condition-dependent traits and how to interpret links between ornamentation and individual characteristics such as nutrient reserves, oxidative state and immunocompetence. I propose that the combined effects of the somatic state, epigenetic state and genotype of an organism determine condition. I define condition as the relative capacity to maintain optimal functionality of vital systems within the body. A condition-dependent trait is a conspicuous feature of an organism that enhances perception of condition. Ornament expression can link to system functionality in at least four ways: (1) resources are traded off between operation of physiological pathways and production of ornaments; (2) a regulatory agent necessary for ornament expression depresses a vital physiological process; (3) ornament production requires a product of a vital physiological process; and (4) pathways are shared between ornament production and vital physiological processes. If the honesty of ornamental traits derives from connections to vital cellular processes then there is no need to invoke a fitness cost of ornamentation to insure signal honesty.

Keywords

Homeostasis, indicator models, individual quality, mate choice, ornamental trait, oxidative stress, sexual selection.

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INTRODUCTION

In a variety of animals, expression of ornamental traits predicts aspects of performance such as recovery from (Lindström & Lundström 2000; Hill & Farmer 2005) and resistance to (Roulin *et al.* 2001) pathogens, capacity to survive an epidemic (Van Oort & Dawson 2005), ability to resist oxidative stress (Perez-Rodriguez *et al.* 2010), cell-mediated immunity (Mougeot 2008), production of functional sperm (Helfenstein *et al.* 2010) and production of better offspring (Huuskonen *et al.* 2009). Behavioural ecologists often conclude that highly ornamented males perform better because these males are in better condition than more poorly ornamented males, and the term 'condition' has become entrenched in the literature on sexual selection and ornamentation. Unless condition is clearly defined, however, invoking condition to explain the success of highly ornamented males offers no real explanation; it is merely another way to describe what is observed.

A clear and unambiguous conceptualization of condition is fundamental for studies of sexual selection and the evolution of ornamental traits because a large body of literature is founded on the premise that ornaments evolve as signals of individual condition. Labs around the world are studying individual condition and ornamental traits in relation to nutrient stores, endocrinological states, immunocompetence, oxidative stress and, most recently, gene expression. A common goal of these studies is to understand why ornamental traits evolved. To date, no theory adequately ties together the diverse physiological processes that have been linked to ornament expression within a single concept of individual condition that is comprehensive and unambiguous.

In this essay, I first discuss the inconsistencies and inadequacies of current definitions of individual condition, and from this starting point, I develop a clear and comprehensive definition of condition. In particular, I show that condition is not synonymous with energy stores. Working from this new conceptualization, I identify the potential mechanisms that can link expression of ornamental traits with condition and discuss how to proceed with studies on condition-dependency in light of the challenges that my approach entails. I make the point that signal honesty does not require resource trade offs or fitness costs. Finally, I conclude with a few examples that illustrate the power and value of a more robust definition of condition.

Poor conceptualization of a fundamental idea

A plethora of papers published in the fields of behavioural, physiological and evolutionary ecology use the term 'condition' in reference to the goodness of an individual, particularly in the contexts of mate choice and sexual selection (reviewed in Andersson 1994; Hill 2002). In conventional usage, individual condition is associated with descriptors such the vigour, viability and desirability. Given the casualness and ubiquity of the use of the terms 'condition' and 'condition-dependent', one would assume that these words are associated with clear and widely agreed-upon definitions. Despite a central place in sexual selection theory, however, the term 'condition' is rarely defined in the literature, and application of the term varies among evolutionary ecologists.

In his influential book *Sexual Selection*, Andersson (1994) defined individual condition as an index of general viability, a definition repeated a decade later in a review of condition-dependency by Cotton *et al.* (2004). In summarizing condition-dependent indicator models of sexual selection, Andersson (page 55) wrote that the 'condition-dependent [ornaments] … develop in proportion to the phenotypic quality of the male'. In a chapter summary, Andersson (page 78) went on to equate condition with the 'nutritional status and health of the male'. Andersson's definitions of condition reflected and reinforced general usage by many behavioural and evolutionary ecologists, but they are neither comprehensive nor unambiguous.

The term 'quality' is often used synonymously with the term 'condition' by researchers, but use of 'quality' is typically just as vague as the application of the term 'condition'. Johnstone *et al.* (2009) made these points explicitly in a recent paper when they wrote: '… the terms quality and condition are rarely defined precisely; … we use them interchangeably …'. An interesting and potentially important distinction between the uses of the terms 'condition' and 'quality' is that the 'genetic quality' of an individual is often distinguished from 'phenotypic quality' (Delhey *et al.* 2006; Weiss 2006). The latter is sometimes presented as being synonymous with condition (Weiss 2006), but the former, often referred to as 'good genes', is usually viewed as distinct from condition (Baratti *et al.* 2010; Ryder *et al.* 2010). Thus, use of the term 'condition' is typically directed at various aspects of the phenotype of an animal (Hegyi *et al.* 2010), but 'quality' encompasses both phenotype and genotype. Each of these generalities is contradicted in the literature.

Several recent reviews have defined individual quality within the framework of quantitative genetics, and in these treatments, authors have equated individual quality with individual fitness or correlates of individual fitness (Hunt *et al.* 2004; Tomkins *et al.* 2004; Wilson & Nussey 2010). These are insightful papers, but there is a level of explanation that is missing from discussions of condition or quality that define the concepts in terms of fitness. Males with better resistance to a pathogen certainly have higher fitness in the presence of the pathogen, but the question of interest is specifically: what qualities of males related to ornamentation makes them more or less susceptible to disease? Quantitative genetic models provide a theoretical mechanism for how natural selection can shape phenotypes, but they leave behavioural and physiological ecologists with little direction for how interpreted data related to the interactions of physiological systems, genetic systems and ornamental traits. There is a critical need for a framework that interprets the relationships between individual condition and ornament display in terms that are rooted more firmly in the animal systems that are the objects of many studies.

NEW DEFINITIONS

In considering the need for a conceptualization of condition that encompasses both genotype and phenotype and that is comprehensive, I propose the following definitions:

Condition is the relative capacity to maintain optimal functionality of essential cellular processes. The environment in which an organism exists acts to disrupt optimal functionality, so another way to state this definition is: *condition is the capacity to withstand environmental challenges*. It follows that: *A condition-dependent display trait is a conspicuous feature of an organism that varies in expression depending on the capacity to withstand environmental challenges*. Condition-dependent traits reveal aspects of condition that are otherwise imperceptible (Fig. 1). I emphasize cellular processes because any emergent characteristics of the organism, such as disease resistance or oxidative state, ultimately depend on performance at the cellular level.

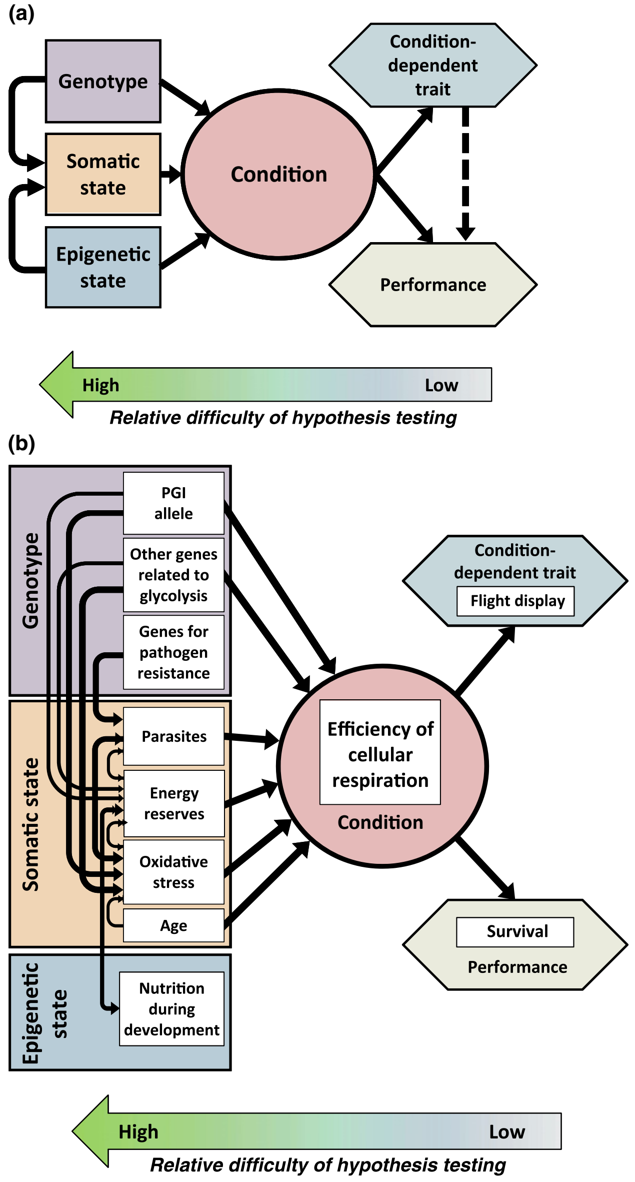

Figure 1 Path diagrams showing pathways through which somatic state, genotype and epigenetic state affect condition, performance and condition-dependent traits. (a) Generic path diagram summarizing the general relationships for any condition-dependent trait. Performance is revealed through the condition-dependent trait (dashed line) even though there need be no causal links between performance and ornamentation. (b) Example of a pathway diagram for a specific condition-dependent trait: flight display in *Colias* butterflies. Watt and colleagues demonstrated the paths linking phosphoglucose isomerase (PGI) genotype to quality of flight displays and performance (reviewed in Wheat *et al.* 2006). Other pathways are hypothetical. For any condition-dependent trait, deducing the pathways between components of condition and the condition-dependent traits will be inherently difficult given the numerous and complex interconnections, whereas the fundamental pathway between the functionality of vital cellular processes (condition) and trait expression should be simpler to test, although knowledge of cellular biochemistry is required. Arrow width is approximately proportional to the predicted strength of interactions.

COMPONENTS OF CONDITION

To better understand the definition of condition that I propose, it is necessary to understand the characteristics of individuals that can contribute to condition. Too often in recent literature, condition is defined as a pool of resources available to an individual (e.g. Rowe & Houle 1996), and this narrow and oversimplified view of condition has lead to a general misunderstanding of what is being signalled by ornamental traits. I recognize three broad components of individual condition – somatic state, genotype and epigenetic state – the sum of which determine the functionality of essential cellular processes (Fig. 1).

Somatic state

Somatic state is the current state of the body of the organism. It includes the phenotype of the organism, but also external influences such as the number of parasites associated with the body, food in the gut, toxins in the bloodstream or stored in the liver or adipose tissue, social status and the quality or quantity of external resources such as food in a territory. The somatic state of an individual also includes damage incurred to the soma, including both physical damage as when a muscle is torn or a shell broken as well as biochemical damage from radiation or chemicals. Somatic state is typically a primary determinant of individual condition.

The aspect of somatic state that is most widely recognized as being related to condition is stored resources and particularly energy reserves. The quantity and quality of stored energy plays a central role in the functionality of many animals. As a matter of fact, reserves of energy are such widely appreciated components of condition that they are often stated as a complete description of condition (Rowe & Houle 1996). Using such definitions, high condition refers to a state of having a large pool of resources available for allocation, and low condition refers to a state of having a small pool of resources.

Despite a tendency to view them as such, energy stores are not a comprehensive description of individual condition. For instance, many wild animals maintain less than maximum fat stores to facilitate mobility, and for such species, there may be little connection between stored fat and condition. Moreover, in captivity and in exceptional circumstances in the wild, animals can accumulate fat stores in excess of what is optimal. These obese individuals have decreased rather than increased their condition by adding to their pool of resources. Even if such circumstances are uncommon, they make the case that stored energy is not synonymous with condition.

Similarly, carotenoid pigments are often considered to be valuable and limiting resources for vertebrates, used both as anti-oxidants and as pigments for ornamental colouration (Olson & Owens 1998; von Schantz *et al.* 1999; Hill 2002). It follows that carotenoid reserves rather than fat stores might equate to condition for some animals. A recent study (Huggins *et al.* 2010), however, showed that accumulation of carotenoid pigments sometimes leads to muscle deterioration. Again, more resource does not inevitably equate to higher condition. No doubt, available resources such as stores of fat or carotenoid pigments are often important components of condition. In many situations in nature, energy stores will be *the* primary determinant of an individual's capacity to withstand environmental challenges, but in other cases energy stores may have little to do with individual condition.

Degree of parasitism is another important component of condition. Individuals that are less compromised by parasites are in better condition than individuals that are more compromised (Wedekind & Folstad 1994; Westneat & Birkhead 1998). Other factors that affect individual 'health' such as toxins in body tissues (Geens *et al.* 2009), auto-immune imbalances (Westneat & Birkhead 1998) and cancerous cell lines (Møller *et al.* 2005) will also affect condition. Many authors also have linked individual condition to the amount of reactive oxidative species (ROS) in tissue – often referred to as oxidative stress (von Schantz *et al.* 1999). It could be argued that, with regard to oxidative state, condition can still be defined as a resource pool if oxidative state is determined by quantities of available anti-oxidants. The level of ROS in tissues, however, is not a simple function of available anti-oxidants (Halliwell & Gutteridge 2007; Costantini 2008). Oxidative stress affects and is affected by parasitism and nutrition, so there is an interplay of factors, a point that becomes important in interpreting how diverse physiological processes are linked to condition-dependent traits (Fig. 1).

Age also affects individual condition. We understand the effects of age most intuitively in our own species: regardless of nutrition, parasitism or oxidative state; a 70-year-old human almost never functions as optimally as a 20-year-old individual. The deterioration of cellular integrity associated with ageing erodes condition (Cote *et al.* 2010).

The sum of factors like available resources, degree of parasitism, oxidative state and age create the somatic state. Somatic state is a key determinant of individual condition, but it is not a complete description of individual condition.

Genotype

Condition is sometimes presented as an entirely phenotypic state, but a genetic component to condition has been recognized as necessary by many authors (e.g. Westneat & Birkhead 1998; Tomkins *et al.* 2004). Good genes models of sexual selection are founded on the premise of genetic-based variation in individual condition (Andersson 1994), and several empirical studies have found significant heritability of measures of condition (reviewed in Gienapp & Merila 2010). The difficulty with including a genetic component to condition is that, at equilibrium, the heritability of fitness must be zero (Fisher 1930). This theoretical constraint is the premise for the lek paradox. A discussion of the lek paradox is beyond the scope of this article; I simply point out that if there is genetic variation related to functionality – such as disease resistance or metabolic efficiency that controls ROS – it will contribute to the condition of an individual.

One aspect of genotype that is widely recognized to affect individual condition – and that is not heritable and hence lays outside of the lek paradox debate – is heterozygosity. In some environments, individuals with higher genome-wide heterozygosity show higher vitality than less heterozygous individuals (Hansson & Westerberg 2002). Inbreeding leads to reduced heterozygosity and is frequently associated with reduced performance. Heterozygosity is an aspect of individual genotype that is likely to play a widespread role in individual condition.

Epigenetic state

Between the genome and the soma lies the epigenome. Events during the life of an individual, and especially during early development, can affect gene expression and hence the phenotype of an animal (Angers *et al.* 2010). Such genetic effects that do not involve changes in the gene sequence can be either pre-transcriptional, involving the packaging of or chemical annotation to DNA (Shilatifard 2006), or can be post-transcriptional (Angers *et al.* 2010). DNA packaging such as occurs through DNA methylation, perhaps the best-studied epigenetic mechanism, can have profound effects on aspects of individual condition like the efficiency and rate of fat deposition (Roemer *et al.* 1997). Epigenetics is a blossoming field in biology, and behavioural and evolutionary ecologists are only beginning to appreciate how an event, such as exposure to a stressor, can have long-term effects on the functionality of an individual (Lynn *et al.* 2010).

Other experiences early in life – particularly molecules transferred from and the environment created by the mother (maternal effects) – which do not involve DNA annotation, can also have life-long and substantial effects on the functionality of vital cellular processes (Mousseau & Fox 1998). The importance of maternal effects to the functionality of adult organisms is abundantly documented in the literature (e.g. Nowicki *et al.* 1998; McGraw *et al.* 2005; Forsberg *et al.* 2011).

Some aspects of condition will only make sense with a consideration of the epigenetic state of the individual. For example, poor nutrition during early development in mice can alter gene expression through methylation of DNA leading to changes throughout adult life in how nutrients are mobilized (reviewed in Gheorghe *et al.* 2010). Studies that include measures of energy mobilization will potentially only make sense if the epigenetic state of each animal is considered. Currently, most data on epigenetic effects come from a few model animals, principally mice among vertebrates, and focus on nutrient reserves, but epigenetic state will be a feature of every organism, and changes in gene expression due to epigenetic effects has the potential to affect a large number of traits.

The growing interest among behavioural ecologists in processes such as gene expression, genetic quality, nutrition, immunology, oxidative pathways, endocrinology and maternal effects demonstrates that the components that I propose as mediators of condition are already being studied, and often being studied within the context of stress responsiveness and sexual signalling (e.g. Buchanan 2000; Mougeot *et al.* 2010b). By formalizing the definition of condition as the capacity to maintain optimal functionality of vital cellular systems – and with the explicit consideration of the genotype, epigenome and somatic state – previously diverse and disparate observations of ornamentation and physiological state can be united within one explanatory umbrella.

DETERMINING OPTIMAL FUNCTIONALITY

By the conceptualization of condition that I propose, the somatic state, epigenetic state and genotype of an organism determine its capacity to cope with environmental challenges. To make use of this concept of condition, researchers need to be able to define the optimal state of body systems and to test whether expression of ornamental traits reflects the capacity to remain near such optima. To make such assessments, researchers will need fundamental understanding of the cellular processes that are proposed to link production of ornamental traits to functionality of vital systems.

In practice, optimality can be determined theoretically or it can be assessed empirically. A theoretical determination of the optimal state of a cellular process is the fundamentally better approach because it provides an objective criterion for how a physiological system would best operate from a design-and-function perspective. In practice, however, we lack sufficient understanding of most vital cellular processes to deduce the optimum state from strictly theoretical considerations. Instead, researchers will typically have to estimate the optimum state from empirical observations. For example, if a researcher wanted to understand the ratio of pro-oxidants to antioxidants in liver cells of House Finches (*Carpodacus mexicanus*) for optimum respiration with minimum tissue damage, he or she would monitor the ROS levels in liver cells in a group of young adult finches that were subjected to no parasitism, had access to excellent diets, were out-bred and had been subjected to no severe stressors during growth and development. The oxidative state in liver cells in response to stressors and its relationship to ornamentation could then be studied relative to the standard established from observations of individuals under minimum environmental duress.

HOMEOSTASIS

The definition of condition that I propose is rooted in the concept of homeostasis, which is the tendency of physiological systems to maintain a stable state (Cannon 1932). If one takes the homeostatic set point as the optimum for functionality, then individual condition as I define it is simply the capacity to maintain homeostasis. This definition of homeostasis, however, deviates from definitions of homeostasis that are commonly adopted in the neurological and endocrinological literature (McEwen 2000; McEwen & Wingfield 2003), which focus more on the neuro-endocrinological processes that guide the body towards a constant internal environment rather than on the homeostatic endpoint *per se* (Day 2005). By defining condition in terms of optimal functionality rather than homeostasis, I avoid the ambiguity that comes with the concept of homeostasis.

Each component system of the body – e.g. the immune system, the neuromuscular system, cellular respiratory system – will have its own critical functions and unique biochemical pathways, and hence each system will have its own homeostatic set point. The sum of the functionality of each component system yields the degree of functionality of the whole organism. It is widely recognized that there can be deviation from homeostasis in one system of the body while numerous other systems maintain high functionality. It is probably frequently the case that poor performance of the body results from deviation from optimal functionality in one or a few component systems. Indeed, a focus on component systems rather than system-wide functionality is a theme in recent studies of individual condition by ecologists. Ornamental traits can potentially signal either whole-organism function or the functionality of single component systems. The ultimate goal of all organisms, however, is optimal performance of the individual as a whole.

Given the different circumstances and variable environments under which homeostasis must be achieved – e.g. during reproduction, migration, periods of muscle exertion – some researchers have proposed the concept of 'allostasis', literally 'stability through change', which is defined 'as the process for actively maintaining homeostasis' (McEwen 2000; McEwen & Wingfield 2003). By this view, homeostasis is a moving target, not a constant set point. From the perspective of studies of condition in the context of sexual selection, it is key to appreciate that the desired functional endpoint for an organism will vary with circumstances and with the environment in which it lives. For example, optimal ROS levels in liver cells for gestating females may not be the same as those for non-breeding males. System optimality must always be defined within the context confronting the study animals.

MECHANISMS LINKING ORNAMENTATION AND SYSTEM FUNCTIONALITY

Expression of display traits can be linked to system functionality in at least four distinct manners (Fig. 2). First, under the Resource Tradeoff Hypothesis, resources needed for a biochemical pathway might also be needed for ornament production (Fig. 2a). It has long been proposed that organisms trade off use of energy for production of ornaments with use of energy for body maintenance (Halliday 1987; Wedekind & Folstad 1994; Westneat & Birkhead 1998). More recently, carotenoid pigments have been proposed to be limiting resources such that organisms must trade off use of carotenoids as ornamental colourants vs. use as anti-oxidants (Lozano 1994; Møller *et al.* 2000). Other resources proposed as necessary for both physiological systems and ornament production include minerals for plumage colouration (McGraw 2003) and alkaloids for pheromone signals in insects (Dussourd *et al.* 1988). This direct trade-off mechanism, often referred to as the 'Y-model' in the life-history literature (Roff & Fairbairn 2007), provides a relatively weak and indirect link between ornament production and the functionality of key body systems, because such a mechanism signals only one aspect of condition – available resources. With such a one-dimensional signal, individuals can, over a short term, produce high ornamentation by over-investing in ornament production, thus diluting the honesty of the signal (Getty 2006). Nevertheless, resource trade off may be a widespread mechanism by which ornament expression is linked to condition.

Shared regulation is a second mechanism that could link production of display traits to key physiological systems (Fig. 2b). Under this Mediator Hypothesis, a regulatory substance exerts opposing effects on vital physiological systems and ornamentation. The first clear articulation of this idea was the influential paper of Folstad & Karter (1992), who proposed that testosterone functions as a two-edged sword – promoting elaboration of ornaments, but suppressing functionality of the immune system. By this idea, only animals with high immune system functionality can withstand the suppression of immune system necessary to produce full expression of ornamentation, and this specific case of the Mediator Hypothesis is widely known as the Immunocompetence Handicap Hypothesis.

Shared regulation of ornaments and vital systems within the body is also the theme of studies on individual condition within a framework of stress response (Buchanan 2000; Bortolotti *et al.* 2009; Mougeot *et al.* 2010b). These studies focus on the hypothalamic–pituitary–adrenal (HPA) axis, which releases glucocorticoid hormones in response to stressors in vertebrates (Buchanan 2000; Bortolotti *et al.* 2009; Mougeot *et al.* 2010b). The HPA axis is the network of communication among body systems, responding to stressors by releasing hormones that stimulate activation or deactivation of a myriad of vital processes including immune defences, respiration and energy mobilization, while at the same time influencing production of ornaments, often through interaction with testosterone.

The Mediator Hypothesis and specifically the Immunocompetence Handicap Hypothesis have been proposed as mechanisms for honest signalling that are distinct from the Resource Tradeoff Hypothesis (Folstad & Karter 1992; Westneat & Birkhead 1998). However, testosterone and glucocorticoids could be viewed as mediators of energy allocation, whereby release of hormones regulates the shunting of energy either to the maintenance of critical systems within the body or to production of displays traits (Wedekind & Folstad 1994). If mediation simply involves energy allocation, then the processes proposed by the Mediator and Resource Tradeoff Hypotheses (Fig. 2a,b) become the same. The strength of the link between condition and ornament expression that emerges from shared regulation depends on the type of shared regulation that is proposed and the constraints that control such mechanisms.

A third and more direct means by which ornamentation might link to the functionality of vital systems is through a dependency of ornament production on the output of a physiological pathway, the Pathway Functionality Hypothesis (Fig. 2c). Ornaments that link to condition in this way are revealing handicaps in the terminology of

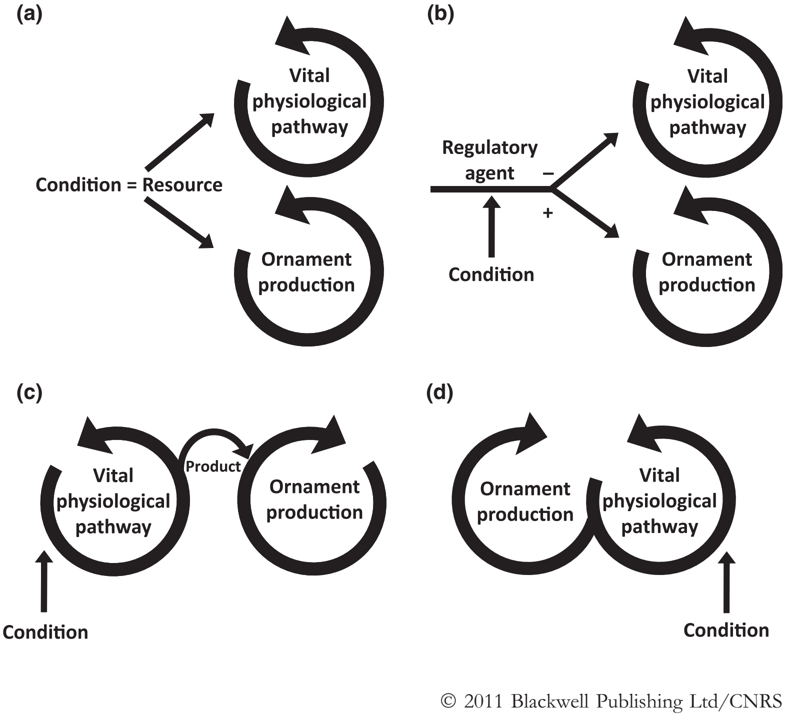

Figure 2 Four mechanisms that could link ornament production with the capacity to maintain the functionality of essential cellular processes. (a) Limiting resources are traded off between vital pathways and ornament production; Resource Tradeoff Hypothesis. (b) A regulatory agent that promotes ornament production depresses a vital pathway; Mediator Hypothesis. (c) Ornament production is proportional to a product of a vital pathway; Pathway Functionality Hypothesis. (d) Ornament production shares a pathway with a vital process; Shared Pathway Hypothesis. Mechanisms are not mutually exclusive.

sexual selection (Andersson 1994). A simple example of this sort of connection between ornament production and vital system functionality involves production of ATP from food through metabolism. If a display trait is tightly linked to ATP availability, such as energy-demanding behavioural displays, then behavioural performance will link to metabolic efficiency (Watt 1992), a basic component of system functionality. Instead of invoking a trade-off in use of stored resources, this mechanism proposes that the efficiency and functionality of basic respiratory pathways – as determined by access to stored energy, but also by other aspects of somatic state as well as the genome and epigenome (see the *Colias* butterfly example below) – dictate the units of energy available for display traits. This mechanism provides a strong link between ornamental traits and pathways related to optimal cellular function because there is a direct intrinsic connection between basic performance of the organism and ornament production.

A fourth means of linking ornament production and systems that are vital to the functionality of the organism is to have pathways shared between vital systems and the systems needed for ornament production, the Shared Pathway Hypothesis (Fig. 2d). Elongated feathers and skeletal features, such as the long tail of male Long-tailed Widowbirds (*Euplectes progne*) and the horns of Bighorn Sheep (*Ovis canadensis*), could represent such ornamental traits that link to system functionality through shared pathways. These ornaments are extensions of structural materials that shape the body, and in this way both critical structural elements of the body and ornamentation rely on the same pathways for production. Production of extra centimetres of tail or additional kilograms of skull is only possible if the systems for feather-keratin synthesis or bone growth are functioning well.

Another potential example of shared pathways linking ornament production to vital processes within the organism concerns feather growth and feather pigmentation. Badyaev & Landeen (2007) observed that hue of carotenoid-based plumage pigmentation in male House Finches is linked to the shape of feathers and hence the processes of feather growth and development. The mechanisms that link feather colour with growth of keratin structures are yet to be resolved, but glycine is required in large amounts for keratinization as well as for maintaining competent levels of the anti-oxidant glutathione. It could be that efficiently functioning redox pathways are vital to both ornamental colour production and basic growth processes in House Finches. The mechanism of shared pathways provides a direct and strong connection between ornamental traits and cellular functionality because the ornament is simply a conspicuous extension of the product of a vital cellular process.

HONESTY WITHOUT PRODUCTION COSTS

The conventional explanation for the maintenance of honest signalling via ornamental traits is that such traits must be costly. The problem with ornaments that exact a maintenance (survival) cost (i.e. Zahavian handicaps; Zahavi 1975), such as a long tail that is a heavy burden to drag around, is the costs of having the ornament counteract the benefits of signalling condition (Maynard Smith 1991). As a result of such difficulties with maintenance costs, recent discussions of indicator models of sexual selection focus on costs related to production of ornamental traits rather than viability costs associated with their maintenance (e.g. Getty 2006). In most contemporary models of sexual selection, the cost of producing an ornament is proportional to the condition of the individual, where condition is typically defined as accumulated resources (i.e. a 'condition-dependent handicap'; reviewed in Andersson 1994). Individuals with abundant resources can invest more in ornament production (pay a lower relative cost for ornament display) than individuals with fewer resources (Zahavi 1977), although Getty (2006) showed mathematically that the relationship between allocation, ornamentation and available energy can be more complicated than originally proposed by Zahavi (1977). Under any of these models, however, this explanation of variation in ornament expression holds only when the primary determinant of condition is the energy stores of individuals (Fig. 2a). Indeed, the notion that honesty requires production costs has bound the concept of condition to being a pool of resources. Growing empirical evidence, however, indicates that even when access to resources is held constant, some individuals will produce more elaborate ornaments than others (Wilkinson *et al.* 1998; Bortolotti *et al.* 2006; Karu *et al.* 2007).

If production of ornaments is inexorably linked to fundamental biochemical pathways (Fig. 2c,d), then ornament expression will be linked to condition – and remain honest – without the need to invoke fitness costs for ornamentation (i.e. it will function as a 'revealing handicap', *sensu* Andersson 1994). This observation potentially solves a critical problem for the concept of signalling quality through ornamentation. Honest signalling decoupled from fitness costs makes the evolution of condition-dependent traits more feasible (Grafen 1990).

EXAMPLES OF DISPLAY TRAITS REVEALING SYSTEM FUNCTIONALITY

Phosphoglucose isomerase and flight displays

The flight displays of butterflies in the genus *Colias* are perhaps the clearest examples of traits that are assessed by females during mate choice and that serve as honest signals of the capacity to maintain high function of essential cellular processes. Flight performance of male *Colias* butterflies hinges critically on the efficiency with which glucose is converted into energy (glycolysis; Watt 1983). A key enzyme in the glycolysis pathway, phosphoglucose isomerase (PGI), is polymorphic in *Colias* populations such that some forms of the enzyme allow for more efficient release of energy from glucose at low temperatures, whereas other allelic variants of PGI allow for greater thermal stability at higher temperatures (Watt 1983, 1992). Depending on environmental conditions, different variants of these enzymes bestow fitness advantages (Watt 1992). The flight display of males makes this key aspect of their genotype perceptible to females choosing mates (Watt *et al.* 1986). These classic studies focused on genotype, but nutritional stores would also certainly affect rate of ATP production and hence flight efficiency. It is likely that factors such as parasites, age and the epigenetic state of the animal could also affect glycolytic efficiency and flight performance (Fig. 1b). Thus, by assessing flight display, a female *Colias* butterfly receives honest and valuable information about the capacity of male *Colias* butterflies to maintain system functionality in the current environment (Watt *et al.* 1986; Watt 1992).

Ornamentation and cellular respiration

A central component of the somatic state of an organism is the level ROS generated during metabolism. More than a decade ago, von Schantz *et al.* (1999) presented an argument that condition-dependent traits as diverse as song, boney protrusions, long feathers, colourful plumage and fleshy growths are especially sensitive to an imbalance of ROS within the body of an individual. These authors proposed that ornamental traits serve as signals for the ability to maintain high functioning of the energy-production systems of organisms. In recent treatments, the idea of von Schantz *et al.* has too often been presented simply as a hypothesis for a trade off of resources – use of carotenoids or other anti-oxidants in ornamental colouration vs. in the detoxification of ROS (Fig. 2b). von Schantz *et al.* briefly presented this idea of anti-oxidants as limited resources, but they did not emphasize a trade off in use of pigments. Rather, the key contribution of the von Schantz *et al.* paper was the hypothesis that the link between condition and ornamentation lies in the connections between ornament production and the efficiency of cellular respiration systems that generate ROS – in other words, in the capacity for high performance by the redox reactions in the mitochondria of cells.

The hypothesis that ornamental traits are signals of the capacity to maintain optimal system functionality holds the potential to make sense of some bewildering sets of studies, such as the literature on oxidative stress, parasitism and carotenoid ornamentation that has been published in the past decade. The hypothesis that carotenoid pigments are critical limiting resources that are parcelled between use in ornamental colouration vs. use in immune defence or to neutralize ROS (Lozano 1994; Møller *et al.* 2000) has been supported in some studies, but not in others (Costantini 2008; Costantini & Møller 2009). A meta-analysis indicates that carotenoids constitute only a small fraction of anti-oxidants used in avian systems (Costantini & Møller 2008), suggesting that the theoretical basis for the pigment trade-off hypothesis is weak. There is a growing consensus that this pigment-trade off hypothesis is inadequate to explain the evolution of carotenoid-based colour signals (Costantini 2008; Costantini & Møller 2009).

There remain, however, tantalizing connections between carotenoid ornamentation, the immune system and the oxidative state of organisms. In many studies, carotenoid supplementation has been shown to enhance ornamental colouration (reviewed in Hill 2006), and in a few studies, carotenoid supplementation has been shown to enhance immune activity (Blount *et al.* 2003; McGraw & Ardia 2003) and growth rate of young (Biard *et al.* 2006; Cucco *et al.* 2006). Stimulation of the immune system has also been shown to affect carotenoid ornamentation (Faivre *et al.* 2003) and oxidative state (Mougeot *et al.* 2010a). If condition is taken as the functionality of vital systems such as the immune system and redox pathways, rather than simply available anti-oxidants, then the complex connections between colouration, disease resistance and oxidative state become more explicable. The prediction from the Pathway Functionality and Shared Pathway Hypotheses is that aspects of carotenoid utilization as well as immune responsiveness are intimately tied to the respiratory reactions that produce free radicals, as proposed by von Schantz *et al.* (1999). In this way, ornamentation reveals the functionality of these systems – the capacity to maintain redox homeostasis. Stressors like pathogens disrupt redox reactions causing among other deviations from homeostasis, a build up of ROS. If the pathways needed for ornament production are linked to such redox pathways, then ornamentation will be diminished with any challenge to these vital systems. A focus on just the pigments misses the key connections between overall system function and ornamentation.

Cognition

Cognitive ability is an important component of fitness in some animals (Keagy *et al.* 2009), and it has been proposed that cognition is associated with individual condition (e.g. Sandi 2004). Neural development and neural processing may represent among the most difficult and demanding cellular processes faced by vertebrates (Gotz & Huttner 2005; Burkitt 2006) such that deviation from optimal functionality in fundamental cellular pathways will be manifested in the performance of neural systems and hence cognition. One would expect behavioural displays, like bird song and complex courtship movements that rely on the same basic neural systems as cognition, to be linked to cognition (Nowicki *et al.* 1998). Perhaps more interesting, recent studies link aspects of cognition with morphological ornaments like plumage colouration (Mateos-Gonzalez *et al.* 2011). At present, there is no proposed mechanism that adequately explains such associations except the Resource Tradeoff Hypothesis, which proposes that high-condition males have the energy needed for both neural development and ornament development. The Pathway Functionality and Shared Pathway Hypotheses, however, provide a novel and potentially more powerful explanation for a positive association between cognition and ornamentation. If the same pathways or products of such pathways are critical for both neural development/processing and production of ornamentation, there would arise a positive association between cognition and ornamentation.

REFOCUSING STUDIES OF ORNAMENTATION

The new concept of condition that I propose in this article is more inclusive and less ambiguous than previous conceptualizations, but such new thinking about condition is only useful if it can be operationalized. How can this new concept of condition be tested and in what ways will it improve the current approach to the study of ornamental traits?

As pointed out in a critique by Prum (2010), any links between positive aspects of individuals and ornamentation have been sufficient in many recent studies to lead to conclusions that an ornament evolved as a condition-dependent signal of individual quality. Such an approach has led to conclusions that nearly all ornamental traits of all animal species are condition dependent. The result is a stagnating literature on ornamental traits with many claims of condition-dependent signalling. To be sure, there have been outstanding studies in the recent literature (which are the foundation of this paper), but there have been relatively few new insights into why and how ornamentation evolved. By recasting the concept of condition as a signal of functionality of vital cellular processes, I challenge researchers to move beyond simple statistical associations. Instead, I encourage a focus on understanding the mechanisms for trait production and how the production of an ornament might link to basic cellular processes. It should not be assumed that all visually striking or conspicuous traits will be associated with fundamental cellular processes, because not all conspicuous traits will be condition-dependent ornaments.

The inadequacies of the current approach being used to study the signal content of ornamental traits can be visualized in a path diagram that outlines my hypothesis for the links between display traits and system functionality (Fig. 1). Many current research programmes test for links between individual components of condition (which I have lined up along the left side of the figure) and ornament expression (illustrated on the right). The interactions among the potential components of condition are generally complex, as indicated by the network of potential pathways, with multiple pathways linking many components and condition. Due to these complex interactions and indirect links among components, studies focused on factors related to condition on the left side of the figure will be inherently difficult to interpret. In contrast, the predicted relationship between cellular functionality and ornament display is more straightforward and easier to interpret in a meaningful way. Testing for this key relationship reveals something fundamental about the signal content of the ornamental trait and allows for a true test of the condition-dependency of an ornament. The challenge in studying links between vital systems and ornamentation lies in the technical difficulties of understanding physiological processes on a cellular level. Once a fundamental link between maintenance of optimal cellular function and ornamentation is established, then working towards the left in the diagram to deduce the contributions of specific components of condition becomes more enlightening.

As an example of the application of the approach that I advocate, consider the current literature on melanin and carotenoid feather colouration as sexual signals. Dozens of studies have looked at the function and condition-dependency of carotenoid and melanin colouration (reviewed in Hill 2007). Clear distinctions have been noted in how these two colour traits correlate with environmental parameters and with the performance of birds, and a series of papers has been published debating whether carotenoid and melanin pigmentation are each condition-dependent signals of quality or not (McGraw & Hill 2000; Jawor & Breitwisch 2003; Griffith *et al.* 2006). As this literature focuses on correlations between colouration and components of condition such as parasites, nutrition and oxidative state, I think that it largely misses the point. The key question is not a simple 'yes' or 'no' concerning whether melanin or carotenoid pigmentation is linked to a vaguely defined state of condition or not; rather, the salient point is understanding the mechanisms by which these two biochemically distinct forms of feather colouration are produced and how each type of pigment production links to fundamental cellular processes.

Already, the study of melanin pigmentation is moving towards a focus on the physiological pathways that might link ornamentation and functionality of basic cellular processes. A link between ornament expression and a range of stress-response mechanisms has recently been proposed for melanin-based colouration. Pro-opiomelanocortin (POMC) genes bind melanocortin-1-receptor, which is a principal controller of amount of melanin production, and hence plays a role in the amount of dark melanin colouration – like dark spots or black throat patches – displayed by an animal. These same POMC genes also bind melanocortin receptors that play a role in the regulation of diverse and basic processes such as immune function, energy regulation and the HPA stress response (Ducrest *et al.* 2008). The details of how these colour-producing and regulatory systems are linked remain unresolved. The intriguing idea is that the same processes that control immune function, energy regulation and the HPA stress response – and hence are intimately tied to the maintenance of optimal functionality at the cellular level – also produce melanin pigments (Ducrest *et al.* 2008). If this hypothesis proves correct, then melanin pigmentation will be shown to be a condition-dependent signal in the sense that animals with extensive melanin pigmentation will be those animals that have a somatic state, genotype and epigenetic state that allow them to maintain a high functioning energy balance and immuno-defensive state. Studies of the mechanisms that might link carotenoid pigmentation to basic cellular processes have not progressed as far as studies of melanin pigmentation, but the links between immune function, ROS and carotenoid pigmentation that I discussed in a previous section of this article suggest that the production of carotenoid pigmentation might link in a different way to basic cellular processes.

The key distinctions between the aspects of animals that are signalled by carotenoid pigmentation vs. melanin pigmentation (Badyaev & Hill 2000; Owens 2006) presumably reflect different pathways to which these two types of pigments are linked. Assessing the links between pigmentation and functionality provides a testable means to reconcile two widespread statements in the literature: carotenoid and melanin are condition-dependent traits; carotenoid and melanin pigmentation relate to different aspects of individual performance.

CONCLUSIONS

The prospect of disentangling the relative contribution of somatic state, genotype and epigenome to individual condition is daunting. These three components of condition are expected to be highly interrelated (Fig. 1). For example, poor nutrition early in life may change the body composition of an animal into adulthood. Such an effect might come in part because the individual must build its adult reserves from a lower starting point, but exposure to a low-food environment early in life might also cause DNA annotation that changes patterns of gene expression that predisposes the animal to absorb less food and carry less fat. These epigenetic factors could never be isolated from effects of genotype or somatic state if one is simply assessing adult animals. For many studies of condition, however, the most important point is appreciating that many components underlie condition and that condition is not simply the fat reserves that an animal carries. Disentangling such interdependent characteristics will not be necessary in most studies. What is measureable is system functionality, and that should be the focus of studies of ornamental traits that are proposed to be condition dependent.

For all its beauty and complexity, an organism is a network of chemical reactions. The ability to effectively survive and reproduce is ultimately dictated by the efficiency and functionality of biochemical systems in the body. There is no more valuable signal to a female choosing a mate or to a territorial male assessing a rival than the functionality of the essential cellular systems of the individual they are assessing. Ornamental traits as signals of the capacity to maintain optimal functionality make sense from the standpoint of most desired information by the receiver.

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