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Sex in a material world: why the study of sexual reproduction and sex-specific traits should become more nutritionally-explicit

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Recent advances in nutritional ecology, particularly arising from Ecological Stoichiometry and the Geometric Framework for nutrition, have resulted in greater theoretical coherence and increasingly incisive empirical methodologies that in combination allow for the consideration of nutrient-related processes at many levels of biological complexity. However, these advances have not been consistently integrated into the study of sexual differences in reproductive investment, despite contemporary emphasis on the material costs associated with sexually selected traits (e.g. condition-dependence of exaggerated ornaments). Nutritional ecology suggests that material costs related to sex-specific reproductive traits should be linked to quantifiable underlying differences in the relationship between individuals of each sex and their foods. Here, we argue that applying nutritionally-explicit thought to the study of sexual reproduction should both deepen current understanding of sex-specific phenomena and broaden the tractable frontiers of sexual selection research. In support of this general argument, we examine the causes and consequences of sex-specific nutritional differences, from food selection and nutrient processing to sex-specific reproductive traits. At each level of biological organization, we highlight how a nutritionally-explicit perspective may provide new insights and help to identify new directions. Based on predictions derived at the individual level, we then consider how sex-specific nutrient limitation might influence population growth, and thus potentially broader patterns of life history evolution, using a simple population dynamics model. We conclude by highlighting new avenues of research that may be more accessible from this integrative perspective.

Organisms live in a material world where fitness is often determined by an individual's ability to effectively translate available resources into reproductive output (Kay et al. 2005). Sexually reproducing organisms are particularly compelling systems for probing components of the pathway from environmental resources to fitness because, despite sharing many aspects of their biology (e.g. diet, genome), each sex solves the problem of converting available resources into reproductive output differently. This assertion is clear from the observation that sexual phenotypes differ in their material requirements, beginning with divergent resource demands during gamete production (i.e. anisogamy, Kodric-Brown and Brown 1987) and becoming more pronounced in species that have evolved materially-costly sexually selected traits (Andersson 1994). Because many sexually-dimorphic traits differ not only in their level of exaggeration, but also their biochemical composition, this implies that the sexes may often differ both in the quantity and composition of resources they require to maximize reproductive output. Thus, we argue that the study of sex-specific traits should become more nutritionally-explicit; that is, research should move beyond manipulations of gross resource availability/quality to consider how individuals of each sex balance the intake of multiple nutrients from often imbalanced foods to meet their reproductive needs (for definition and further discussion on nutritional explicitness see Raubenheimer et al. 2009). Integration of concepts and methods from the growing field of nutritional ecology into current sexual selection research provides just such a path.

In support of this general argument, we begin by outlining a heuristic schema that highlights salient components on the path from available resource pools to individual fitness and beyond (Fig. 1). We then describe conceptual advances and empirical methodologies stemming from two contemporary nutritionally-explicit paradigms, the Geometric Framework for nutrition and Ecological Stoichiometry. Building on this perspective, we consider the ways in which the sexes might be able to pursue different nutritional optima, using foraging

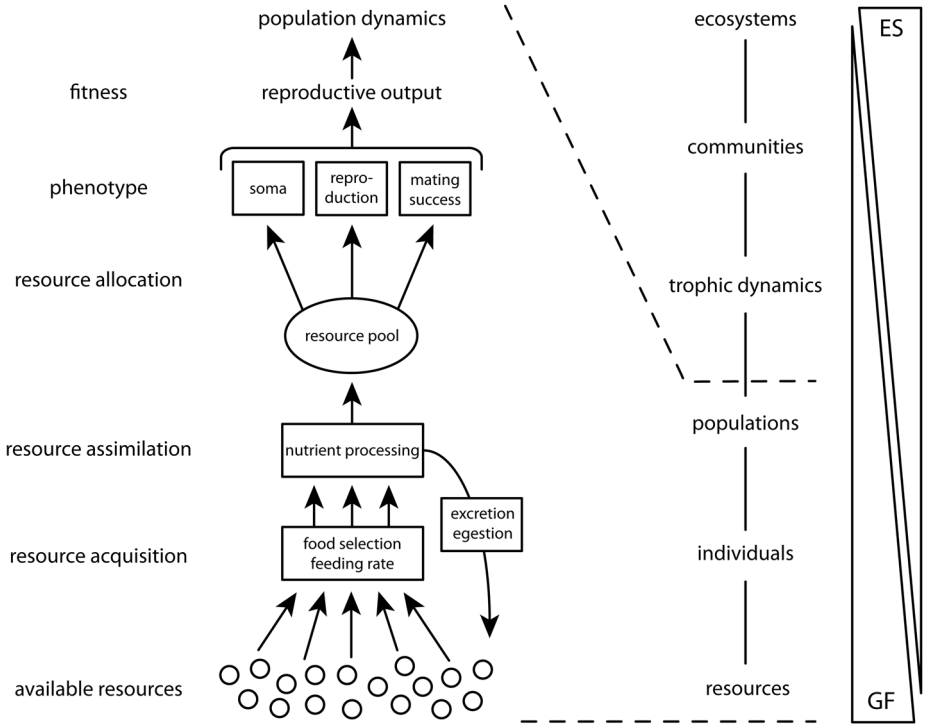

Figure 1. Schematic representation of the nutrient dynamics and processes involved in the translation of available resources to organismal fitness and beyond. The present manuscript focuses on phenomena at lower levels of biological organization, expanded on the left. However, insights arising from nutritionally-explicit consideration of these phenomena may help to inform patterns at broader scales (on right). Integration of techniques and concepts from Ecological Stoichiometry (ES) and the Geometric Framework for nutrition (GF) allows for increased nutritional-explicitness across all levels represented, with GF offering greatest resolution at lower levels, matched by the strength of ES to characterize dynamics at higher levels of biological complexity.

tactics and post-ingestive nutrient processing. We then discuss the potential for a nutritionally-explicit perspective to inform the evolution of sex-specific reproductive traits, including exaggerated ornaments and parental investment. To probe how such trait- and individual-level phenomena may translate into broader patterns of life history evolution, we consider the fitness consequences of sexual divergence in nutritional optima by exploring patterns of population growth using a mathematical model. Lastly, we describe scientific frontiers further afield that we see as extensions made more accessible by our core arguments. Throughout the manuscript, our coverage of the scientific literature on the broad subject of nutrition and sex is far from exhaustive. Rather, we hope that the selected examples we present serve to persuade the reader that a deeper integration of sexual selection and nutritional ecology will help to generate new tactics for addressing questions of current interest and debate, and open new avenues of research in sexual selection and evolutionary biology.

Translating available resources to organismal fitness and beyond: a heuristic schema

In evolutionary biology, the relationship between environmental resource availability and organismal fitness has traditionally been described as the product of two processes, resource acquisition and resource allocation to phenotypic traits (Stearns 1992). As such, organisms can maximize fitness by either increasing resource acquisition (i.e. increasing the size of their resource pool) and/or optimizing patterns of resource allocation (Fig. 1). In situations where acquired resources are insufficient to support the construction of an optimal phenotype, tradeoffs are expected to occur between phenotypic traits (van Noordwijk and de Jong 1986). Research motivated by this theoretical framework has expanded our knowledge of how resource acquisition and allocation interact to produce variation in life history parameters and fitness (Reznick et al. 2000, Boggs 2003, Hunt et al. 2004a). However, much of this work has generated experimental variation in resource acquisition via gross manipulations of resource quantity (e.g. ad libitum vs food restriction) and/or quality (e.g. via diet dilution or large shifts in food types), which obscures many of the important nutrient-specific dynamics underlying organismal responses to diet.

Recent advances in nutritional ecology indicate that resource acquisition is a complex process best understood by comparing the balance of nutrients available in food to that required by an organism's phenotype (Raubenheimer and Simpson 1997, Sterner and Elser 2002, Frost et al. 2005). In the simplest (and least common) case, the nutritional composition of food matches the nutritional requirements of the organism (i.e. the organism's food is 'balanced'). In such situations, resource acquisition can be adequately understood (and manipulated) in terms of intake rate alone because an organism can respond to increases in their resource demands

by simply ingesting higher quantities of food. However, when the nutritional composition of available foods is imbalanced in relation to an organism's nutritional requirements, individuals must compensate via patterns of food selection, intake rate, post-ingestive nutrient processing, and in many cases shifts in resource allocation (Fig. 1, Frost et al. 2005). Thus, properly understanding the organismal consequences of feeding on nutritionally imbalanced diets requires attention to a suite of traits (e.g. food selection, nutrient processing, etc.) above and beyond intake rate alone.

Based on well-established connections between dietary intake and reproductive performance (Hunt et al. 2004a, Partridge et al. 2005, Lee et al. 2008) as well as the potentially distinct biochemical demands of sex-specific reproductive traits (although more work is needed to document such patterns in detail), we expect each sex to have different optimal intake targets for a suite of nutrients, both at molecular (e.g. micronutrients such as vitamins; macronutrients such as proteins) and elemental levels (e.g. trace elements such as selenium; mineral elements such as phosphorus). Two contemporary nutritionally-explicit frameworks, the Geometric Framework for nutrition (GF) and Ecological Stoichiometry (ES), provide the necessary tools for examining such multidimensional links between nutritional physiology and sex-specific fitness. At the center of both these approaches is the knowledge that individuals will perform optimally (e.g. growth, development, reproduction or fitness) when the composition of acquired nutrients closely matches nutritional requirements (Raubenheimer and Simpson 1997, Sterner and Elser 2002, Frost et al. 2005, Kay et al. 2005). When the intake of a particular nutrient falls below the required level, performance will be impaired, particularly in the poorest quality individuals (Houle and Kondrashov 2002, Hunt et al. 2004a). On the other hand, nutrient consumption in excess of an organism's requirements may result in reduced growth and viability (Raubenheimer and Simpson 2004, Raubenheimer et al. 2005, Boersma and Elser 2006). Thus, the value of consuming more or less of a given food must be considered in terms of the balance between over and under-ingestion of the food's constituent nutrients.

In GF, foods are viewed within a multidimensional nutritional landscape whose axes represent the relevant nutrients of the food that influence fitness (Raubenheimer and Simpson 1997). Foods of different nutritional contents are thus represented by different trajectories within this nutritional landscape, known as 'nutritional rails'. Individuals can manipulate their nutritional intake to meet the demand for specific nutrient combinations by either eating more or less of a single food item thereby moving along a nutritional rail, or by selecting between foods of different ratios, thereby moving within the nutritional space bounded by the rails (Raubenheimer and Simpson 1997). One of the strengths of this 'geometric' approach is that by selecting appropriate nutritional rails (i.e. foods), researchers can uncover both the target nutritional intake an organism selects when allowed to compose its own diet (called the 'intake target'), as well as what priority rules an organism abides by when it is restricted to a single nutritional rail that does not allow it to access its intake target (i.e. an imbalanced food). Applying these techniques to each sex should reveal whether divergent nutrient requirements associated with sex-specific traits translate into different intake targets and/or different priority rules under nutritional imbalance for males and females.

As a complementary perspective, ES uses the basic elemental composition of organisms to explore the balance of energy and materials in living systems (Sterner and Elser 2002), reciprocally linking the availability of resources to key organismal functions (e.g. growth, reproduction, excretion). While the abstraction of nutrients to their constituent elements results in some loss of resolution at the level of organismal responses to macronutrient availability (Anderson et al. 2004, Raubenheimer and Simpson 2004, Raubenheimer et al. 2009), this simplification gives ES greater power in resolving the contribution of processes at higher levels of organization (e.g. population, ecosystem) to features of an organism's nutritional environment (Fig. 1, Elser et al. 2000, Elser and Hamilton 2007). In addition, because the elemental composition of biological tissues can often be readily measured, the ES framework lends itself to comparisons of the material requirements of specific traits across broad phylogenetic scales (Fagan et al. 2002). This latter characteristic also offers a facile way to consider the contribution of a specific trait to the overall elemental budget of an organism (e.g. the proportion of adult nitrogen devoted to male coloration vs seminal fluids).

While ES and GF have accrued empirical successes often at different levels of biological organization (ES for community, population and ecosystem levels, GF at organismal levels; Fig. 1), we consider application of techniques from both frameworks to be important for implementing a broadly integrative, nutritionally-explicit approach to the study of sex-specific traits and associated nutritional optima. In this review we aim to highlight how a unified nutritional framework that incorporates both GF and ES can enable the importance of nutrition to the evolution of sex-specific traits to be examined across all scales, from the physiology of individuals to the level of populations and beyond (see also discussions in Elser et al. 2000, Raubenheimer and Simpson 2004, Raubenheimer et al. 2009). In the sections below, we follow this logical progression from the selective acquisition and processing of nutrients through to the population consequences of sex-specific nutritional requirements.

Sex-differences in food selection and nutrient uptake

Given that the nutrient requirements associated with reproduction may differ between the sexes (Maklakov et al. 2008) and that sub-optimal consumption of key nutrients may impose fitness costs (Raubenheimer et al. 2005, Boersma and Elser 2006), we expect males and females to differ in optimal dietary intake, and hence differ in patterns of food selection. Examining the foraging ecology literature reveals a wealth of information regarding differences between males and females in the efficiency with which they search for food, the composition of their diets, and the habitat or 'patches' in which each sex is typically found foraging (Ruckstuhl 1998, Mysterud 2000, Beck et al. 2005, Tucker et al. 2009). However, while these studies are important for demonstrating that males and females may differ in

their active acquisition of nutrients, they have rarely connected the resulting compositional differences of ingested nutrients to sex-specific fitness optima (thus identifying sex-specific 'nutritional optima'). Characterization of sex-specific nutritional optima is of clear utility for probing the behavioral and physiological mechanisms governing how each sex forages.

Conceptual advances arising from GF provide three food selection tactics that relate foraging behavior to the optimal intake of an organism (Simpson and Raubenheimer 1996, Raubenheimer and Simpson 1997). First, in species where reproductive investment depends on the acquisition of limiting trace minerals or compounds, sex specific optima may be achieved through supplementary foraging for specific food sources rich in the needed nutrient (Raubenheimer and Simpson 2006). Second, each sex can select combinations of complementary foods that are individually nutritionally imbalanced, but together allow an animal to reach its multidimensional intake target. Third, males and females can vary in the type and amount of nutrients that are most tightly regulated during food selection. In these situations it is common for compensatory feeding to occur where intake of a key limiting nutrient is prioritized, resulting in the overconsumption of other nutrients in lower demand. While supplementary, complementary and compensatory feeding processes have been shown to be widespread phenomena in nutritional ecology (Raubenheimer and Simpson 1997), empirical evidence for sex-specific differences in the implementation of these mechanisms is rather limited. Thus, efforts to connect the material requirements of sex-specific traits to divergent nutritional optima should improve our understanding of how and why sex differences in foraging tactics and food selection may arise.

Once a food is selected, males and females face another set of challenges at the physiological level based on the nutritional composition of the selected food. In a simple two nutrient model, organisms must: 1) sequester and/or increase processing efficiency of the limiting nutrient (e.g. phosphorus or protein), and 2) store and/or decrease processing efficiency of the surplus nutrient (often carbon or carbohydrates). There is growing evidence for such sex differences in nutrient processing. For example, differences in the utilization of metabolic substrates during exercise have now been well established in humans, where females metabolize proportionately more lipids and less carbohydrates and protein than do males (Tarnopolsky and Saris 2001). However, more work is clearly needed to better understand how differences in post-ingestive processing relate to the specific demands imposed by reproduction in each sex.

The resource pool that results from both feeding responses and post-ingestive processing provides the raw materials for allocation to phenotypic traits (e.g. an organism's 'condition' sensu Rowe and Houle 1996). In the ideal case, organisms are able to fully bridge the gap between food and phenotype, resulting in a precise match between the pool of acquired resources and the material requirements that maximize fitness. However, nutritional imbalances arising from an organism's resource environment often translate into imbalances in an organism's resource pool, in which case organisms must respond via changes in resource allocation that may lead to reductions in fitness (e.g. detrimental accumulations of excess nutrients, such as obesity). Thus, patterns of phenotypic trait expression (i.e. their 'condition-dependence') can be more completely understood by considering both the biochemical/elemental composition of food resources and the success with which an organism has been able to selectively bias the uptake of specific nutrients from their food to approach their nutritional optima. This perspective suggests that nutritional ecology may offer concrete ways for researchers to quantify an organism's condition, a parameter central to both sexual selection and life history theory that continues to be empirically elusive (Jakob et al. 1996, Gosler and Harper 2000, Green 2001, Cotton et al. 2004).

Sexually-selected ornaments

Sexually selected armaments and ornaments often represent large collections of particular nutrients, such as the large calcium and phosphorous deposits represented by ungulate antlers (Lincoln 1992). This suggests that the production of sexually selected traits should be tightly linked to an organism's underlying nutrient budget in ways that can be inferred from their biochemical composition (e.g. temporary osteoporosis induced by high calcium needs during ungulate antler formation, Baxter et al. 1999). Further, the exaggeration of such traits via directional sexual selection should progressively bias the nutritional requirements of the ornamented sex, thus driving divergence of nutritional optima between the sexes and the underlying traits that connect individual resource pools to environmental resource availability (e.g. food selection, feeding rate and post-ingestive nutrient processing). Here, we highlight two sexually selected traits, carotenoid coloration in birds and male song in crickets, which illustrate both the empirical traction afforded by nutritional explicitness, and the ways in which our understanding of sex-specific traits can be deepened by further integration of insights from nutritional ecology.

Carotenoid coloration in birds has become a textbook example of the role that diet can play in determining the signaling value of a sexual ornament. Carotenoids cannot be synthesized by animals, and therefore must be acquired from dietary sources (McGraw 2006). Once acquired, carotenoids may be invested into color ornaments or employed as antioxidants in a variety of immune functions (Møller et al. 2000, McGraw 2005). Thus, arguments regarding female preferences for male carotenoid coloration have revolved around the potential information females might gain regarding male foraging success and/or health (Olson and Owens 1998). However, while male carotenoid plumage appears to be responsive to dietary carotenoid manipulations in the lab in a variety of species (McGraw 2006), connecting these patterns to dynamics in the field has been more challenging. In particular, the hypothesis that males advertise their foraging abilities to females via carotenoid-rich plumage traits is based on the assumption that carotenoids are scarce in diet, and either that males acquire carotenoids as part of their regular diet (and therefore males who have been able to acquire more food also have more carotenoids) or that males engage in supplementary feeding on foods particularly rich in carotenoids.

Verifying these assumptions is not only critical to understanding the signal content of carotenoid-based plumage,

but also how the acquisition of carotenoids interacts with the acquisition of other nutrients. However, studies of the carotenoid content of the diets of free-ranging birds are relatively few (Slagsvold and Lifjeld 1985, Linville and Breitwisch 1997, Hill et al. 2002). Likewise, while males of ornamented species are known to acquire higher concentrations of carotenoids from their diet than females (Møller et al. 2000, Hill et al. 2002, McGraw and Gregory 2004), the relative role of male foraging behaviors per se versus sex differences in carotenoid uptake mechanisms from the digestive tract remains poorly understood. For example, in several bird species males acquire higher levels of carotenoids from diet than do females even when reared on a common diet (Negro et al. 2001, McGraw et al. 2005). Further, a recent attempt to characterize differences in the foraging strategies of sexually-dichromatic birds did not detect any sex differences in food selection or intake relevant to carotenoid acquisition (McGraw et al. 2003). More work is clearly needed to tease apart the relative contributions of food selection, food intake and nutrient processing. We suggest that this challenge may be profitably approached using techniques from nutritional ecology (e.g. characterizing the influence of dietary carotenoids on sex-specific intake targets).

The fact that carotenoids must be derived by animals directly from food has proven to be extremely useful in exploring the nutrient dynamics associated with carotenoid-based traits. However, many sexually-selected traits are dependent on more basic dietary precursors, such as carbohydrates and proteins, which will inevitably be allocated to a broad range of important functions beyond the sexual ornament. The development of a similarly sophisticated understanding of the nutritional economics related to such traits has been more empirically challenging. Nevertheless, notable progress has been accomplished by incorporating insights from nutritional ecology. Male calling behavior in crickets provides a case in point. Early work on the dietary dependence of male advertisement calls in crickets reported variable responses of male calls to gross manipulations of diet, ranging from strong effects of diet on energetic investment in male song (Wagner and Hoback 1999, Hunt et al. 2004a, Judge et al. 2008) to a complete lack of dietary influence on the structural properties of male calls (Gray and Eckhardt 2001). Constructing a cohesive understanding of the nutritional basis underlying variation in male calling behavior from this work remains difficult because the diet manipulations employed were not sufficiently well characterized to provide a means for comparison. However, recent work has begun to provide a more detailed picture by quantifying the responses of male calling behavior to variation in key nutrients. In particular, work by Bertram and colleagues has revealed a link between male calling effort and the supply of dietary phosphorous (Bertram et al. 2006, 2009), a commonly limiting mineral in animal nutrition (Sterner and Elser 2002). The authors argue that increased supply of dietary phosphorous may support faster repair of proteins damaged by free radicals generated during energetically expensive calling. This work highlights the power of nutritionally-explicit approaches in that they readily generate testable hypotheses at other relevant levels of organization (e.g. connecting male calling behavior to physiological repair mechanisms).

A recent study by Maklakov et al. (2008) further characterizes the influence of diet on male song by quantifying male calling effort across a nutritional landscape defined by variation in both carbohydrates and protein. First, these authors characterize how various combinations of dietary protein and carbohydrates correspond to male calling effort across a defined nutritional landscape. Second, the male-specific nutritional optimum for calling effort was directly compared to the dietary composition that maximizes female egg production. By identifying the nutritional optima of each sex simultaneously, these researchers develop a more complete picture of the nutritional ecology of this species, revealing that males and females maximize their fitness in different regions of nutritional space. Following up on this finding, these researchers employed techniques from GF to test the prediction that males and females should defend distinct intake targets that correspond to their nutritional optima. However, rather than finding that males and females are able to achieve their respective nutritional optima via food selection, this work revealed that males and females share an intake target that represents a compromise between their respective nutritional optima. Thus, both male calling effort and female reproductive output may be constrained by the nutritional optima of the opposite sex. Such constraints may have important consequences for population dynamics, a point that we return to later in the manuscript.

Taken together, these examples illustrate the power of adopting a more nutritionally-explicit approach to sexually-selected ornamental traits. Research along these lines provides a means for better understanding the costs associated with such traits by relating their material demands to the nutritional environment of the organism, how such material requirements interact with the nutrient demands of other life history characters, and how features of the nutritional ecology of the opposite sex may constrain or enable their expression and exaggeration. Considering these insights across broader spatial and temporal scales may reveal new avenues for future research, such as the influence of anthropogenic nutrient inputs on sexual signaling.

Parental investment

Parental investment in offspring represents both a critical departure and point of unification for the nutritional economies of the sexes. The divergent roles of the sexes in relation to offspring provisioning begin at the stage of gamete production, where female nutritional investment in individual gametes typically exceeds that of males (Kodric-Brown and Brown 1987), and often continue through pre-natal and post-natal care. However, in species where males contribute materially to offspring, either through brood provisioning or nutrient contributions to females during copulation (e.g. nuptial gifts), parental investment represents a touchpoint between the nutritional economies of each sex. Specifically, increased nutrient investment by one sex may help to relax the nutrient demands imposed by reproduction on the opposite sex. To illustrate how a nutritionally-explicit perspective can expand on current understanding of parental investment, we consider maternal investment during pregnancy and lactation in mammals, and male investment in nuptial gifts in insects.

In mammals, offspring are exclusively reliant on the resources provided by females, both during embryonic

development and subsequent post-natal development in the form of lactation (Langer 2008). Maternal nutrient provisioning has generally been characterized in terms of energy sources and protein, although minerals such as calcium and trace elements such as selenium and zinc also play critical roles (Allen and Ullrey 2004). Thus female (and male partner) fitness is directly related to the capacity of the mother to satisfy the nutritional demands of offspring, both in quantity and composition. Mothers can meet these demands by both increasing nutrient intake and mobilizing endogenous nutrient reserves (Bronson and Heideman 1994). These two nutrient sources can complement each other, with the mobilization of endogenous reserves often compensating for limited availability of a key nutrient in food (Allen and Ullrey 2004). For example, there is considerable evidence that female mammals lose bone during pregnancy and lactation as a consequence of elevated calcium mobilization to support skeletal ossification in offspring (Kovacs 2005), and that the amount of bone loss is inversely correlated with dietary calcium intake (Bawden and McIver 1964, Rasmussen 1977, Janakiraman et al. 2003). Thus, understanding how females successfully provision offspring requires characterizing both female nutritional status at fertilization and the capacity for females to augment nutrient inputs from their nutritional environment during pregnancy and lactation.

While the nutritional dynamics underlying offspring provisioning in mammals are clearly complex, nutritional ecology provides a number of useful inroads for understanding the tactics employed by gravid mothers during pregnancy and post-natal provisioning. First, the resource demands of offspring should alter the nutritional intake targets and associated priority rules governing food selection of reproductive females relative to males and non-reproductive females. In particular, these biases should become increasingly apparent as gestation and lactation progress. Evidence for shifts in the nutritional goals of pregnant mothers exists for humans (Molina-Font 1998), but these shifts appear to be motivated by a mix of cultural and physiological cues (Urgell et al. 1998). Similar evidence is lacking in free-ranging mammals (Allen and Ullrey 2004). However, in both humans and free-ranging mammals, nutritionally-explicit characterization of shifts in maternal dietary intake and food selection should illuminate how gravid females balance the intake of multiple nutrients to satisfy the costs of reproduction. Similar efforts (but without reference to sexual or reproductive differences) have been recently met with success in free-ranging primates (Felton et al. 2009), indicating that such methods are tractable in field scenarios.

Nutritional ecology may also shed light on broader evolutionary patterns of maternal reproductive traits. For example, omnivorous mammals may be better able than specialist herbivores to accommodate the multivariate nutrient demands of reproduction via flexible shifts in food selection, resulting in phylogenetic differences in reproductive traits such as lactation. Preliminary support for this idea comes from Krockenberger and colleagues (1998), who suggested that the low daily production and low protein/lipid content of female koala milk is an adaptation to the low protein/lipid content of their specialized diet of *Eucalyptus* foliage. Similar reductions in maternal investment in lactation appear in other folivorous marsupials (Munks and Green 1995), but more work is needed to consider this hypothesis within a broader phylogenetic context.

While mammalian reproduction represents a case where offspring provisioning is largely the responsibility of females, in other taxa the nutritional demands associated with offspring production are often shared more evenly by the two sexes. In such situations, the nutritional dynamics of both sexes are intertwined in the pursuit of fitness. The role of male-donated nutrients in female reproduction in gift-giving insects provides a useful illustration of this point. In some insects, males transfer significant quantities of nutrients (carbohydrates, lipids, proteins, phosphorous) to females during copulation in the form of prey items, spermatophores or other somatic-contributions (Vahed 1998, Markow et al. 2001). These nutrient resources are often utilized by females to satisfy the nutritional demands of oogenesis and somatic maintenance (Boggs and Gilbert 1979, Vahed 1998, Markow et al. 2001). In a number of species (reviewed by Vahed 1998, Gwynne 2008), considerable evidence now exists linking the size of the nuptial gift received by a female to both longevity and fecundity (Vahed 2007, Wedell et al. 2008, but see Sakaluk et al. 2006). Particularly in environments where food resources are scarce, females may rely on these male contributions to supplement their resource budgets (Gwynne and Simmons 1990, Simmons 1992, Simmons and Gwynne 1993). However, while it appears that the nutrient composition (e.g. phosphorous content, Markow et al. 2001) of nuptial gifts can potentially influence their utility to females and thus their impact on the fitness of both sexes, we currently know little about how diet influences the composition or size of male nuptial gifts (Will and Sakaluk 1994, Hall et al. 2008). Further, because females are unlikely to be able to assess the quality of spermatophores of prospective mates directly, probing relationships between male nuptial provisioning and other male ornaments is important (Gwynne 1982, Fedorka and Mousseau 2002).

Considering patterns of spermatophore investment across broader phylogenetic scales may also allow for new insights regarding the co-evolution of male and female nutritional investment in offspring. For example, work by Karlsson (1995, 1996) suggests that increasing levels of polyandry in gift-giving butterflies may result in shifts in the source of reproductive reserves from females to males (particularly nitrogenous reserves such as proteins and amino acids). Thus, polyandrous females may 'forage' for proteins needed to augment fecundity by pursuing multiple copulations over the course of their lifetime. Such phylogenetic patterns provide an arena for considering how the nutrient budgets of the sexes may interact across evolutionary time.

Lastly, while we have focused on the role of nuptial gifts as male investment in offspring, in many cases these contributions may serve simply as mating effort or may operate to manipulate female receptivity and re-mating rate (Gwynne 2008). Again, we argue that employing nutritionally-explicit methods to probe the relationship between nuptial gifts and male (and female) nutrient budgets may help to disentangle the various roles that nuptial gifts may play in mediating intersexual interactions (i.e. by indicating the nutritional cost of nuptial gifts to males, and their nutritional value to females, as characterized within the context of the multivariate nutrient budget of each sex).

Population-level consequences of sex-specific nutrient limitation

Following arguments above, we expect that nutritional optima may commonly differ between the sexes. This implies that individual fitness may be maximized when the sexes are able to independently pursue their distinct nutritional targets. However, from an evolutionary perspective, this poses a problem as males and females share a common genome and any allele that enhances fitness in males by allowing them to reach their optimal nutrient intake may conversely reduce fitness when expressed in females (Lande 1980). Accordingly, intralocus sexual conflict may constrain each sex from reaching its own fitness optima, resulting in compromises in the expression of shared traits (Bonduriansky and Chenoweth 2009) and thus reductions in the average fitness of members of a population (Lande 1980). Alternatively, the ability for the sexes to achieve distinct nutritional intakes may be constrained by the composition and/or abundance of available (but shared) resources. This suggests that differences in the nutritional optima of the sexes, and each sex's capacity to pursue such nutritional optima, may have important consequences for population growth and dynamics.

In this section, we explore the fitness consequences of sex-specific nutrient limitation using a simple population dynamics approach. Our intent is to provide initial theoretical insights on this topic, as empirical evidence is currently lacking. We design our models to account for the different roles of males and females in population growth, thus allowing us to ask questions about the fitness consequences of sex-specific patterns of nutrient limitation. In our models, the role of males in population growth is dictated by their influence on the fertilization success of females, which allows us to further incorporate variation in the Allee effect (i.e. male rarity reduces population growth rates because females cannot find a partner, McCarthy 1997). While there are several ways of modeling population dynamics by including sex structure and the Allee effect (Courchamp et al. 2009), we opt here for the simple scenario proposed by Rankin and Kokko (2007) to derive our models.

Below, we consider two situations where sex-specific nutrient limitations may influence population dynamics. First, we consider that nutrient limitations impact population growth rates via direct effects on reproductive traits in each sex (e.g. male sexual advertisement, female fecundity, case 1). We then develop a model where population growth rates are instead influenced by nutrient limitations on sex-specific maturation rates (case 2). In both models, we mainly focus on exploring the importance of the capacity for males and females to achieve their sex-specific nutritional optima.

Case 1. Nutrient limitation on fertilization and fecundity

First, we consider that nutrient limitation in males reduces per-female fertilization probability as a result of reduced male reproductive investment (e.g. frequency of sexual advertisement or sperm number), while nutrient limitation in females suppresses their potential fecundity. We model these aspects as follows:

$$\frac{dM}{dt} = s_F f[F,M] brF - (F+M) d_M M \quad (1a)$$

$$\frac{dF}{dt} = s_F f[F,M] b(1-r)F - (F+M) d_F F \quad (1b)$$

where M and F represent male and female abundance, respectively, r is the primary sex ratio, b is the maximum reproductive rate of a fertilized female and f is the per-female fertilization probability. d_i (i = M or F) determines the density-dependent mortality of sex i. Although we do not consider the dynamics of food abundance per se, this term implies that populations may crash due to starvation. In terms of nutrition, s_i ($0 \leq s_i \leq 1$) represents the effect of food nutrient content (e.g. protein:carbohydrate content or phosphorous:carbon content) on reproductive effort of sex i, including negative effects due to both nutrient limitation and the metabolic costs of excreting or storing excess nutrients. A high value of s_i means that individuals of sex i are able to acquire food that closely matches their nutritional requirements. It should be noted that we formulate s_M and s_F as independent parameters, but the model can describe a situation where males and females are constrained to share a common food resource by further defining the relationship between s_M and s_F.

In the model, we assume that the per-female fertilization probability is affected by male reproductive effort as well as by male proportion within the population, as follows (Rankin and Kokko 2007):

$$f[F,M] = \frac{s_M M/(M+F)}{a + s_M M/(M+F)} \quad (2)$$

where a represents the strength of the Allee effect. When the Allee effect is present (i.e. $a > 0$), the fertilization probability increases with both male reproductive effort and male proportion, but saturates for higher values. Thus, this formulation includes a range of situations, including scenarios where females do not experience sperm limitation (i.e. $a = 0$) or where male reproductive effort is not constrained by nutrient limitation (i.e. $s_M = 1$).

Using this model, we explore the influence of sex-specific nutrient limitation (s_M and s_F) by examining the parameter dependence of the equilibrium total population size (see Appendix 1 for analysis). We find the following when s_M and s_F are independent (Fig. 2). When the Allee effect is weak (i.e. a is small), population size is predominantly determined by nutrient limitations on females. Nutrient limitations on male reproductive effort have minor effects on the population size, as illustrated by $N^* = b(1-r)s_F/d_F$ for $a = 0$. This is because female fertilization probability should be high even when males are less active. However, when the Allee effect is strong (i.e. large a), the population size is determined by nutrient limitations on both sexes. These results suggests that the capacity for males and females to independently optimize nutrient intake (i.e. $s_M = s_F = 1$) may be important for population growth.

However, as we have noted above, the degree to which each sex is able to achieve its own nutritional optima may be constrained either genetically or environmentally. If the sexes must compromise on a single food of a given nutritional content, what point along a gradient of food nutritional

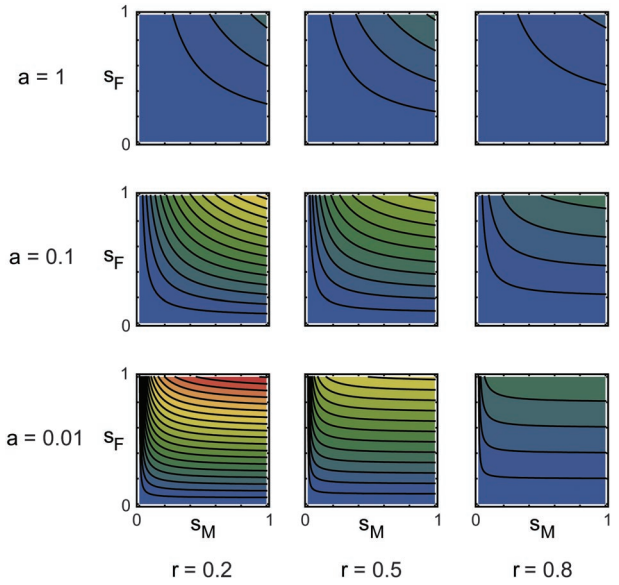

Figure 2. Parameter dependence of equilibrium total population size in case 1. In each small panel, the horizontal and vertical axes represent nutritional effects on male and female reproductive performance (s_M and s_F), respectively. Panels are arranged left to right by primary sex ratio (r = 0.2, 0.5, and 0.8) and top to bottom by the strength of the Allee effect (a = 0.01, 0.1, and 1). In each case, equilibrium population sizes are color coded, with red corresponding to the highest values and blue the lowest. b = 50 and d_i = 10.

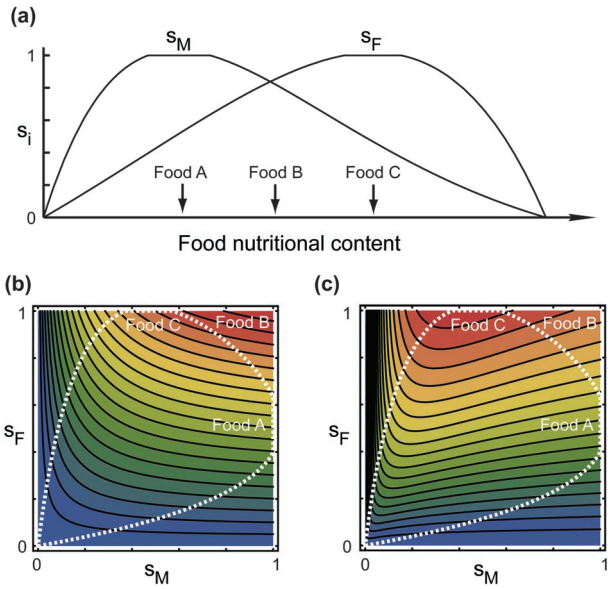

Figure 3. Effects of food nutritional content on equilibrium total population size. (a) Two curves representing imaginary relationships between sex-specific reproductive performance and food nutritional content (e.g. phosphorous:carbon). Arrows label nutrient contents of three imaginary foods (food A, B and C) on the x-axis. (b, c) White lines indicate the trajectory of (s_M, s_F) on the plane where the equilibrium population size is represented by colors as in Fig. 2. Imaginary foods indicated in (a) are also labeled on the plane in (b, c) for reference. (b) case 1 and (c) case 2. b = 50, d_i = 10, a =0.1, r = 0.5 and m_i = 5. Color coding has been rescaled for clarity.

content results in the highest population growth rates? We can characterize this by modeling that both s_M and s_F vary along a gradient of food nutritional content (e.g. phosphorous:carbon), where peak values (i.e. s_i =1) for each sex lie at distinct points along the gradient. Here we model an idealized case where the functional relationship between food nutritional content and s_i is unimodal for both sexes but truncated at s_i = 1 (Fig. 3a). In Fig. 3a, we assume that foods A and C maximize male and female reproductive performance, respectively. The nutritionally-mediated relationship between male and female performance is then plotted (white line in Fig. 3b) on the plane (s_M, s_F) where equilibrium population size is presented. In this scenario, population sizes are maximized when individuals select a common food source that lies between the male and female optima (e.g. food B, Fig. 3b).

Case 2. Sex-specific nutrient limitations on maturation rate

Nutrient limitations may also differentially affect the developmental trajectories of each sex, (e.g. growth rates, Sterner and Elser 2002), which should in turn influence population growth rates. Here, we explore population consequences when nutrient limitations delay maturation in males and females. We propose a model with both sex and stage structure:

$$\frac{dJ_M}{dt} = f[F,M]brF - s_M m_M J_M - d_J J_M \tag{3a}$$

$$\frac{dJ_F}{dt} = f[F,M]b(1-r)F - s_F m_F J_F - d_J J_F \tag{3b}$$

$$\frac{dM}{dt} = s_M m_M J_M - (M+F)d_M M \tag{3c}$$

$$\frac{dF}{dt} = s_F m_F J_F - (M+F)d_F F \tag{3d}$$

where J_i (i = M or F) represents the juvenile abundance of sex i. We denote the other variables and some parameters as in the first model. d_j is the density-independent juvenile mortality rate. m_i is maturation rate of sex i, which is constrained by nutrient limitations characterized by the parameter s_i ($0 \le s_i \le 1$). Female fertilization probability depends on the proportion of males within the population (Rankin and Kokko 2007):

$$f[F,M] = \frac{M/(M+F)}{a + M/(M+F)} \tag{4}$$

As in case 1, we examine the parameter dependence of the total population size (Fig. 4; see Appendix 2 for analysis). We find that population growth is limited by nutrient availability for both sexes when the Allee effect is strong (i.e. large a) and the sex primary ratio is female-biased (i.e. small r). This

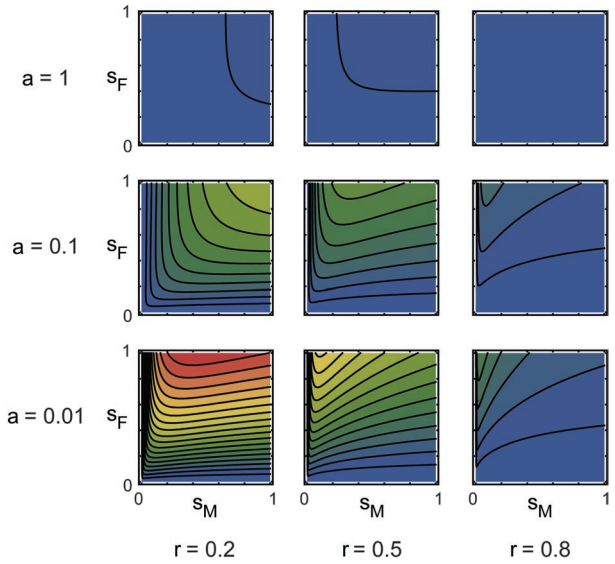

Figure 4. Parameter dependence of equilibrium population size in case 2. In each small panel, the horizontal and vertical axes represent nutritional effects on male and female maturation rates (s_M and s_F), respectively. Conditions are identical to those in Fig. 3c.

implies that if the sexes are constrained to share the same food resource in such situations, population growth may be maximized when individuals preferentially select food that lies between male and female optima (e.g. as shown in Fig. 3a). On the other hand, we find that the total population size is maximized at low levels of s_M, when the Allee effect was weak (i.e. small a) or primary sex ratio is male-biased (i.e. large r). In contrast to the previous finding, this result suggests that population growth rates may be maximized when individuals utilize a food resource that is biased toward the female nutritional optimum (i.e. small s_M and large s_F; Fig. 3c). Intriguingly, this result suggests that independent optimization of nutrient intake for both sexes (i.e. $s_M = s_F = 1$) may negatively influence population growth. This apparently paradoxical result is explained by intersexual competition; that is, the increased adult male abundance due to high male maturation rate (i.e. large s_M) suppresses the adult female abundance and thus total population size through the density-dependent mortality. Increased adult female abundance due to large s_F can also have a negative effect on the total population size when intersexual competition considerably suppresses male abundance and thus female fertilization probability (data not shown).

Together our two models highlight how the effect of nutrient limitation on fertilization and maturation may have fundamental implications at the population level. For example, our first model (case 1) suggests that fitness (i.e. population growth rate) may increase when males and females are able to select food based on their sex-specific nutrient requirements. This finding is consistent with the central arguments we develop from empirical data. However, if males and females are constrained in their ability to differentially select food (Maklakov et al. 2008), fitness may be maximized by foraging for foods that lie between the nutritional optima of each sex (e.g. Fig. 3b). Interestingly, the results from case 2 indicate that population growth rates may in certain circumstances be maximized when the sexes share a common food resource that does not correspond to the 'optimal' food nutritional content of one or both sexes (e.g. Fig. 3c). Thus, mismatches between sex-specific nutritional optima and realized nutritional intake may not always translate in to decreases in population growth, a possibility that requires further exploration.

While we have employed simple models, our results nevertheless suggest that conflict between the sexes in their ability to reach their own sex-specific optima may have important consequences for population growth. More detailed models should expand these preliminary insights to better understand more specific cases (e.g. vertebrates and invertebrates, capital and income breeders, monogamy and polygamy, semelparity and iteroparity), as well as the importance of temporal and spatial variability in nutrient composition of available foods (Muller et al. 2001, Grover 2003, Andersen et al. 2004, Hall 2004, Moe et al. 2005).

Conclusions and future directions

We have highlighted how nutritionally explicit frameworks can generate new hypotheses about the eco-evolutionary forces driving differences between the sexes. We have also presented a number of key areas where nutritionally-explicit approaches such as the Geometric Framework and Ecological Stoichiometry can further our understanding of sex-specific reproductive investment. In particular, an understanding of the material demands of sex-specific traits should readily lead to testable hypotheses regarding variation in trait expression at different times (e.g. seasonal), and places (e.g. habitats, ecosystems) when/where the balance of constituent nutrients may vary. Testing such predictions should further our quest to capture and explain the great diversity in sex-specific phenotypes.

Further, fundamental and operational definitions of 'resource' as required by nutritionally-explicit approaches described herein should allow for new and incisive ways to test theoretical predictions at various levels of organization. Of particular interest is how sex-specific fitness optima could be permitted either through the evolution of sex-linkage (Rice 1984) or through sex-biased gene expression of autosomal loci (Ellegren and Parsch 2007). Knowing the nutritional optima of the sexes will allow for informed analysis of data generated from high-throughput methods (e.g. transcriptome) to identify such predicted sex-linkage and differential expression, because gene functions and their substrates are often described in their elemental or molecular form in the various databases (e.g. KEGG, <www.genome.jp/kegg/>).

In addition, such nutritionally-explicit and empirically amenable approaches should also contribute much to understanding the role of condition and genetic quality in the process of sexual selection (Hunt et al. 2004b) by offering a quantifiable metric of 'condition'. For example, defining condition in terms of the ability of mates to acquire, assimilate, and allocate a key nutrient (e.g. an essential amino acid) or suite of nutrients required for some aspect of reproduction will not only allow for a quantitative assessment of condition, but also illuminate the underlying genetic and molecular pathways that determine condition. As such, this

approach should provide a mechanistic basis for critically testing several important predictions generated from recent advances in sexual selection research (Radwan 2008).

In conclusion, we have discussed how males and females differ in their nutritional requirements specifically in relation to reproductive traits, and have highlighted some of the mechanisms that each sex can use to reach their associated nutritional optima. Such nutritionally-explicit thought generates novel predictions and new empirical pathways for considering the evolution of sex-specific traits. Defining key parameters (e.g. 'resource', 'condition') involved in sexual selection in nutritionally-explicit terms should lend greater empirical amenability, while being generally applicable to a wide variety of organisms. Moreover, by expanding these concepts to the broader consequences of sex-specific nutrient limitation on population growth we illustrate the potential to approach higher levels of biological complexity provided by a unified nutritional framework incorporating both the Geometric framework and Ecological stoichiometry (Kay et al. 2005, Raubenheimer et al. 2009). Clearly, nutritionally-explicit thought has much to contribute to contemporary issues surrounding the evolution of sex-specific traits.

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References

Allen, M. E. and Ullrey, D. E. 2004. Relationships among nutrition and reproduction and relevance for wild animals. – Zoo Biol. 23: 475–487.

Andersen, T. et al. 2004. Stoichiometry and population dynamics. – Ecol. Lett. 7: 884–900.

Anderson, T. R. et al. 2004. Stoichiometry: linking elements to biochemicals. – Ecology 85: 1193–1202.

Andersson, M. 1994. Sexual selection. – Princeton Univ. Press.

Bawden, J. W. and McIver, F. T. 1964. Distribution of Ca^{45} during pregnancy under conditions of calcium deficiency in rats. – J. Dent. Res. 43: 563–567.

Baxter, B. J. et al. 1999. Bone turnover associated with antler growth in red deer (*Cervus elaphus*). – Anat. Rec. 256: 14–19.

Beck, C. A. et al. 2005. Blubber fatty acids of gray seals reveal sex differences in the diet of a size-dimorphic marine carnivore. – Can. J. Zool. 83: 377–388.

Bertram, S. M. et al. 2006. Signalling and phosphorous: correlations between mate signalling effort and body elemental composition in crickets. – Anim. Behav. 72: 899–907.

Bertram, S. M. et al. 2009. Phosphorus availability influences cricket mate attraction displays. – Anim. Behav. 77: 525–530.

Boersma, M. and Elser, J. J. 2006. Too much of a good thing: on stoichiometrically balanced diets and maximal growth. – Ecology 87: 1325–1330.

Boggs, C. L. 2003. Environmental variation, life histories and allocation. – In: Boggs, C. L. et al. (eds), Butterflies: ecology and evolution taking flight. Univ. of Chicago Press, pp. 185–206.

Boggs, C. L. and Gilbert, L. E. 1979. Male contribution to egg-production in butterflies: evidence for transfer of nutrients at mating. – Science 206: 83–84.

Bonduriansky, R. and Chenoweth, S. F. 2009. Intralocus sexual conflict. – Trends Ecol. Evol. 24: 280–288.

Bronson, F. H. and Heideman, P. D. 1994. Seasonal regulation of reproduction in mammal. – In: Knobil, E. and Neill, J. D. (eds), The physiology of reproduction. Raven Press, pp. 541–583.

Cotton, S. et al. 2004. Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? – Proc. R. Soc. Lond. B 271: 771–783.

Courchamp, F. et al. 2009. Allee effects in ecology and conservation. – Oxford Univ. Press.

Ellegren, H. and Parsch, J. 2007. The evolution of sex-biased genes and sex-biased gene expression. – Nat. Rev. Genet. 8: 689–698.

Elser, J. J. and Hamilton, A. 2007. Stoichiometry and the new biology: the future is now. – PLoS Biol. 5: e181.

Elser, J. J. et al. 2000. Biological stoichiometry from genes to ecosystems. – Ecol. Lett. 3: 540–550.

Fagan, W. F. et al. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. – Am. Nat. 160: 784–802.

Fedorka, K. M. and Mousseau, T. A. 2002. Nuptial gifts and the evolution of male body size. – Evolution 56: 590–596.

Felton, A. M. et al. 2009. Protein content of diets dictates the daily energy intake of a free-ranging primate. – Behav. Ecol. 20: 685–690.

Frost, P. C. et al. 2005. Are you what you eat? Physiological constraints on organismal stoichiometry in an elementally imbalanced world. – Oikos 109: 18–28.

Gosler, A. G. and Harper, D. 2000. Assessing the heritability of body condition in birds: a challenge exemplified by the great tit *Parus major* L. (Aves). – Biol. J. Linn. Soc. 71: 103–117.

Gray, D. A. and Eckhardt, G. 2001. Is cricket courtship song condition dependent? – Anim. Behav. 62: 871–877.

Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? – Ecology 82: 1473–1483.

Grover, J. P. 2003. The impact of variable stoichiometry on predator–prey interactions: a multinutrient approach. – Am. Nat. 162: 29–43.

Gwynne, D. T. 1982. Mate selection by female katydids (Orthoptera: Tettigoniidae, *Conocephalus nigropleurum*). – Anim. Behav. 30: 734–738.

Gwynne, D. T. 2008. Sexual conflict over nuptial gifts in insects. – Annu. Rev. Entomol. 53: 83–101.

Gwynne, D. T. and Simmons, L. W. 1990. Experimental reversal of courtship roles in an insect. – Nature 346: 172–174.

Hall, M. D. et al. 2008. The effect of diet quality and wing morph on male and female reproductive investment in a nuptial feeding ground cricket. – PLoS ONE 3: e3437.

Hall, S. R. 2004. Stoichiometrically explicit competition between grazers: species replacement, coexistence, and priority effects along resource supply gradients. – Am. Nat. 164: 158–172.

Hill, G. E. et al. 2002. Dietary carotenoids predict plumage coloration in wild house finches. – Proc. R. Soc. Lond. B 269: 1119–1124.

Houle, D. and Kondrashov, A. S. 2002. Coevolution of costly mate choice and condition-dependent display of good genes. – Proc. R. Soc. Lond. B 269: 97–104.

Hunt, J. et al. 2004a. High-quality male field crickets invest heavily in sexual display but die young. – Nature 432: 1024–1027.

Hunt, J. et al. 2004b. What is genetic quality? – Trends Ecol. Evol. 19: 329–333.

Jakob, E. M. et al. 1996. Estimating fitness: a comparison of body condition indices. – Oikos 77: 61–67.

Janakiraman, V. et al. 2003. Calcium supplements and bone resorption in pregnancy: a randomized crossover trial. – Am. J. Prev. Med. 24: 260–264.

Judge, K. A. et al. 2008. Condition dependence of male life span and calling effort in a field cricket. – Evolution 62: 868–878.
Karlsson, B. 1995. Resource allocation and mating systems in butterflies. – Evolution 49: 955–961.
Karlsson, B. 1996. Male reproductive reserves in relation to mating system in butterflies: a comparative study. – Proc. R. Soc. Lond. B 263: 187–192.
Kay, A. D. et al. 2005. Toward a stoichiometric framework for evolutionary biology. – Oikos 109: 6–17.
Kodric-Brown, A. and Brown, J. H. 1987. Anisogamy, sexual selection, and the evolution and maintenance of sex. – Evol. Ecol. 1: 95–105.
Kovacs, C. S. 2005. Calcium and bone metabolism during pregnancy and lactation. – J. Mammary Gland Biol. 10: 105–118.
Krockenberger, A. K. et al. 1998. Production of milk and nutrition of the dependent young of free-ranging koalas (*Phascolarctos cinereus*). – Physiol. Zool. 71: 45–56.
Langer, P. 2008. The phases of maternal investment in eutherian mammals. – Zoology 111: 148–162.
Lande, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. – Evolution 34: 292–305.
Lee, K. P. et al. 2008. Lifespan and reproduction in *Drosophila*: new insights from nutritional geometry. – Proc. Natl Acad. Sci. USA 105: 2498–2503.
Lincoln, G. A. 1992. Biology of antlers. – J. Zool. 226: 517–528.
Linville, S. U. and Breitwisch, R. 1997. Carotenoid availability and plumage coloration in a wild population of northern cardinals. – Auk 114: 796–800.
Maklakov, A. A. et al. 2008. Sex-specific fitness effects of nutrient intake on reproduction and lifespan. – Curr. Biol. 18: 1062–1066.
Markow, T. A. et al. 2001. How *Drosophila* males make eggs: it is elemental. – Proc. R. Soc. Lond. B 268: 1527–1532.
McCarthy, M. A. 1997. The Allee effect, finding mates and theoretical models. – Ecol. Modell. 103: 99–102
McGraw, K. J. 2005. The antioxidant function of many animal pigments: are there consistent health benefits of sexually selected colourants? – Anim. Behav. 69: 757–764.
McGraw, K. J. 2006. Mechanics of carotenoid-based coloration. – In: Hill, G. E. and McGraw, K. J. (eds), Bird coloration: mechanisms and measurements. Harvard Univ. Press, pp. 177–242.
McGraw, K. J. and Gregory, A. J. 2004. Carotenoid pigments in male American goldfinches: what is the optimal biochemical strategy for becoming colourful? – Biol. J. Linn. Soc. 83: 273–280.
McGraw, K. J. et al. 2003. Diet, plasma carotenoids, and sexual coloration in the zebra finch (*Taeniopygia guttata*). – Auk 120: 400–410.
McGraw, K. J. et al. 2005. The physiological costs of being colourful: nutritional control of carotenoid utilization in the American goldfinch, *Carduelis tristis*. – Anim. Behav. 69: 653–660.
Moe, S. J. et al. 2005. Recent advances in ecological stoichiometry: insights for population and community ecology. – Oikos 109: 29–39.
Molina-Font, J. A. 1998. Nutrition and fetal growth. – Early Hum. Dev. 53: S51–S60.
Møller, A. P. et al. 2000. Carotenoid-dependent signals: indicators of foraging efficiency, immunocompetence or detoxification ability? – Avian Poult. Biol. Rev. 11: 137–159.
Muller, E. B. et al. 2001. Stoichiometric food quality and herbivore dynamics. – Ecol. Lett. 4: 519–529.
Munks, S. A. and Green, B. 1995. Energy allocation for reproduction in a marsupial arboreal folivore, the common ringtail possum (*Pseudocheirsu peregrinus*). – Oecologia 101: 94–104.
Mysterud, A. 2000. The relationship between ecological segregation and sexual body size dimorphism in large herbivores. – Oecologia 124: 40–54.
Negro, J. J. et al. 2001. Sex-and age-related variation in plasma carotenoids despite a constant diet in the red-legged partridge *Alectoris rufa*. – Ardea 89: 275–280.
Olson, V. A. and Owens, I. P. F. 1998. Costly sexual signals: are carotenoids rare, risky or required? – Trends Ecol. Evol. 13: 510–514.
Partridge, L. et al. 2005. Sex and death: what is the connection? – Cell 120: 461–472.
Radwan, J. 2008. Maintenance of genetic variation in sexual ornaments: a review of the mechanisms. – Genetica 134: 113–127.
Rankin, D. J. and Kokko, H. 2007. Do males matter? The role of males in population dynamics. – Oikos 116: 335–348.
Rasmussen, P. 1977. Calcium deficiency, pregnancy, and lactation in rats: some effects on blood-chemistry and skeleton. – Calc. Tiss. Res. 23: 87–94.
Raubenheimer, D. and Simpson, S. J. 1997. Integrative models of nutrient balancing: application to insects and vertebrates. – Nutr. Res. Rev. 10: 151–179.
Raubenheimer, D. and Simpson, S. J. 2004. Organismal stoichiometry: quantifying non-independence among food components. – Ecology 85: 1203–1216.
Raubenheimer, D. and Simpson, S. J. 2006. The challenge of supplementary feeding: can geometric analysis help save the kakapo? – Notornis 53: 100–111.
Raubenheimer, D. et al. 2005. Does Bertrand's rule apply to macronutrients? – Proc. R. Soc. Lond. B 272: 2429–2434.
Raubenheimer, D. et al. 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. – Funct. Ecol. 23: 4–16.
Reznick, D. et al. 2000. Big houses, big cars, superfleas and the costs of reproduction. – Trends Ecol. Evol. 15: 421-–425.
Rice, W. R. 1984. Sex-chromosomes and the evolution of sexual dimorphism. – Evolution 38: 735–742.
Rowe, L. and Houle, D. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. – Proc. R. Soc. Lond. B 263: 1415–1421.
Ruckstuhl, K. E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. – Anim. Behav. 56: 99–106.
Sakaluk, S. K. et al. 2006. Cryptic sexual conflict in gift-giving insects: chasing the chase-away. – Am. Nat. 167: 94–104.
Simmons, L. W. 1992. Quantification of role reversal in relative parental investment in a bush cricket. – Nature 358: 61–63.
Simmons, L. W. and Gwynne, D. T. 1993. Reproductive investment in bushcrickets: the allocation of male and female nutrients to offspring. – Proc. R. Soc. Lond. B 252: 1–5.
Simpson, S. J. and Raubenheimer, D. 1996. Feeding behaviour, sensory physiology and nutrient feedback: a unifying model. – Entomol. Exp. Appl. 80: 55–64.
Slagsvold, T. and Lifjeld, J. T. 1985. Variation in plumage color of the great tit *Parus major* in relation to habitat, season and food. – J. Zool. 206: 321–328.
Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.
Sterner, R. W. and Elser, J. J. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. – Princeton Univ. Press.
Tarnopolsky, M. A. and Saris, W. H. M. 2001. Evaluation of gender differences in physiology: an introduction. – Curr. Opin. Clin. Nutr. 4: 489–492.
Tucker, S. et al. 2009. Sources of variation in diets of harp and hooded seals estimated from quantitative fatty acid signature analysis (QFASA). – Mar. Ecol. Prog. Ser. 384: 287–302.
Urgell, M. R. et al. 1998. Maternal nutritional factors: significance for the fetus and the neonate. – Early Hum. Dev. 53: S61–S76.

Vahed, K. 1998. The function of nuptial feeding in insects: review of empirical studies. – Biol. Rev. Camb. Philos. Soc. 73: 43–78.
Vahed, K. 2007. All that glisters is not gold: sensory bias, sexual conflict and nuptial feeding in insects and spiders. – Ethology 113: 105–127.
van Noordwijk, A. J. and de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. – Am. Nat. 128: 137–142.
Wagner, W. E. and Hoback, W. W. 1999. Nutritional effects on male calling behaviour in the variable field cricket. – Anim. Behav. 57: 89–95.
Wedell, N. et al. 2008. Nuptial gifts fail to resolve a sexual conflict in an insect. – BMC Evol. Biol. 8: 204.
Will, M. W. and Sakaluk, S. K. 1994. Courtship feeding in decorated crickets: is the spermatophylax a sham? – Anim. Behav. 48: 1309–1315.

Appendix 1

Equilibrium population size in case 1
At equilibrium, males and females have the following equilibrium abundances.

$$M^* = \frac{bd_F r^2(1-r)s_M s_F}{\{d_M(1-r)+d_F r\}[a\{d_M(1-r)+d_F r\}+d_F r s_M]} \tag{A1a}$$

$$F^* = \frac{bd_M r(1-r)^2 s_M s_F}{\{d_M(1-r)+d_F r\}[a\{d_M(1-r)+d_F r\}+d_F r s_M]} \tag{A1b}$$

Local stability analysis demonstrates that the equilibrium is always stable (not shown). The total population size is given by

$$N^* = M^* + F^* = \frac{br(1-r)s_M s_F}{a\{d_M(1-r)+d_F r\}+d_F r s_M} \tag{A2}$$

Appendix 2

Equilibrium population size in case 2
At equilibrium, juvenile and adult males and females have the following abundances:

$$J_M^* = \frac{br^2(1-r)d_M d_F m_M m_F s_M s_F (d_J + m_F s_F)}{(1-r)ad_J d_M m_F s_F (d_J + m_M s_M) + r(1+a)d_F m_M s_M (d_J + m_F s_F)} X \tag{B1a}$$

$$J_M^* = \frac{br(1-r)^2 d_M d_F m_M m_F s_M s_F (d_J + m_M s_M)}{(1-r)ad_J d_M m_F s_F (d_J + m_M s_M) + r(1+a)d_F m_M s_M (d_J + m_F s_F)} X \tag{B1b}$$

$$M^* = rd_F m_M s_M (d_J + m_F s_F) X \tag{B1c}$$

$$F^* = (1-r)d_M m_F s_F (d_J + m_M s_M) X \tag{B1d}$$

where

$$X = \frac{br(1-r)m_M m_F s_M s_F}{d_A\{(1-r)d_J m_F s_F + m_M s_M (rd_J + m_F s_F)\}\{(1-r)ad_J d_M m_F s_F (d_J + m_M s_M) + r(1+a)d_F m_M s_M (d_J + m_F s_F)\}} \tag{B2}$$

By numerical simulations, we confirmed that the equilibrium was generally stable (data not shown). The total population size is given by JM*+ JF*+ M*+ F*.