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Functional Approach to Condition

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Introduction

Animal signaling is commonly thought to be costly. Signaling costs can arise via a variety of avenues, including energy expenditure, predator attraction, and so on (reviews in Zuk and Kolluru, 1998; Kotiaho, 2001), and are predicted to increase with signal expression (e.g., size, amplitude, and intensity; Johnstone, 1997). Due to these costs, signaler condition, which is hypothesized to be a reflection of a signaler's genetic quality, is expected to influence the level of signal expression one can afford (Zahavi, 1975), resulting in a positive correlation between signaler condition and signal expression – that is, condition-dependent signaling (Zahavi, 1977; West-Eberhard, 1979; Andersson, 1982; Nur and Hasson, 1984; Zeh and Zeh, 1988; von Schantz et al., 1999).

Despite the wealth of theoretical and empirical work on condition-dependent signaling, the term condition itself is somewhat enigmatic. An individual's condition is a theoretical construct associated with the acquisition and allocation of nutritional resources, and is assumed to be an integral part of an individual's health, vigor, and viability (Andersson, 1982; Nur and Hasson, 1984; Zeh and Zeh, 1988). Condition is often thought of as polygenic in nature, capturing much of the additive genetic variance responsible for viability, spanning numerous loci across the genome (Andersson, 1982; Rowe and Houle, 1996); however, like other quantitative traits, condition is also influenced by the environment as well as by interactions between an individual's genotype and the environment (Hunt et al., 2004b).

In this chapter, we use a widely accepted working definition of condition provided by Rowe and Houle (1996)—a pool of resources acquired from the environment, which is available for allocation to various fitness-related traits (see Figure 9.1). An individual's condition sums numerous processes throughout its lifespan and is constantly fluctuating as resources are acquired and allocated to different functions (Figure 9.1). This broad definition of condition incorporates information on the resources available throughout an individual's life—it encompasses the resources used during development to create structures (including those used for resource acquisition), the resources used in the normal functioning of an individual (i.e., its physiology), and the resources currently available in an individual's energy stores (Figure 9.1). The decisions directing resource acquisition and allocation strategies (Figure 9.1) are ultimately influenced by both an individual's environment (e.g., presence/absence of predators and food abundance) and its genotype (e.g., heritable traits related to foraging ability, digestion, and learning).

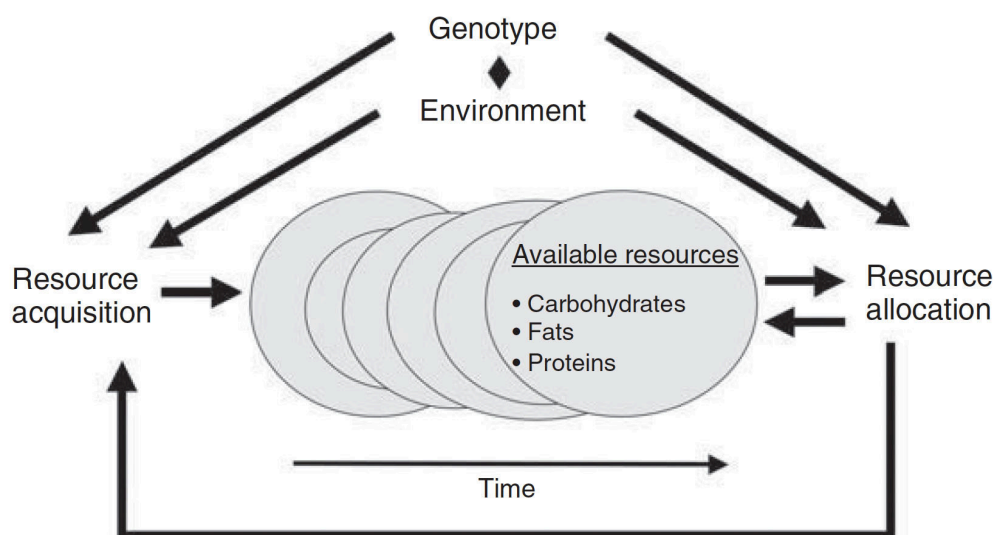


Figure 9.1. A representation of the complex interactions (indicated by diamond) between an individual's genotype and environment and their interactions with resource acquisition, available resource pool, and resource allocation. Resource acquisition and/or resource allocation can vary over the lifespan of individuals, resulting in different sizes of resource pools (i.e., condition) over time.

Practical Approaches to Condition

Proxies of Current Energy Reserves

Scientists interested in condition-dependent signaling typically consider an individual's current condition (or current energy stores) by utilizing proxies such as body condition (a variety of indices have been used to estimate this; see Table 9.1). Some studies use measures of overall body weight or volume, while others measure the physical size of body parts assumed to be indicative of energy reserves (e.g., shape of abdomen in birds; Owen, 1981). While potentially easy to quantify, these absolute measurements are confounded with body size, which may give little or no information about differences in current energy reserves (Piersma and Davidson, 1991), but instead could reflect larger quantities of non-energy related compounds (e.g., water, bone; Tomkins et al., 2004).

The vast majority of indices currently used attempt to control for body size by investigating the relationship between a dynamic body variable thought to represent energy reserves and a static, or less dynamic, estimate of overall body size (Jakob et al., 1996). Commonly, scientists use body weight or volume, measures that are known to change rapidly with resource acquisition, and control for body size using the length/width of skeletal (or exoskeletal in invertebrates) structures that are either fixed during certain life stages or remain effectively static over the time period of interest. Such methods vary tremendously and are the topic of much debate (e.g., Jakob et al., 1996; Garcia-Berthou, 2001; Peig and Green, 2010). Here, we simply highlight a few of the more common body condition indices and direct our readers to the relevant literature regarding the issues associated with each.

The simplest body condition index is the ratio index, which is calculated as body weight, or volume, divided by a linear measure of body size. Ratio indices provide a good descrip-

TABLE 9.1. Examples of Proxies Used to Estimate Body Condition Across Taxa

Proxy	Measure	Group	Citation
<i>Estimates of Reserves via Absolute Body Measures</i>			
Body size	Wing size	Insects	Hooper <i>et al.</i> (1999); David <i>et al.</i> (2000); Blanckenhorn and Hosken (2003); Van Homrigh <i>et al.</i> (2007)
Mass	Shape of abdomen	Birds	Owen (1981)
	Pectoral muscle size	Birds	Perez-Rodriguez <i>et al.</i> (2006)
		Birds	Gonzalez <i>et al.</i> (1999); Hill (2000); McGraw and Hill (2000);
Volume		Insects	Johnsen <i>et al.</i> (2003); Perez-Rodriguez <i>et al.</i> (2006)
			Kotiaho <i>et al.</i> (2001); Kotiaho (2002); Rantala <i>et al.</i> (2003);
		Spiders	Scheuber <i>et al.</i> (2003a)
		Birds	Mappes <i>et al.</i> (1996); Rundus <i>et al.</i> (2011)
Growth rate		Birds	Sibly <i>et al.</i> (1987)
Trait asymmetry		Birds	Zuk <i>et al.</i> (1990); Keyser and Hill (1999)
		Birds	McGraw <i>et al.</i> (2002)
<i>Estimates of Reserves Controlling for Body Size</i>			
Relative weight		Fish	Neuman and Flammang (1997)
Density	Weight/volume	Spiders	Moya-Larano <i>et al.</i> (2008)
Ratio	Weight/fixed body measure	Amphibians	Arntzen <i>et al.</i> (1999)
		Fish	Tonn <i>et al.</i> (1989); Greenstreet (1992); Candolin (2000)
Slope adjusted ratio		Lizards	van Berkum <i>et al.</i> (1989); van Marken Lichtenbelt <i>et al.</i> (1993)
		Birds	Moller (1987); Evans and McMahon (1987);
		Spiders	Shamble <i>et al.</i> (2009); Wilgers and Hebets (2011)
Residual	Dynamic body part/static body part	Spiders	Anderson (1974); Watson (1990); Jakob (1991)
	Weight/(body size) ^a /slope ^a	Fish	Kulling and Milinski (1992); Nicoletto (1993)
	Weight/body size	Insects	Pierce <i>et al.</i> (1985); Juliano (1986); Baker (1989)
		Birds	Andersson (1992); Carranza and Hidalgo de Trucios (1993); Hamer and Furness (1993);

(continued)

TABLE 9.1. (Continued)

Proxy	Measure	Group	Citation
			Schluter and Gustafsson (1993); Veiga (1993); Qvarnstrom (1999); Weatherhead <i>et al.</i> (1999); Merila <i>et al.</i> (2001); Moller and Petrie (2002); Doucet and Montgomerie (2003); Sarasola <i>et al.</i> (2004); Ardia (2005); Bize <i>et al.</i> (2006)
			Jennions and Backwell (1998)
			Marden and Rollins (1994); Wagner and Hoback (1999); Gray and Eckhardt (2001);
			Holzer <i>et al.</i> (2003); Scheuber <i>et al.</i> (2003b)
			Dobson (1992); Dobson and Michener (1995); Woodroffe (1995); Dobson <i>et al.</i> (1999)
			Fisher (1999); Schulte-Hostedde <i>et al.</i> (2001); Blackwell (2002)
			Murphy (1994); Judge and Brooks (2001)
			Dunlap and Mathies (1993); Weatherhead <i>et al.</i> (1995); Keller <i>et al.</i> (1997);
			Cuadrado (1998); Shine <i>et al.</i> (2001)
			Uetz <i>et al.</i> (2002); Hoefler <i>et al.</i> (2008); Wilder and Rypstra (2008);
ANCOVA	Weight with body size covariate	Birds	Lomborg and Toft (2009); Wilgers <i>et al.</i> (2009); Taylor <i>et al.</i> (2011)
			Torok <i>et al.</i> (2003); Parker and Garant (2004)
			Lomborg and Toft (2009); Wilder and Rypstra (2008)
			Bize <i>et al.</i> (2006)
PCA	Factor loading with size and mass	Birds	Peig and Green (2009); Peig and Green (2010)
			Peig and Green (2009)
			Peig and Green (2009)
Scaled mass index	Body mass scaled by mass/length relationship	Mammals	
		Reptiles	

PCA, principal component analysis.
“Slope of relationship determined from entire population.

tive index that is comparable across groups or populations and has been used consistently in the literature (Table 9.1). However, the ratio index is often not independent of body size, which limits conclusions on body condition alone (for criticisms, see Blem, 1984; Ranta et al., 1994; Jakob et al., 1996). Additional methods to quantify body condition separate the effects of energy reserves and body size by incorporating size measures as a covariate in analysis of covariance (ANCOVA) models, and analyzing variation in body weight or other dynamic measures (Garcia-Berthou, 2001). Alternatively, researchers use the residuals from a linear regression of body weight against some linear measure of body size. The use of residuals has become increasingly common over the last two decades (reviewed in Green, 2001). However, numerous studies have cautioned their use due to potential violations of statistical assumptions (e.g., linear relationships and independence; Green, 2001), alterations of trait allometric relationships (Kotiaho, 1999), or limitations in comparisons across individuals varying in size (Kotiaho, 1999) and across heterogeneous groups (e.g., populations; Jakob et al., 1996). Ultimately, the choice of body condition index is non-trivial as results and conclusions often vary widely, based on the chosen index (Bolger and Connolly, 1989; Jakob et al., 1996; Moya-Larano et al., 2008; Peig and Green, 2010).

Body condition indices have at times been found to be good predictors of specific energy reserves (Sibly et al., 1987; Schulte-Hostedde et al., 2001; Cattet et al., 2002; Ardia, 2005; Schulte-Hostedde et al., 2005); however, as mentioned previously, variation in these proxies may also simply reflect variation in other compounds (e.g., water; Schulte-Hostedde et al., 2001, 2005). Additionally, these snapshot indices do not provide information regarding specific types of energy stores, or how these energy stores vary throughout development. Given that different animals, and even different developmental stages, may have different nutritional requirements and may require different essential elements, the black box approach commonly used to estimate body condition provides little information as to the mechanisms underlying condition, and how they may differ across taxa (Lailvaux and Irschick, 2006). Condition indices also fail to illuminate variation in the ratios of specific energy reserves, which may be important as measures of different types of energy reserves do not necessarily correlate with one another and can even provide contradictory results (e.g., Blanckenhorn and Hosken, 2003). As such, a more detailed approach incorporating direct measurements of specific energy reserves for allocation to fitness-related traits may prove to be important for a detailed understanding of the evolution of condition-dependent signaling.

Direct Measures of Current Energy Reserves

Organisms convert newly ingested organic matter into three main groups of compounds: carbohydrates, fats, and proteins. Simple carbohydrates, such as glucose, are used to fuel metabolism, which may be important for energy-demanding behavioral displays. If not used immediately, simple carbohydrates are converted to energy storage compounds, such as starch and glycogen (complex carbohydrates), which can be later accessed as an energy source to fuel aerobic or anaerobic metabolism. Due to storage constraints associated with glycogen (i.e., size, hydrophilic), the majority of excess carbohydrates are broken down to synthesize compact long-term energy storage, like fats.

Fats serve both metabolic and structural functions. They are likely an important energy reserve for animals where feeding is limited for long periods of time. Importantly, fat stores can be accumulated in one life stage for use in another. Additionally, fats are useful for delivering other important resources, such as carotenoids, which are known to perform a variety of physiological functions (reviewed in Olson and Owens, 1998).

Proteins serve important structural and functional roles, and have been found to be necessary for normal development in a variety of animals (e.g., Eagle, 1959; House, 1961). The amino acids required for protein synthesis can either be consumed or be synthesized in the body. Proteins also serve as a long-term energy storage molecule; however, the efficiency and extent to which proteins can be effectively digested by certain taxa may vary (e.g., insects; Chapman, 1998). Unlike fats, there is no specialized store for proteins and thus energy must come from catabolism of both structural and functional organs (e.g., muscles, digestive organs), where excessive depletion can harm animal performance (Jenni and Jenni-Eiermann, 1998). Because of this, the relative protein contribution to the energy budget is, for example, only about 5% in migrating birds (Jenni and Jenni-Eiermann, 1998), and protein catabolism for metabolic energy is typically only utilized when other energy stores are depleted (king penguins: Robin et al., 1988; green sea turtles: Jessop et al., 2004).

Given differences in their accessibility, their storage, and their potential use, detailed knowledge of an organism's (i) nutritional requirements, (ii) abundance of specific energy resources (e.g., quantification of carbohydrates, fats, and/or proteins) across their lifespan, and (iii) allocation strategies will aid our understanding of targets of selection surrounding condition-dependent signaling.

Manipulating Energy Reserves

An initial first step toward documenting condition-dependent signaling often involves quantification of signal/display expression in wild caught animals and subsequent correlations with some proxy of condition (e.g., body condition index and parasite load; Hoglund et al., 1992; Buchholz, 1995; Thompson et al., 1997; Doucet and Montgomerie, 2003). While such an approach is informative, it cannot provide information about the relative influence of genotype versus environment in determining the witnessed variation. Thus, often in conjunction with such field-based correlative approaches, scientists employ more controlled environmental manipulations to experimentally alter current body condition and examine corresponding changes in signal expression.

Manipulating nutrition (quantity and quality), density, parasite load, temperature, and so on can lead to measurable differences among treatment groups in various proxies associated with condition (reviewed in Cotton et al., 2004). Regardless of the manipulation, treatments commonly represent two extremes (e.g., high vs low nutrient levels, parasitized vs unparasitized). While using such extreme manipulations increases the power to detect a relationship between current condition and signal expression, it removes much of the potentially relevant middle of the population distribution in phenotype response. Therefore, Cotton et al. (2004) suggest the use of a broader set of manipulations, providing a more comprehensive assessment of the relationship between various proxies of condition and signal expression.

The majority of studies of condition-dependent signaling thus far have utilized either phenotypic manipulations across randomly sampled individuals or genetic controls (e.g., Kodric-Brown, 1989; Houde and Torio, 1992; Birkhead et al., 1998; Grether, 2000). Such approaches can either swamp out or eliminate potential genetic variation among individuals and thus do not allow variation in condition to manifest solely as a result of additive genetic variation among individuals (Cotton et al., 2004). Given that many hypotheses relating to the evolution of condition-dependent signal expression (e.g., various indicator mechanisms) assume phenotypic quality/viability (i.e., condition) to be heritable (e.g., Andersson, 1982; Hamilton and Zuk, 1982; Iwasa et al., 1991; Iwasa and Pomiankowski, 1999),

future studies are needed which focus more on the genetic basis of condition (Tomkins et al., 2004).

Condition and Animal Performance

Allocation of Energy Reserves

The pool of current energy reserves that an individual possesses is expected to directly relate to its ability to afford costly activities, such as the development of elaborate morphological characters and the production of behavioral displays that may enhance reproductive success, and/or the engagement in other behaviors and physiological processes that may enhance survival. As such, variation in this pool of resources should translate into variation in animal performance, where performance is defined as an organism's ability to conduct various ecologically relevant tasks related to survival (e.g., foraging, running speed, and overall endurance) and/or reproduction (e.g., fighting ability and courtship displays; see Lailvaux and Irschick, 2006; Irschick et al., 2008). Here, we discuss the relationship between various measures of energy reserves and animal performance, highlighting studies in which detailed knowledge of energy stores has been crucial.

Body condition indices have been shown to correlate with various fitness measures—individuals in better body condition survive better (e.g., Naef-Daenzer et al., 2001; Shine et al., 2001; Murray, 2002; Morrison et al., 2007) and have overall higher reproductive success (e.g., Chastel et al., 1995; Dobson and Michener, 1995; Otronen, 1995; Wauters and Dhondt, 1995). Direct links between available carbohydrates and animal performance have also been documented. During hovering flight in the broadtailed hummingbird (*Selaphorus platycercus*), fasting individuals switch from primarily metabolizing fats to oxidizing mainly carbohydrates 20–60 minutes after a meal (Welch et al., 2006). Similarly, up to 78% of the fuel required for hovering flight in the nectarivorous bat, *Glossophaga soricina*, was shown to come from recently ingested carbohydrates (Welch et al., 2008). For such animals that engage in energy-demanding behavioral displays, we might expect a relationship between display performance and exogenous sugar uptake, making the direct measurement of carbohydrates potentially informative. Ingested carbohydrates are also an important energy source for sex pheromone expression in the cockroach, *Nauphoeta cinerea* (South et al., 2011) and when given a choice, males consumed diets with higher carbohydrate content (South et al., 2011).

In addition to the immediate use of carbohydrates, glycogen stores are also known to be important in energy-demanding behavioral displays. In the mosquito, *Anopheles freeborni*, males feed on nectar during the night and store the acquired carbohydrates as glycogen for use during swarming flight the next day (Yuval et al., 1994). In fiddler crabs, males wave a single large claw during courtship displays to attract females. One of the primary stores of energy in decapod crustaceans is glycogen, which is readily mobilized into blood glucose for ATP synthesis during fights and leg-waving displays. Matsumasa and Murai (2005) found variability in resting male blood glucose levels, suggesting standing variation in male quality. Additionally, they found that males who waved their legs more frequently had higher lactate levels, a byproduct of glucose catabolism, in their bloodstream, suggesting a positive correlation between glycogen energy reserves and performance. Glycogen is also a known energy source for frogs during metabolically demanding calling activity (Bevier, 1997).

Both survival and fecundity have been shown to increase with increased fat reserves across a variety of taxa (Elowe and Dodge, 1989; Atkinson and Ramsay, 1995; Vleck and

Vleck, 2002) and fat stores accumulated during early developmental stages are known to influence subsequent life stages. For example, accumulation of fat stores by juveniles has been found to be crucial for terrestrial survival post-metamorphosis in amphibians (Scott et al., 2007) and for reproductive success in damselflies (Plaistow and Siva-Jothy, 1996). Studies on birds also provide evidence that body condition during juvenile stages can influence adult body condition (e.g., fat reserves), and that these fat reserves are important for survival during strenuous activities, such as migration (Merila and Svensson, 1997). Given the above-demonstrated relationships between early life fat storage and later life performance, fats provide an excellent example of the need for a more inclusive (incorporating more than simply current body condition indices) and detailed (quantifying fats vs carbohydrates or proteins) examination of an animal's energy reserves when relating it to performance.

Proteins are commonly used in the development of a variety of structures, including bird feathers, which are produced by keratins. In dark-eyed juncos, *Junco hyemalis*, birds on protein-enriched diets expressed faster feather growth rates along with larger and brighter white plumage ornaments on the tail, suggesting the intake of specific energy compounds (i.e., diet quality) can result in condition-dependent expression (McGlothlin et al., 2007). Similar results have been found in house sparrows, *Passer domesticus*, where male house sparrows on protein-enriched diets have large white wing bars (Poston et al., 2005). In addition, male house sparrows had brighter (i.e., not as black) but not bigger melanin-based black bibs when fed diets lacking melanin-precursors compared to males fed normal diets (Poston et al., 2005).

In many cases, energy-demanding activities, such as flight, do not rely solely on one energy resource type. For example, long-distance migrations require tremendous energy reserves from multiple sources (e.g., glycogen, fats, proteins). In several species, protein catabolism increases when fat reserves are near depletion (<5–10%; Schwilch et al., 2002; Bauchinger and Biebach, 2001). Nonetheless, the relative utilization of different compounds varies across birds and has been found to be a function of their diet (Gannes, 2001), suggesting a direct link between the types and amounts of resources acquired and those used during performance.

Trade-Offs in Resource Allocation

The allocation of resources from a finite pool (although the pool is rarely finite as currently available resources are frequently used for additional nutrient acquisition – e.g., to sustain foraging) is expected to result in trade-offs in resource allocation, such that allocating resources to one trait reduces the available resources for allocation to other traits (Rowe and Houle, 1996; Zera and Harshman, 2001). For individuals with fewer energy reserves, it might be necessary to allocate more resources to basic survival requirements, making investment in other traits (e.g., reproductive) relatively more costly. However, an individual's optimal resource allocation among traits aims to maximize overall fitness and thus depends not only on the amount of available resources, but also on the strengths of various selection sources (Rowe and Houle, 1996). For example, in reproductive systems exemplified by strong female choice, signalers might maximize fitness by allocating greater resources to secondary sexual traits (e.g., ornamentation and displays), or other traits under selection via females, thereby gaining increased reproductive success even at a cost to other life-history traits. Such a trade-off has been found in the field cricket, *Teleogryllus commodus*, in which high body-condition males invest so many resources to their sexual displays that they tend to die younger than lower condition males (Hunt et al., 2004a).

Similarly, in *Hygrolycosa rubrofasciata* wolf spiders, males induced to court at higher rates suffered greater mortality and lost more weight over the trial than did males that courted at lower rates, suggesting that allocation of energy reserves to courtship reduced their availability for allocation to survival (Mappes et al., 1996). However, within the high courting group, males that maintained high courtship levels survived better, suggesting variation in an individual's ability to afford the high energetic costs associated with the display (Mappes et al., 1996). This variation could be attributed to body condition, where larger resource pools may afford greater levels of reproductive trait expression while simultaneously experiencing greater viability (Jennions et al., 2001).

Signaling systems, in which there is a working knowledge of the resources utilized during costly signal expression and how these resources are used in other fitness-related functions, can facilitate our understanding of the details surrounding the selection and subsequent evolution of condition-dependent signaling. For example, carotenoid-based coloration is found in numerous animal taxa (e.g., birds, fish, amphibians, reptiles, insects, mollusks, crustaceans; Matsuno, 2001; McGraw et al., 2005), producing some of the most brilliant coloration in the animal kingdom (Olson and Owens, 1998). Carotenoid pigments (e.g., carotenes, xanthophylls) cannot be synthesized by animals; instead they must be acquired through consumption of carotenoid-rich food. Carotenoids also play important roles throughout the body (e.g., enhancing immune system function: antioxidants, free-radical absorbers; reviews in Lozano, 1994; Shykoff and Widmer, 1996; Lozano, 2001; and serving as photo-protectants: example in Japanese Quail; Thomson et al., 2002), yet despite these important roles, carotenoids appear to be readily allocated to a signaling function. Prior research has shown that individuals in good nutritional condition (i.e., high reserves of carotenoids) and in good overall health can afford to allocate greater resources to a colorful carotenoid-based display (e.g., McGraw and Hill, 2000; McGraw and Ardia, 2003; Saks et al., 2003; Mougeot et al., 2007), and females favor those males with larger or brighter displays (examples in guppies: Endler, 1983; house finches: Hill, 1990; three-spined sticklebacks: Bakker and Mundwiler, 1994). The putative trade-off in carotenoid resource allocation within males and the seeming importance of this trait in female mate choice can lead us to generate testable predictions about the strength of sexual selection for condition-dependent carotenoid-based signaling. For example, we might expect females to pay more attention to carotenoid-based signals in environments with low carotenoid resource availability. Grether (2000) tested this hypothesis in the guppy, *Poecilia reticulata*, across a gradient of carotenoid availabilities and found no support. Nonetheless, by understanding the physiology underlying signal expression, we gain further insights into traits that compete for limited resources within the body and the precise trade-offs that might result.

Time Scales for Resource Allocation

Resource allocation is dynamic in nature and condition-dependent signals involved in reproductive behavior can potentially reflect the pool of available resources at different time scales (Johnstone, 1995). For example, morphological traits associated with signaling can potentially provide receivers with information about the resource pool available to an individual throughout the development of a particular structure (e.g., deer antlers: Clutton-Brock et al., 1982; Suttie and Kay, 1983; horns in beetles: Emlen, 1994; spider coloration: Shamblé et al., 2009; Rundus et al., 2011; Taylor et al., 2011). Alternatively, morphological traits such as carotenoid coloration may reflect more recent or even current resource pools (e.g., Grether, 2000; Rosen and Tarvin, 2006). To complicate matters further, many behavioral displays (e.g., acoustic and vibratory song, body movements) require intense

motor performance, which is known to raise metabolic rates considerably, and thus require substantial immediate energy reserves. Such elaborate displays may also require complex structures (e.g., muscles) and motor skills acquired during development (Byers et al., 2010), and thus reflect resource pools available at earlier life stages. Ultimately, the production of costly displays can provide information about both current energy reserves (Mappes et al., 1996; Hoefler et al., 2008) as well as energy reserves available during development (Nowicki et al., 2002); thus, knowing the relative influence of each may be important for understanding the selection pressures associated with condition-dependent signal evolution.

Condition and Mate Choice

The evolution of condition-dependent signaling is often attributed to sexual selection. Male-male competition provides an intuitive relationship between body condition, signaling performance, and direct fitness outcomes (e.g., access to females); and numerous examples evidence condition-dependent signals that are used in male-male competition (e.g., review in Berglund et al., 1996; Veiga, 1993; Vanpé et al., 2007). Female choice is also frequently touted as being involved in the evolution of condition-dependent signaling (Bondurianski, 2007), yet the connections here are less intuitive. It is the relationship between female choice and condition-dependent signaling that we will focus on subsequently.

It is hypothesized that females indirectly assess a potential mate's quality by examining courtship signal expression, ultimately resulting in the evolution of stable female preferences and corresponding exaggeration of costly male secondary sexual traits (Andersson, 1986; Heywood, 1989; Hoelzer, 1989; Grafen, 1990; Iwasa et al., 1991; Iwasa and Pomiankowski, 1999). In support of this, there exists a wealth of consistent evidence demonstrating that females prefer to mate with males that exhibit more elaborate traits/displays (e.g., larger, brighter, and louder; reviews in Andersson, 1994; Johnstone, 1995; but see Griffith et al., 1999; Lebas and Marshall, 2001; Shamble et al., 2009 for examples of no evidence of female choice). For these choosy females, mate choice can be costly (e.g., Alatalo et al., 1988; Rowe, 1994), suggesting that these choosy females are receiving some benefit from their choice of mates. Females could benefit directly through increased paternal care, increased nutritional resources, better quality territories, or reduced parasitism risk (among others). Hypothesized direct benefits such as these generate a clear prediction – a positive correlation should exist between a signaler's condition and the direct benefits conveyed to females. Indeed, condition-dependent signals have been found to correlate with paternal care (e.g., birds; Hill, 1991; Senar et al., 2002), with the quantity of sperm transferred (e.g., guppies; Matthews et al., 1997; crickets; Wagner and Harper, 2003) and with the production of nutritional benefits, such as spermatophores (e.g., crickets; Wagner and Harper, 2003) and nuptial gifts (e.g., fireflies; Crastley, 2004). The ability to quantify the direct benefits females receive and to then relate them to proxies of signaler condition makes direct benefits a compelling, and readily testable, hypothesis regarding female mate choice on condition dependent signals.

Choosy females are also expected to benefit indirectly if preferred mates pass "good genes" to their offspring that increase their fitness. Evidence for underlying heritable additive genetic variance for body condition is slowly accumulating (Merila, 1996; Merila and Svensson, 1997; Sheldon et al., 1997; Grether, 2000; Kotiaho et al., 2001; Merila et al., 2001; Blanckenhorn and Hosken, 2003), as are examples demonstrating that condition-dependent signals covary with genetic variance (i.e., genic capture; e.g., David et al., 2000; Brandt and Greenfield, 2004; Parker and Garant, 2004; Missoweit et al., 2008). Additionally,

there is some evidence that the additive genetic variance in sexually selected traits results in viability benefits to offspring (Moller and Alatalo, 1999), although the effects may be relatively minor (Alatalo et al., 1998; Moller and Alatalo, 1999). Regardless of the magnitude, offspring from highly ornamented males in good body condition have been found to experience benefits in a variety of fitness-related traits, where offspring feed at higher rates (tree frogs: Doty and Welch, 2001), survive better (guppies: Evans et al., 2004), are in better body condition (collared flycatchers: Sheldon et al., 1997), have increased resistance to parasites (sticklebacks: Barber et al., 2001), and have better larval development (tree frogs: Welch et al., 1998). However, these measurements fall short of evidencing true fitness benefits to females, which should be measured minimally by the number of offspring that each offspring produces (i.e., grandchildren; Hunt et al., 2004b).

Similar to the previously highlighted variation in proxies used for estimating male condition (see Table 9.1), scientists also use a variety of different proxies for estimating female and offspring fitness, including condition itself, making it difficult to obtain an overall picture of the evidence for females receiving fitness benefits from mate choice decisions based on condition-dependent signals. Furthermore, while examples do exist that suggest benefits, both direct and indirect, to females for these choices, the evidence is surprisingly sparse (especially for indirect benefits) and the current viewpoint may be exaggerated due to publication bias toward positive results (Kotiaho and Puurtinen, 2007). We suggest that the relative scarcity of examples may reflect an insufficient approach to condition-dependent signal evolution. For example, proxies of current body condition may not accurately reflect resources relevant to female fitness, as it may be the case that the details about energy reserves that are important to females and/or reflective of energy reserves available at a different time scale (e.g., during juvenile development) are crucial. Additionally, the relative influences of the environmental component, additive genetic variance, and their interactions on body condition and corresponding offspring fitness need to be more firmly established, as signal reliability, especially in condition-dependent signaling systems with proposed indirect benefits, is hypothesized to be compromised (Greenfield and Rodriguez, 2004; Hunt et al., 2004b).

Summary

Evidence of condition-dependent signaling abounds. Such signals are thought to have had important effects on the evolution of animal communication systems (Iwasa et al., 1991). However, the ambiguous and broad nature of condition makes it currently un-measurable, causing scientists to rely on brief snapshots of body condition to estimate an individual's current energy reserves. The variety of proxies used to estimate body condition both across and within taxa has allowed considerable progress in advancing our understanding of ultimate explanations of animal signaling; however, using readily quantifiable proxies of body condition may cloud this understanding and slow our advance. We advocate that a more proximate approach is now in order. We argue that a focus on the physiological basis of condition, on the processes underlying resource allocation, and on the relationship between these and measures of whole organism performance will provide a more complete understanding of underlying mechanisms resulting in a signal's condition-dependence (Lailvaux and Irschick, 2006). Additionally, more proximate approaches to understanding the relationship between condition-dependent signal expression and female mating decisions, and the putative associated fitness benefits, will improve our understanding of selection pressures that might influence the evolution of condition-dependent signaling in

a reproductive context. Focusing on more proximate physiological underpinnings of what condition means and how it directly influences signal expression and female fitness benefits lays the foundation for future comparisons across taxa that share similar mechanisms, which may illuminate interesting broad-scale patterns.

References

- Alatalo, R.V., Carlson, A., and Lundberg, A. (1988) The search cost in mate choice of the pied flycatcher. *Animal Behavior*, 36, 289–291.
- Alatalo, R.V., Kotiaho, J.S., Mappes, J., and Parri, S. (1998) Mate choice for offspring performance: major benefits or minor costs? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 1998, 2297–2301.
- Anderson, J.F. (1974) Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). *Ecology*, 55, 576–585.
- Andersson, M. (1982) Sexual selection, natural selection and quality advertisement. *Biological Journal of the Linnean Society*, 17, 375–393.
- Andersson, M. (1986) Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution*, 40, 804–816.
- Andersson, M. (1994) *Sexual Selection*, Princeton University Press, Princeton, NJ.
- Andersson, S. (1992) Female preference for long tails in lekking Jackson's widowbirds: experimental evidence. *Animal Behaviour*, 43, 379–388.
- Ardia, D.R. (2005) Super size me: an experimental test of the factors affecting lipid content and the ability of residual body mass to predict lipid stores in nestling European Starlings. *Functional Ecology*, 19, 414–420.
- Arntzen, J.W., Smithson, A., and Oldham, R.S. (1999) Marking and tissue sampling effects on body condition and survival in the newt *Triturus cristatus*. *Journal of Herpetology*, 33, 567–576.
- Atkinson, S.N. and Ramsay, M.A. (1995) The effects of prolonged fasting on the body composition and reproductive success of female polar bears (*Ursus maritimus*). *Functional Ecology*, 9, 559–567.
- Baker, R.L. (1989) Condition and size of damselflies: a field study of food limitation. *Oecologia*, 81, 111–119.
- Bakker, T.C.M. and Mundwiler, B. (1994) Female mate choice and male red coloration in a natural three-spined stickleback (*Gasterosteus aculeatus*) population. *Behavioral Ecology*, 5, 74–80.
- Barber, I., Arnott, S.A., Braithwaite, V.A., Andrew, J., and Huntingford, F.A. (2001) Indirect fitness consequences of mate choice in sticklebacks: offspring of brighter males grow slowly but resist parasitic infections. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 268, 71–76.
- Bauchinger, U. and Biebach, H. (2001) Differential catabolism of muscle protein in Garden Warblers (*Sylvia borin*): flight and leg muscle act as a protein source during long-distance migration. *Journal of Comparative Physiology B*, 171, 293–301.
- Berglund, A., Bisazza, A., and Pilastro, A. (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, 58, 385–399.
- Bevier, C.R. (1997) Utilization of energy substrates during calling activity in tropical frogs. *Behavioral Ecology and Sociobiology*, 41, 343–352.
- Birkhead, T.R., Fletcher, F., and Pellatt, E.J. (1998) Sexual selection in the zebra finch *Taeniopygia guttata*: condition, sex traits and immune capacity. *Behavioral Ecology and Sociobiology*, 44, 179–191.
- Bize, P., Piau, R., Moureau, B., and Heeb, P. (2006) A UV signal of offspring condition mediates context-dependent parental favouritism. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 273, 2063–2068.
- Blackwell, G.L. (2002) A potential multivariate index for condition of small mammals. *New Zealand Journal of Zoology*, 29, 195–203.
- Blanckenhorn, W.U. and Hosken, D.J. (2003) Heritability of three condition surrogates in the yellow dung fly. *Behavioral Ecology*, 14, 612–618.
- Blem, C.R. (1984) Ratios in avian physiology. *Auk*, 101, 153–155.
- Bolger, T. and Connolly, P.L. (1989) The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology*, 34, 171–182.
- Bondurianski, R. (2007) The evolution of condition-dependent sexual dimorphism. *American Naturalist*, 169, 9–19.
- Brandt, L.S.E. and Greenfield, M.D. (2004) Condition-dependent traits and the capture of genetic variance in male advertisement song. *Journal of Evolutionary Biology*, 17, 821–828.
- Buchholz, R. (1995) Female choice, parasite load and male ornamentation in wild turkeys. *Animal Behaviour*, 50, 929–943.
- Byers, J., Hebets, E., and Podos, J. (2010) Female mate choice based on male motor performance. *Animal Behav-*

- our, 79, 771–778.
- Candolin, U. (2000) Increased signalling effort when survival prospects decrease: male–male competition ensures honesty. *Animal Behaviour*, 60, 417–422.
- Carranza, J. and Hidalgo de Trucios, S.J. (1993) Condition-dependence and sex traits in the male great bustard. *Ethology*, 94, 187–200.
- Cattet, M.R.L., Caulkett, N.A., Obbard, M.E., and Stenhouse, G.B. (2002) A body-condition index for ursids. *Canadian Journal of Zoology*, 80, 1156–1161.
- Chapman, R.F. (1998) *The Insects: Structure and Function*, 4th edn, Harvard University Press, Cambridge, Massachusetts.
- Chastel, O., Weimerskirch, H., and Jouventin, P. (1995) Influence of body condition on reproductive decision and reproductive success in the blue petrel. *The Auk*, 4, 964–972.
- Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. (1982) *Red Deer. Behavior and Ecology of Two Sexes*, University of Chicago Press, Chicago, IL.
- Cotton, S., Fowler, K., and Pomiankowski, A. (2004) Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271, 771–783.
- Crastley, C.K. (2004) Flash signals, nuptial gifts and female preferences in *Photinus* fireflies. *Integrative and Comparative Biology*, 44, 238–241.
- Cuadrado, M. (1998) The influence of female size on the extent and intensity of mate guarding by males in *Chamaeleo chamaeleon*. *Journal of Zoology (London)*, 246, 351–358.
- David, P., Bjorksten, T., Fowler, K., and Pomiankowski, A. (2000) Condition-dependent signalling of genetic variation in stalk-eyed flies. *Nature*, 406, 186–188.
- Dobson, F.S. (1992) Body mass, structural size, and life history patterns of the Columbian ground squirrel. *American Naturalist*, 140, 109–125.
- Dobson, F.S. and Michener, G.R. (1995) Maternal traits and reproduction in Richardson's ground squirrels. *Ecology*, 76, 851–862.
- Dobson, F.S., Risch, T.S., and Murie, J.O. (1999) Increasing returns in the life-history of Columbian ground squirrels. *Journal of Animal Ecology*, 68, 73–86.
- Doty, G.V. and Welch, A.M. (2001) Advertisement call duration indicates good genes for offspring feeding rate in gray tree frogs (*Hyla versicolor*). *Behavioral Ecology and Sociobiology*, 49, 150–156.
- Doucet, S.M. and Montgomerie, R. (2003) Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. *Behavioral Ecology*, 14, 503–509.
- Dunlap, K.D. and Mathies, T. (1993) Effects of nymphal ticks and their interaction with malaria on the physiology of male fence lizards. *Copeia*, 1993, 1045–1048.
- Eagle, H. (1959) Amino acid metabolism in mammalian cell cultures. *Science*, 130, 432–437.
- Elowe, K.D. and Dodge, W.E. (1989) Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management*, 53, 962–968.
- Emlen, D.J. (1994) Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 256, 131–136.
- Endler, J.A. (1983) Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes*, 9, 173–190.
- Evans, J.P., Kelley, J.L., Bisazza, A., Finazzo, E., and Pilastro, A. (2004) Sire attractiveness influences offspring performance in guppies. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271, 2035–2042.
- Evans, R.M. and McMahon, B.F. (1987) Within-brood variation in growth and condition in relation to brood reduction in the American white pelican. *Wilson Bulletin*, 99, 190–201.
- Fisher, D.O. (1999) Offspring sex-ratio variation in the brindled nailtail wallaby, *Onychogalea fraenata*. *Behavioral Ecology and Sociobiology*, 45, 411–419.
- Gannes, L.Z. (2001) Comparative fuel use of migrating passerines: effects of fat stores, migration distance, and diet. *The Auk*, 118, 665–677.
- García-Berthou, E. (2001) On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *Journal of Animal Ecology*, 70, 708–711.
- Gonzalez, G., Sorci, G., Moler, A.P., Ninni, P., Haussey, C., and De Lope, F. (1999) Immunocompetence and condition-dependent sexual advertisement in male house sparrows (*Passer domesticus*). *Journal of Animal Ecology*, 68, 1225–1234.
- Grafen, A. (1990) Sexual selection unhandicapped by the Fisher process. *Journal of Theoretical Biology*, 144, 473–516.
- Gray, D.A. and Eckhardt, G. (2001) Is cricket courtship song condition dependent? *Animal Behaviour*, 62, 871–877.
- Green, A.J. (2001) Mass/length residuals: measures of body condition or generators of spurious results? *Ecology*, 82, 1473–1483.
- Greenfield, M.D. and Rodriguez, R.L. (2004) Genotype–environment interaction and the reliability of mating

- signals. *Animal Behaviour*, 68, 1461–1468.
- Greenstreet, S.P.R. (1992) Migration of hatchery reared juvenile Atlantic salmon, *Salmo salar* L. down a release ladder. 2. Effect of fish developmental strategy on speed and pattern of movement. *Journal of Fish Biology*, 40, 667–681.
- Grether, G.F. (2000) Carotenoid limitation and mate preference evolution: a test of the indicator hypothesis in guppies (*Poecilia reticulata*). *Evolution*, 54, 1712–1724.
- Griffith, S.C., Owens, I.P.F., and Burke, T. (1999) Female choice and annual reproductive success favour less-ornamented male house sparrows. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266, 765–770.
- Hamer, K.C. and Furness, R.W. (1993) Parental investment and brood defence by male and female great skuas *Catharacta skua*: the influence of food supply, laying date, body size and body condition. *Journal of Zoology*, 230, 7–18.
- Hamilton, W.D. and Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites? *Science*, 218, 384–387.
- Heywood, J.S. (1989) Sexual selection by the handicap mechanism. *Evolution*, 43, 1387–1397.
- Hill, G.E. (1990) Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behavior*, 40, 563–572.
- Hill, G.E. (1991) Plumage coloration is a sexually selected indicator of male quality. *Nature*, 350, 337–339.
- Hill, G.E. (2000) Energetic constraints on expression of carotenoid-based plumage coloration. *Journal of Avian Biology*, 31, 559–566.
- Hoeftler, C.D., Persons, M.H., and Rypstra, A.L. (2008) Evolutionarily costly courtship displays in a wolf spider: a test of viability indicator theory. *Behavioral Ecology*, 19, 974–979.
- Hoelzer, G.A. (1989) The good parent process of sexual selection. *Animal Behaviour*, 40, 1067–1078.
- Hoglund, J., Alatalo, R.V., and Lundberg, A. (1992) The effects of parasites on male ornaments and female choice in the lek-breeding black grouse (*Tetrao tetrix*). *Behavioral Ecology and Sociobiology*, 30, 71–76.
- Holzer, B., Jacot, A., and Brinkhof, M.W.G. (2003) Condition-dependent signaling affects male sexual attractiveness in field crickets, *Gryllus campestris*. *Behavioral Ecology*, 14, 353–359.
- Hooper, R.E., Tsubaki, Y., and Siva-Jothy, M.T. (1999) Expression of a costly, plastic secondary sexual trait is correlated with age and condition in a damselfly with two male morphs. *Physiological Entomology*, 24, 364–369.
- Houde, A.E. and Torio, A.J. (1992) Effect of parasitic infection on male color pattern and female choice in guppies. *Behavioral Ecology*, 3, 346–351.
- House, H.L. (1961) Insect nutrition. *Annual Review of Entomology*, 6, 13–26.
- Hunt, J., Brooks, R., Jennions, M.D., Smith, M.J., Bentsen, C.L., and Bussiere, L.F. (2004a) High-quality male field crickets invest heavily in sexual display but die young. *Nature*, 432, 1024–1027.
- Hunt, J., Bussiere, L.F., Jennions, M.D., and Brooks, R. (2004b) What is genetic quality? *Trends in Ecology and Evolution*, 19, 329–333.
- Irschick, D.J., Meyers, J.J., Husak, J.F., and Le Galliard, J.-F. (2008) How does selection operate on whole organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research*, 10, 177–196.
- Iwasa, Y. and Pomiankowski, A. (1999) Good parent and good genes models of handicap evolution. *Journal of Theoretical Biology*, 200, 97–109.
- Iwasa, Y., Pomiankowski, A., and Nee, S. (1991) The evolution of costly mate preferences. 2. The handicap principle. *Evolution*, 45, 1431–1442.
- Jakob, E.M. (1991) Costs and benefits of group living for pholcid spiderlings: losing food, saving silk. *Animal Behaviour*, 41, 711–722.
- Jakob, E.M., Marshall, S.D., and Uetz, G.W. (1996) Estimating fitness: a comparison of body condition indices. *Oikos*, 77, 61–67.
- Jenni, L. and Jenni-Eiermann, S. (1998) Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology*, 29, 521–528.
- Jennions, M.D. and Backwell, P.R.Y. (1998) Variation in courtship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behavioral Ecology*, 9, 605–611.
- Jennions, M.D., Moller, A.P., and Petrie, M. (2001) Sexually selected traits and adult survival: a meta-analysis. *Quarterly Review of Biology*, 76, 3–36.
- Jessop, T.S., Hamann, M., and Limpus, C.J. (2004) Body condition and physiological changes in male green turtles during breeding. *Marine Ecology Progress Series*, 276, 281–288.
- Johnsen, A., Delhey, K., Andersson, S., and Kempenaers, B. (2003) Plumage colour in nestling blue tits: sexual dichromatism, condition dependence and genetic effects. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 270, 1263–1270.
- Johnstone, R.A. (1995) Sexual selection, honest advertisement and the handicap principle – reviewing the evidence. *Biological Reviews of the Cambridge Philosophical Society*, 70, 1–65.
- Johnstone, R.A. (1997) The evolution of animal signals, in *Behavioral Ecology: An Evolutionary Approach* (eds

- J.R. Krebs and N.B. Davies), Wiley-Blackwell, USA.
- Judge, K.A. and Brooks, R.J. (2001) Chorus participation by male bullfrogs, *Rana catesbeiana*: a test of the energetic constraint hypothesis. *Animal Behaviour*, 62, 849–861.
- Juliano, S. (1986) Food limitation of reproduction and survival for populations of *Brachinus* (Coleoptera: Carabidae). *Ecology*, 67, 1036–1045.
- Keller, C., Diaz-Paniagua, C., and Andreu, A.C. (1997) Post-emergent field activity and growth rates of hatchling spur-thighed tortoises, *Testudo graeca*. *Canadian Journal of Zoology*, 75, 1089–1098.
- Keyser, A.J. and Hill, G.E. (1999) Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266, 771–777.
- Kodric-Brown, A. (1989) Dietary carotenoids and male mating success in the guppy: an environmental component to female choice. *Behavioral Ecology and Sociobiology*, 25, 393–401.
- Kotiaho, J.S. (1999) Estimating fitness: comparison of body condition indices revisited. *Oikos*, 87, 399–400.
- Kotiaho, J.S. (2001) Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biological Reviews*, 76, 365–376.
- Kotiaho, J.S. (2002) Sexual selection and condition dependence of courtship display in three species of horned dung beetles. *Behavioral Ecology*, 13, 791–799.
- Kotiaho, J.S. and Puurtinen, M. (2007) Mate choice for indirect genetic benefits: scrutiny of the current paradigm. *Functional Ecology*, 21, 638–644.
- Kotiaho, J.S., Simmons, L.W., and Tomkins, J.L. (2001) Towards a resolution of the lek paradox. *Nature*, 410, 684–686.
- Kulling, D. and Milinski, M. (1992) Size-dependent predation risk and partner quality in predator inspection of sticklebacks. *Animal Behaviour*, 44, 949–955.
- Lailvaux, S. and Irschick, D.J. (2006) A functional perspective on sexual selection: insights and future prospects. *Animal Behavior*, 72, 263–273.
- Lebas, N.R. and Marshall, N.J. (2001) No evidence of female choice for a condition-dependent trait in the agamid lizard, *Ctenophorus ornatus*. *Behaviour*, 138, 965–980.
- Lomborg, J.P. and Toft, S. (2009) Nutritional enrichment increases courtship intensity and improves mating success in male spiders. *Behavioral Ecology*, 20, 700–708.
- Lozano, G.A. (1994) Carotenoids, parasites, and sexual selection. *Oikos*, 70, 309–311.
- Lozano, G.A. (2001) Carotenoids, immunity, and sexual selection: comparing apples and oranges? *American Naturalist*, 158, 200–203.
- Mappes, J., Alatalo, R.V., Kotiaho, J.S., and Parri, S. (1996) Viability costs of condition-dependent sexual male display in a drumming wolf spider. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 263, 785–789.
- Marden, J.H. and Rollins, R.A. (1994) Assessment of energy reserves by damselflies engaged in aerial contests for mating territories. *Animal Behaviour*, 44, 949–955.
- Matsumasa, M. and Murai, M. (2005) Changes in blood glucose and lactate levels of male fiddler crabs: effects of aggression and claw waving. *Animal Behaviour*, 69, 569–577.
- Matsuno, T. (2001) Aquatic animal carotenoids. *Fisheries Science*, 67, 771–783.
- Matthews, I.M., Evans, J.P., and Magurran, A.E. (1997) Male display rate reveals ejaculate characteristics in the Trinidadian guppy *Poecilia reticulata*. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 264, 695–700.
- McGlothlin, J.W., Duffy, D.L., Henry-Freeman, J.L., and Ketterson, E.D. (2007) Diet quality affects an attractive white plumage pattern in dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology and Sociobiology*, 61, 1391–1399.
- McGraw, K.J. and Ardia, D.R. (2003) Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. *American Naturalist*, 162, 704–712.
- McGraw, K.J. and Hill, G.E. (2000) Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 267, 1525–1531.
- McGraw, K.J., Hudon, J., Hill, G.E., and Parker, R.S. (2005) A simple and inexpensive chemical test for behavioral ecologists to determine the presence of carotenoid pigments in animal tissues. *Behavioral Ecology and Sociobiology*, 57, 391–397.
- McGraw, K.J., Mackillop, E.A., Dale, J., and Hauber, M.E. (2002) Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology*, 205, 3747–3755.
- Merila, J. (1996) Genetic variation in offspring condition: an experiment. *Functional Ecology*, 10, 465–474.
- Merila, J., Kruuk, L.E.B., and Sheldon, B.C. (2001) Natural selection on the genetical component of variance in

- body condition in a wild bird population. *Journal of Evolutionary Biology*, 14, 918–926.
- Merila, J. and Svensson, E. (1997) Are fat reserves in migratory birds affected by condition in early life? *Journal of Avian Biology*, 28, 279–286.
- Missoweit, M., Engqvist, L., Lubjuhn, T., and Sauer, K.P. (2008) Nuptial feeding in the scorpionfly *Panorpa vulgaris*: maintenance of genetic variance in sexual advertisement through dependence on condition influencing traits. *Evolutionary Ecology*, 22, 689–699.
- Moller, A. (1987) Variation in badge size in male house sparrows *Passer = domesticus*: evidence for status signalling. *Animal Behaviour*, 35, 1637–1644.
- Moller, A.P. and Alatalo, R.V. (1999) Good-genes effects in sexual selection. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266, 85–91.
- Moller, A.P. and Petrie, M. (2002) Condition dependence, multiple sexual signals, and immunocompetence in peacocks. *Behavioral Ecology*, 13, 248–253.
- Morrison, R.I.G., Davidson, N.C., and Wilson, J.R. (2007) Survival of the fattest: body stores on migration and survival in red knots *Calidris canutus islandica*. *Journal of Avian Biology*, 38, 479–487.
- Mougeot, F., Perez-Rodriguez, L., Martinez-Padilla, J., Leckie, F., and Redpath, M. (2007) Parasites, testosterone and honest carotenoid-based signalling of health. *Functional Ecology*, 21, 886–898.
- Moya-Larano, J., Macias-Ordenez, R., Blanckenhorn, W.U., and Fernandez Montravela, C. (2008) Analysing body condition: mass, volume or density? *Journal of Animal Ecology*, 77, 1099–1108.
- Murphy, C.G. (1994) Determinants of chorus tenure in barking treefrogs (*Hyla gratiosa*). *Behavioral Ecology and Sociobiology*, 34, 285–294.
- Murray, D.L. (2002) Differential body condition and vulnerability to predation in snowshoe hares. *Journal of Animal Ecology*, 71, 614–625.
- Naef-Daenzer, B., Widmer, F., and Nuber, M. (2001) Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology*, 70, 730–738.
- Neuman, R.M. and Flammang, M.K. (1997) Relative weight as a body condition index for chain pickerel. *Journal of Freshwater Ecology*, 12, 19–26.
- Nicoletto, P.F. (1993) Female sexual response to condition-dependent ornaments in the guppy, *Poecilia reticulata*. *Animal Behaviour*, 46, 441–450.
- Nowicki, S., Searcy, W.A., and Peters, S. (2002) Brain development, song learning and mate choice in birds: a review and experimental test of the “nutritional stress hypothesis”. *Journal of Comparative Physiology A*, 188, 1003–1014.
- Nur, N. and Hasson, O. (1984) Phenotypic plasticity and the handicap principle. *Journal of Theoretical Biology*, 110, 275–297.
- Olson, V.A. and Owens, I.P.F. (1998) Costly sexual signals: are carotenoids rare, risky or required? *Trends in Ecology and Evolution*, 13, 510–514.
- Otronen, M. (1995) Energy reserves and mating success in males of the yellow dung fly, *Scathophaga stercoraria*. *Functional Ecology*, 9, 683–688.
- Owen, M. (1981) Abdominal profile – a condition index for wild geese in the field. *The Journal of Wildlife Management*, 45, 227–230.
- Parker, T.H. and Garant, D. (2004) Quantitative genetics of sexually dimorphic traits and capture of genetic variance by a sexually-selected condition-dependent ornament in red junglefowl (*Gallus gallus*). *Journal of Evolutionary Biology*, 17, 1277–1285.
- Peig, J. and Green, A.J. (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos*, 118, 1883–1891.
- Peig, J. and Green, A.J. (2010) The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology*, 24, 1323–1332.
- Perez-Rodriguez, L., Blas, J., Vinuela, J., Marchant, T.A., and Bortolotti, G.R. (2006) Condition and androgen levels: are condition-dependent and testosterone-mediated traits two sides of the same coin? *Animal Behaviour*, 72, 97–103.
- Pierce, C., Crowley, P., and Johnson, D. (1985) Behavior and ecological interactions of larval Odonata. *Ecology*, 66, 1504–1512.
- Piersma, T. and Davidson, N.C. (1991) Confusion of mass and size. *Auk*, 108, 441–444.
- Plaistow, S. and Siva-Jothy, M.T. (1996) Energetic constraints and male mate-securing tactics in the damselfly *Calopteryx splendens xanthostoma* (Charpentier). *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 263, 1233–1239.
- Poston, J.P., Hasselquist, D., Stewart, I.R.K., and Westneat, D.F. (2005) Dietary amino acids influence plumage traits and immune responses of male house sparrows, *Passer domesticus*, but not as expected. *Animal Behaviour*, 70, 1171–1181.
- Qvarnstrom, A. (1999) Genotype-by-environment interactions in the determination of the size of a secondary

- sexual character in the collared flycatcher (*Ficedula albicollis*). *Evolution*, 53, 1564–1572.
- Ranta, E., Laurila, A., and Elmberg, J. (1994) Reinventing the wheel: analysis of sexual dimorphism in body size. *Oikos*, 70, 313–321.
- Rantala, M.J., Kortet, R., Kotiaho, J.S., Vainikka, A., and Suhonen, J. (2003) Condition dependence of pheromones and immune function in the grain beetle *Tenebrio molitor*. *Functional Ecology*, 17, 534–540.
- Robin, J.P., Frain, M., Sardet, C., Groscolas, R., and Le Maho, Y. (1988) Protein and lipid utilization during long-term fasting in emperor penguins. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology*, 254, R61–R68.
- Rosen, R.F. and Tarvin, K.A. (2006) Sexual signals of the male American goldfinch. *Ethology*, 112, 1008–1019.
- Rowe, L. (1994) The costs of mating and mate choice in water striders. *Animal Behavior*, 48, 1049–1056.
- Rowe, L. and Houle, D. (1996) The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 263, 1415–1421.
- Rundus, A.S., Sullivan-Beckers, L., Wilgers, D.J., and Hebets, E.A. (2011) Females are choosier in the dark: environment-dependent reliance on courtship components and its impact on fitness. *Evolution*, 65, 268–282.
- Saks, L., Ots, I., and Horak, P. (2003) Carotenoid-based plumage coloration of male greenfinches reflects health and immunocompetence. *Oecologia*, 134, 301–307.
- Sarasola, J.H., Negro, J.J., and Travaini, A. (2004) Nutritional condition and serum biochemistry for free-living Swainson's hawks wintering in central Argentina. *Comparative Biochemistry and Physiology A*, 137, 697–701.
- Scheuber, H., Jacot, A., and Brinkhof, M.W.G. (2003a) Condition dependence of a multicomponent sexual signal in the field cricket *Gryllus campestris*. *Animal Behaviour*, 65, 721–727.
- Scheuber, H., Jacot, A., and Brinkhof, M.W.G. (2003b) The effect of past condition on a multicomponent sexual signal. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 270, 1779–1784.
- Schluter, D. and Gustafsson, L. (1993) Maternal inheritance of condition and clutch size in the collared flycatcher. *Evolution*, 47, 658–667.
- Schulte-Hostedde, A.I., Millar, J.S., and Hickling, G.J. (2001) Evaluating body condition in small mammals. *Canadian Journal of Zoology*, 79, 1021–1029.
- Schulte-Hostedde, A.I., Zinner, B., Millar, J.S., and Hickling, G.J. (2005) Restitution of mass-size residuals: validating body condition indices. *Ecology*, 86, 155–163.
- Schwilch, R., Grattarola, A., Spina, F., and Jenni, L. (2002) Protein loss during long-distance migratory flight in passerine birds: adaptation and constraint. *Journal of Experimental Biology*, 205, 687–695.
- Scott, D.E., Casey, E.D., Donovan, M.F., and Lynch, T.K. (2007) Amphibian lipid levels at metamorphosis correlate to post-metamorphic terrestrial survival. *Oecologia*, 153, 521–532.
- Senar, J.C., Figuerola, J., and Pascual, J. (2002) Brighter yellow blue tits make better parents. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 269, 257–261.
- Shamble, P.S., Wilgers, D.J., Swoboda, K.A., and Hebets, E.A. (2009) Courtship effort is a better predictor of mating success than ornamentation for male wolf spiders. *Behavioral Ecology*, 20, 1242–1251.
- Sheldon, B.C., Merila, J., Qvarnstrom, A., Gustafsson, L., and Ellegren, H. (1997) Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 264, 297–302.
- Shine, R., LeMaster, M.P., Moore, I.T., Olsson, M.M., and Mason, R.T. (2001) Bumpus in the snake den: effects of sex, size, and body condition on mortality of red-sided garter snakes. *Evolution*, 55, 598–604.
- Shykoff, J.A. and Widmer, A. (1996) Parasites and carotenoid-based signal intensity: how general should the relationship be? *Naturwissenschaften*, 83, 113–121.
- Sibly, R.M., Jones, P.T., and Houston, D.C. (1987) The use of body dimensions of lesser black-backed gulls *Larus fuscus* to indicate size and estimate body reserves. *Functional Ecology*, 1, 275–279.
- South, S.H., House, C.M., Moore, A.J., Simpson, S.J., and Hunt, J. (2011) Male cockroaches prefer a high carbohydrate diet that makes them more attractive to females: implications for the study of condition-dependence. *Evolution*, 65, 1594–1606.
- Suttie, J.M. and Kay, R.N.B. (1983) The influence of nutrition and photoperiod on the growth of antlers of young red deer, in *Antler Development in Cervidae* (ed R.D. Brown), Caesar Kleberg Wildlife Research Institute, Kingsville, TX.
- Taylor, L.A., Clark, D.L., and McGraw, K.J. (2011) Condition dependence of male display coloration in a jumping spider (*Habronattus pyrrithrix*). *Behavioral Ecology and Sociobiology*, 65, 1133–1146.
- Thompson, C.W., Hillgarth, N., Leu, M., and McClure, H.E. (1997) High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. *American Naturalist*, 149, 270–294.
- Thomson, L.R., Toyoda, Y., Langner, A., Delori, K.M., Garnett, K.M., Craft, N., Nichols, C.R., Cheng, K.M., and Dorey, C.K. (2002) Elevated retinal zeaxanthin and prevention of light-induced photoreceptor cell death in quail. *Investigative Ophthalmology and Visual Science*, 43, 3538–3549.
- Tomkins, J.L., Radwan, J., Kotiaho, J.S., and Tregenza, T. (2004) Genic capture and resolving the lek paradox.

- Trends in Ecology and Evolution, 19, 323–328.
- Tonn, W.M., Paszkowski, C.A., and Holopainen, I.J. (1989) Responses of crucian carp populations to different predation pressure in a manipulated pond. *Canadian Journal of Zoology*, 67, 2841–2849.
- Torok, J., Hegyi, G., and Garamszegi, L.Z. (2003) Depigmented wing patch size is a condition-dependent indicator of viability in male collared flycatchers. *Behavioral Ecology*, 14, 382–388.
- Uetz, G.W., Papke, R., and Kilinc, B. (2002) Influence of feeding regime on body size, body condition and a male secondary sexual character in *Schizocosa ocreata* wolf spiders (Araneae, Lycosidae): condition-dependence in a visual signaling trait. *Journal of Arachnology*, 30, 461–469.
- van Berkum, F., Huey, R., Tsuji, J., and Garland, T. Jr. (1989) Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird and Girard). *Functional Ecology*, 3, 97–105.
- van Homrigh, A., Higgie, M., McGulgan, K., and Blows, M.W. (2007) The depletion of genetic variance by sexual selection. *Current Biology*, 17, 528–532.
- van Marken Lichtenbelt, W.D., Wesselingh, R.A., Vogel, J.T., and Albers, K.B.M. (1993) Energy budgets in free living iguanas in a seasonal environment. *Ecology*, 74, 1157–1172.
- Vanpé, C., Gaillard, J.M., Kjellander, P., Mysterud, A., Magnien, P., Delorme, D., van Laere, G., Klein, F., Liberg, O., and Hewison, A.J.M. (2007) Antler size provides an honest signal of male phenotypic quality in roe deer. *The American Naturalist*, 169, 481–493.
- Veiga, J.P. (1993) Badge size, phenotypic quality, and reproductive success in the house sparrow: a study on honest advertisement. *Evolution*, 47, 1161–1170.
- Vleck, C.M. and Vleck, D. (2002) Physiological condition and reproductive consequences in Adelie penguins. *Integrative and Comparative Biology*, 42, 76–83.
- von Schantz, T., Bensch, S., Grahm, M., Hasselquist, D., and Wittzell, H. (1999) Good genes, oxidative stress and condition-dependent sexual signals. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266, 1–12.
- Wagner, W.E. and Harper, C.J. (2003) Female life span and fertility are increased by the ejaculates of preferred males. *Evolution*, 57, 2054–2066.
- Wagner, W.E. and Hoback, W.W. (1999) Nutritional effects on male calling behaviour in the variable field cricket. *Animal Behaviour*, 57, 89–95.
- Watson, P.J. (1990) Female-enhanced male competition determines the first mate and principal sire in the spider *spurthighed litigiosa* (Linyphiidae). *Behavioral Ecology and Sociobiology*, 26, 77–90.
- Wauters, L.A. and Dhondt, A.A. (1995) Lifetime reproductive success and its correlates in female Eurasian red squirrels. *Oikos*, 72, 402–410.
- Weatherhead, P.J., Barry, F.E., Brown, G.P., and Forbes, M.R.L. (1995) Sex ratios, mating behavior and sexual size dimorphism of the northern water snake, *Nerodia sipedon*. *Behavioral Ecology and Sociobiology*, 36, 301–311.
- Weatherhead, P.J., Dufour, K.W., Loughheed, S.C., and Eckert, C.G. (1999) A test of the good-genes-as-heterozygosity hypothesis using red-winged blackbirds. *Behavioral Ecology*, 10, 619–625.
- Welch, A.M., Semlitsch, R.D., and Gerhardt, H.C. (1998) Call duration as an indicator of genetic quality in male gray tree frogs. *Science*, 280, 1928–1930.
- Welch, K.C. Jr., Bakken, B.H., del Rio, C.M., and Suarez, R.K. (2006) Hummingbirds fuel hovering flight with newly ingested sugar. *Physiological and Biochemical Zoology*, 79, 1082–1087.
- Welch, K.C. Jr., Herrera, G.M., and Suarez, R.K. (2008) Dietary sugar as a direct fuel for flight in the nectarivorous bat *Glossophaga soricina*. *Journal of Experimental Biology*, 211, 310–316.
- West-Eberhard, M.J. (1979) Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society*, 123, 222–234.
- Wilder, S.M. and Rypstra, A.L. (2008) Diet quality affects mating behaviour and egg production in a wolf spider. *Animal Behaviour*, 76, 439–445.
- Wilgers, D.J. and Hebets, E.A. (2011) Complex courtship displays facilitate male reproductive success and plasticity in signalling across variable environments. *Current Zoology*, 57, 175–186.
- Wilgers, D.J., Nicholas, A.C., Reed, D.H., Stratton, G.E., and Hebets, E.A. (2009) Condition-dependent alternative mating tactics in a sexually cannibalistic wolf spider. *Behavioral Ecology*, 20, 891–900.
- Woodroffe, R. (1995) Body condition affects implantation date in the European badger, *Meles meles*. *Journal of Zoology (London)*, 236, 183–188.
- Yuval, B., Holliday-Hanson, M.L., and Washing, R.K. (1994) Energy budget of swarming male mosquitos. *Ecological Entomology*, 19, 74–78.
- Zahavi, A. (1975) Mate selection – selection for a handicap. *Journal of Theoretical Biology*, 53, 205–214.
- Zahavi, A. (1977) The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, 67, 603–605.
- Zeh, D.W. and Zeh, J.A. (1988) Condition-dependent sex ornaments and field tests of sexual selection theory. *American Naturalist*, 132, 454–459.

- Zera, A.J. and Harshman, L.G. (2001) The physiology of life history trade-offs in animals. *Annual Review of Ecological Systems*, 32, 95–126.
- Zuk, M. and Kolluru, G.R. (1998) Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology*, 73, 415–438.
- Zuk, M., Thornhill, R., Ligon, J.D., and Johnson, K. (1990) Parasites and mate choice in red jungle fowl. *American Zoologist*, 30, 235–244.