CHAPTER TWO

Integrating nutritional and behavioral ecology: Mutual benefits and new frontiers

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1. Introduction

Although behavioral ecology and nutritional ecology have many shared interests, these fields were conceived and developed largely independently of one another. The historical focus in behavioral ecology has been on unraveling the adaptive functions of behavior, both in relation to ecological interactions, principally resource acquisition, and social interactions

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including animal signaling, mate choice, and the evolution of cooperation (Birkhead & Monaghan, 2010). Methodologically, there has been strong emphasis on quantitative models, including optimization models, game theory, and models of multilevel selection (Dugatkin & Reeve, 1998; Martins & Hansen, 1997; Nowak & Sigmund, 2004; Traulsen & Nowak, 2006). The framework used in behavioral ecology for studying resource acquisition, optimal foraging theory, generally assumes that the specific nutritional goal of foraging is net energy gain, sometimes subject to constraints set by other food components (Illius, Tolkamp, & Yearsley, 2002; Raubenheimer & Simpson, 2018; Stephens & Krebs, 1986).

In contrast, the field of nutritional ecology coalesced around the question of which factors govern food selection and processing in animals (Choat & Clements, 1998; Raubenheimer & Simpson, 1997; Raubenheimer, Simpson, & Mayntz, 2009; Van Soest, 1994). Methodologically, nutritional ecology centered on the interplay between field studies of animal ecology and experiments measuring the behavioral (food selection), physiological (food utilization) and functional (survival, development, growth, and reproduction) responses of animals to foods (Raubenheimer et al., 2009). In contrast to the emphasis of behavioral ecology on energy as the primary foraging currency, historically nutritional ecology focused more heavily on nutrients, most prominently protein (often measured as nitrogen content of foods, e.g. Mattson, 1980; McNeill & Southwood, 1978; White, 1993).

This emphasis on different nutritional currencies is not surprising given that optimal foraging theorists in behavioral ecology worked largely with predators, animal parasites and graminivores, whose foods were considered to be of high nutritional quality (i.e., including adequate protein), but limited in quantity (Stephens & Krebs, 1986). In contrast, nutritional ecology researchers predominantly worked on herbivores, whose growth can be strongly constrained by the nutritional quality of foods, including access to sufficient protein in their diet (Simpson, Sibly, Lee, Behmer, & Raubenheimer, 2004). Also relevant are the different timescales of the behaviors which optimal foraging theorists and nutritional ecologists tend to study. Optimal foraging theorists often focus on short-term, energy-fueled foraging behaviors and their long-term evolutionary origins and maintenance (Stephens & Krebs, 1986), whereas nutritional ecologists have often focused on the intermediate-level, protein-intensive, processes of growth and reproduction (e.g., Harrison, Raubenheimer, Simpson, Godin, & Bertram, 2014; Lee et al., 2008; Maklakov et al., 2008; Raubenheimer et al., 2009; South, House, Moore, Simpson, & Hunt, 2011; but see

Raubenheimer, Simpson, & Tait, 2012 for discussion of the broadening range of timescales under investigation by nutritional ecologists).

The historical focus in behavioral ecology and nutritional ecology on single nutrient currencies was driven not so much by a theoretical commitment to the biological importance of energy or protein, as by methodological pragmatism. It has long been known that animals are dependent on several essential nutrients (Richter, Holt, & Barelare, 1938; Waldbauer & Friedman, 1991), and the importance of nutrient balance had been experimentally established when both nutritional and behavioral ecology were in their infancy (House, 1969). However, what was missing was a methodological approach for modeling the complexities of nutrient balance (Raubenheimer et al., 2009). For this purpose, Raubenheimer and Simpson (1993) introduced a state-space geometric framework for nutritional ecology (Raubenheimer & Simpson, 1993; Simpson & Raubenheimer, 1993). This Geometric Framework for nutrition has since been applied to a wide range of animal systems and biological questions (Simpson & Raubenheimer, 2012). These studies have demonstrated that the behavior, physiology and performance of animals are influenced more strongly by nutrient balance than by any particular nutrient on its own. This critical insight, that nutrition is best understood as a multivariate challenge, has yet to be fully inculcated into behavioral ecology research.

Recent conceptual shifts in behavioral ecology regarding behavioral traits parallel nutritional ecology's transition from univariate to multivariate emphases regarding nutritional inputs. Early efforts to understand variation in individual behavior typically focused on single focal behaviors, to the exclusion of other nominally unrelated aspects of an organism's phenotype. However, recent theoretical and empirical work has underlined the importance of considering focal traits within the broader life-history context of the whole organism (e.g., Biro & Stamps, 2008; Hatchwell & Komdeur, 2000; Linden & Møller, 1989; Morehouse, 2014; Stearns, 2000). In much the same way that organisms must balance their nutritional intake, individuals must balance trade-offs between behaviors and morphological traits (Morehouse, 2014). These trade-offs can arise due to temporal constraints between behaviors such as foraging and mating (Abrahams, 1993; Boggs, 1992; Mangel & Clark, 1986), or through nutritional constraints that lead to resource competition between morphological and behavioral traits (Badyaev, 1997; Badyaev & Ghalambor, 2001; Badyaev & Qvarnström, 2002; Gustafsson, Qvarnström, & Sheldon, 1995; Morehouse, 2014). Behavioral ecology researchers have thus moved away from studying behaviors in isolation, and instead are increasingly studying behaviors within a life-history framework. For example, a number of research groups have begun making headway in understanding causal links between mating success and foraging ability in instances where sexual signals are reliant on limiting nutritional resources (Gray, Simpson, & Polak, 2018; Harrison et al., 2014; Hebets, Wesson, & Shamble, 2008; Mehlis, Rick, & Bakker, 2015; Reifer, Harrison, & Bertram, 2018; Whattam & Bertram, 2011). Similarly, the recent surge in interest in behavioral syndromes has highlighted that suites of behaviors may often be connected by individual differences in boldness or activity level (Han & Dingemanse, 2015; Serrano-Davies, O'Shea, & Quinn, 2017; Sih, Bell, & Johnson, 2004; Wolf & Weissing, 2012). Researchers are now probing whether these individual differences in activity level are driven by underlying variation in metabolism (Biro & Stamps, 2008; Careau, Beauchamp, Bouchard, & Morand-Ferron, 2019). These more recent advances in behavioral ecology argue for the need to consider behavioral performance as a multivariate trait, subject to extensive trade-offs with other seemingly unrelated aspects of an organism's life history (Morehouse, 2014; Morehouse, Nakazawa, Booher, Jeyasingh, & Hall, 2010). Research in nutritional ecology could benefit from the insights derived from these more holistic approaches to behavioral performance when considering how animals balance the nutritional demands imposed by their lifestyles or vice versa (Oudman et al., 2016).

The emerging emphasis on how organisms balance resource acquisition (nutritional ecology) and behavioral performance (behavioral ecology) suggest that deeper evolutionary understanding would come from investigating how these processes are connected. Such investigations could come in the form of (1) behavioral ecologists adopting new approaches from nutritional ecology to improve theory and empirical work (e.g., expanding from simple food restriction to nutrient-specific approaches), (2) nutritional ecologists explicitly tackling evolutionary hypotheses when examining links between diet and behavior through integration of key issues in behavioral ecology (e.g., sexual conflict, behavioral syndromes), or (3) the design of new experiments at the interface between nutritional and behavioral ecology. Of course, the latter implementation of a multivariate perspective for both nutrition and behavior can be experimentally challenging, particularly for some study systems. Here we highlight why such an integration may be worth the extra effort, describe methods that researchers might adopt to this end, and provide examples from reproductive biology that illustrate how this highly integrative perspective has already started revealing novel insights into several systems.

2. The multivariate nature of nutrition

Researchers studying nutrition have long understood that organisms must balance their intake of multiple important resources. However, focused study of the rules that govern such balancing, as well as the outcomes of nutritional imbalance, only began in earnest with the introduction of the Geometric Framework for nutrition (reviewed in Simpson & Raubenheimer, 2012). Although there are other frameworks for considering the material basis for the evolution of behavior (e.g., ecological stoichiometry, Sterner & Elser, 2002), the Geometric Framework approach, with its multivariate and nutritionally explicit perspective, differs in several respects that make it particularly well suited to the nutritional ecology-behavioral ecology integration we argue for here (Raubenheimer et al., 2012).

In the Geometric Framework, models are constructed around a *nutrient space* subtended by two or more nutritional axes, each of which represents a different food component (Fig. 1; Raubenheimer & Simpson, 1993).

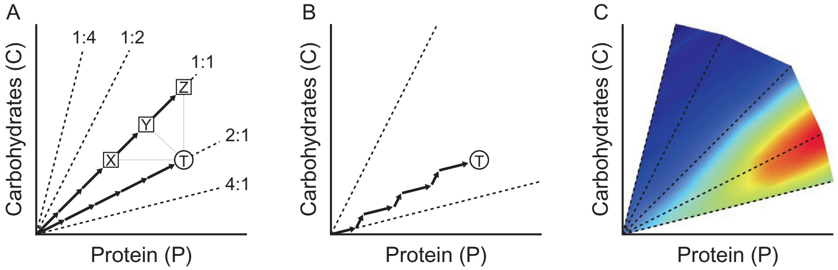

Fig. 1 Schematics showing the basic elements of the Geometric Framework for nutrition. The X and Y axes represent two possible nutritional axes (protein and carbohydrates) that bound the nutrient space. Food compositions (e.g., P:C ratios) are represented by nutritional rails (dashed lines radiating from the origin, labeled with their respective P:C ratios in A). Animals navigate through this nutrient space by consuming foods (arrows), with the goal of reaching their optimal nutritional state or intake target (T). In (A) two eating scenarios are represented: one in which the food source is nutritionally balanced, allowing the animal to reach its intake target simply by eating a single food (2:1 nutritional rail), and another in which the available food is nutritionally imbalanced (1:1), forcing the animal to under-ingest P to avoid over-ingesting C (X), over-ingest C to ingest sufficient P (Z) or adopt a compromise between under-ingesting P and over-ingesting C (Y). In (B) the focal animal has access to nutritionally complementary foods, allowing it to arrive at its intake target by alternating ingestion of two imbalanced foods. (C) By measuring focal outcomes from animals restricted to specific foods and plotting these outcomes on an orthogonal axis (here represented as a heatmap), researchers can map regions of this nutrient space that maximize metrics of organismal performance.

The nutrient space thus provides a geometric model within which the nutritional components can be represented in common terms and quantitatively interrelated. The optimal nutritional state that can be achieved by the animal (i.e., that which under the stipulated circumstances would maximize fitness) is represented by a point or area called an *intake target* (T in Fig. 1). The animal "navigates" through nutrient space, with the goal of reaching the intake target, by selecting foods and regulating the amount of each eaten. Foods are represented by lines, called *nutritional rails*, radiating through nutrient space at an angle that is determined by the balance of nutrients they contain. For example, in a nutrient space defined by axes for protein and carbohydrate, a food that contains a 1:1 ratio of protein: carbohydrate would be represented by a 45° rail, whereas foods with proportionately more protein or carbohydrate would be represented by shallower or steeper rails, respectively. As the animal eats, it ingests the nutrients in the same proportion as they are present in the chosen food, and its nutritional state thus changes along a trajectory that is coincident with the rail for that food. The nutritional consequences of eating are therefore dependent on the relationship between the animal's current state, its optimal state (the position of the intake target), and the composition of the food that it is eating (angle of the rail).

The Geometric Framework allows researchers to investigate a number of important nutritional challenges that organisms face within a nutritionally explicit context (Raubenheimer et al., 2009). One eating scenario would be where the chosen food rail intersects both the animal's current nutritional state and its target state (the intake target; 2:1 nutritional rail in Fig. 1A). By eating this food, the animal can navigate directly to the intake target; the food is *nutritionally balanced* with respect to the animal's requirements. A second eating scenario would be where the chosen food rail does not intersect the intake target—it is *nutritionally imbalanced* and does not on its own enable the animal to reach its target. The animal can nonetheless reach the intake target by combining its intake from this food with another food whose rail falls on the opposite side of the intake target (Fig. 1B). Such foods, which are individually imbalanced but collectively enable the animal to compose a compound trajectory to the target, are *nutritionally complementary* with respect to the modeled nutrients. A third eating scenario would be where the animal neither has access to nutritionally balanced, nor nutritionally complementary foods. In this case the animal would have to settle on a trade-off between over-ingesting some nutrients and under-ingesting others (X, Y, or Z in Fig. 1A). Like the position of the intake target, such trade-offs, termed *rules of compromise*, reflect a matrix of costs and benefits, and are subject to evolution by natural selection (Simpson & Raubenheimer, 2012).

An important goal of Geometric Framework is to ascertain the nutritional phenotypes of animals and understand the balance of costs and benefits that underpin their evolution. However, nutritional state is not on its own a particularly informative route to understanding the evolution of nutritional strategies. For that, the model needs to include measures that are more directly linked to fitness, such as mortality rates, longevity, growth rates, and reproduction. Since these variables cannot be expressed in nutritional terms, they are incorporated using a response axis that is orthogonal to the nutrient space. A powerful way of doing this is to use response surfaces that map the consequences (in terms of survival, growth, reproduction, etc.) for the animal at a given point in nutrient space at a stipulated time (Fig. 1C; Simpson & Raubenheimer, 2012). Recently, this approach has become even more powerful with the development of a standard quantitative method for analyzing these nutritional data; this method can both accurately assess nutritional trade-offs in complex nutrient spaces and compare trade-offs within and across species (e.g., Morimoto & Lihoreau, 2019).

The Geometric Framework thus offers a way for relating nutrition not only to fitness, but also to the evolved phenotypes that are associated with fitness. We argue that adoption of Geometric Framework approaches will substantially improve behavioral ecology inferences regarding the material basis of behavior and related traits (Fig. 2, bottom row). We refer interested readers to more extensive descriptions of the Geometric Framework and its applications elsewhere (e.g., Raubenheimer & Simpson, 1993, 2009; Simpson & Raubenheimer, 2012).

3. An integrative approach to nutritional ecology and behavioral ecology

The nutritionally explicit fitness surfaces offered by Geometric Framework provide a powerful starting point for greater integration of nutritional ecology and behavioral ecology, an integration that would benefit from formalizing several additional steps (Fig. 2). First, how animals manage their pursuit of different behavioral activities (e.g., courtship vs foraging, sleeping, and antipredatory behavior) can strongly determine their nutritional requirements (nutrient demand) and foraging activities (nutrient supply). Energetically costly behaviors such as mate attraction or territory defense may increase carbohydrate needs (Gillooly & Ophir, 2010;

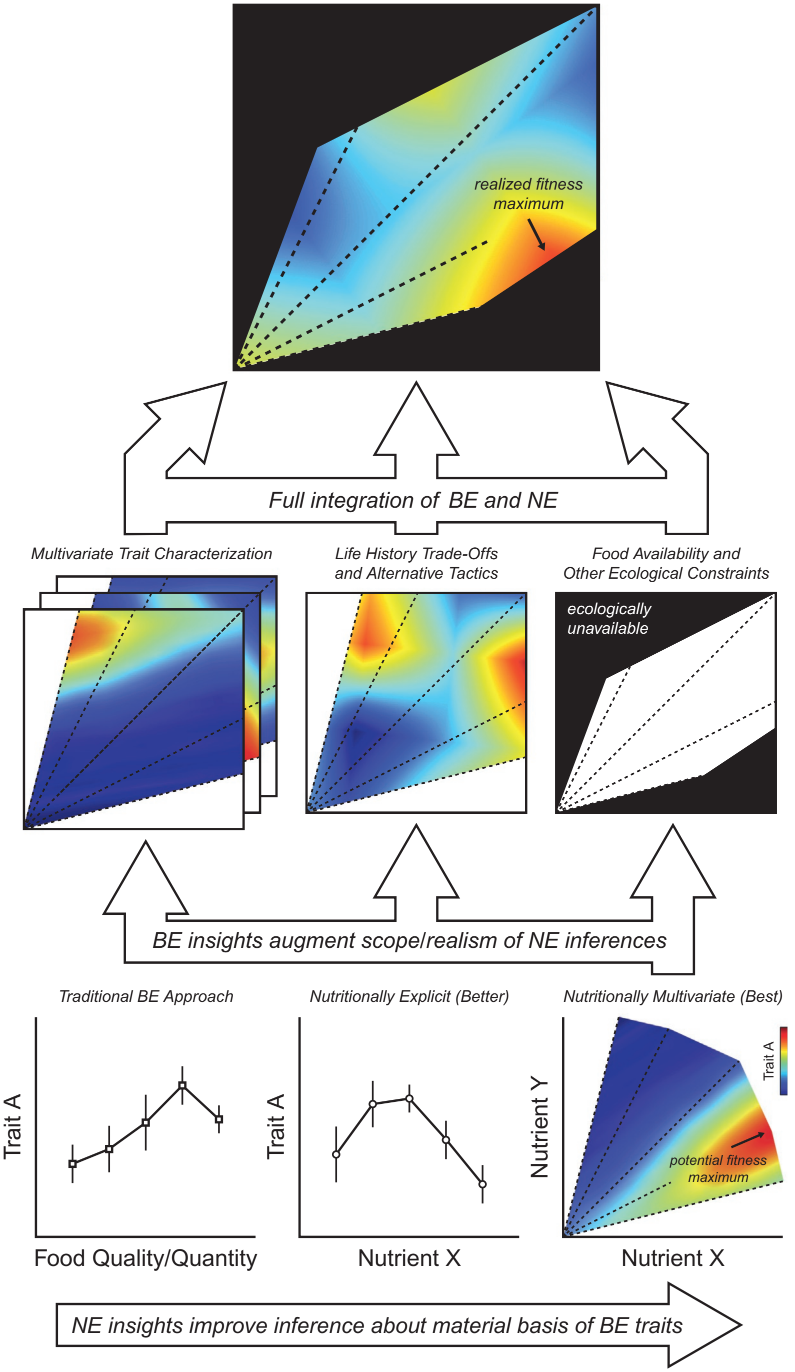

Fig. 2 See figure legend on opposite page.

Marler, Walsberg, White, & Moore, 1995; Plaistow & Siva-Jothy, 1996; Prestwich, 1994; Thomson, Darveau, & Bertram, 2014), whereas the rapid growth of conspicuous color signals or armaments may instead require high inputs of other currencies like pigments or minerals (Badyaev & Hill, 2000; Hill, Caron, & Montgomerie, 2002; Hill & McGraw, 2006a, 2006b; Morehouse, 2014). Trade-offs between these different activities are addressed by the evolution of life histories (Fig. 2, middle row, middle panel). Thus, knowledge of both the nutritional needs imposed by different behaviors as well as how those behaviors are balanced within organismal life histories is essential to understanding how and why organisms manage their nutrition (Morehouse, 2014). Such insights are unlikely to come from studies of animals whose behavioral repertoires are severely limited by experimental conditions (an issue for lab-based studies in nutritional and behavioral ecology alike). Instead, careful comparison of results from both captive and free-living populations will be essential for proper inference. This is also an instance where nutritional ecology research will benefit from drawing on the rich history of work in behavioral ecology, be it for grounding their work in the broader behavioral repertoire of a focal species or considering the evolutionary history of the phenotypes under investigation.

Second, what animals can eat is of course determined by what is available in their environment (Fig. 2, middle row, right panel). Availability is determined by both the foods that are present and the accessibility of these foods, the latter being influenced by factors such as spatial and temporal variation in food supply, competitors, and predators (e.g., Behmer, Raubenheimer, & Simpson, 2001; Bojarska & Selva, 2012;

Fig. 2 Schematic showing the steps and associated benefits involved in integration of behavioral ecology (BE) and nutritional ecology (NE). BE benefits from adopting new NE approaches (moving left to right on bottom row), especially nutritionally multivariate approaches like the Geometric Framework for nutrition, through improved insights into the material basis of behaviors and associated morphological traits. Nutritionally explicit methods (i.e., those which quantitatively manipulate individual nutrients in experimental foods) are a useful first step toward multivariate nutrition in less tractable study systems. NE also benefits from attention to new BE insights (middle row) through increasingly informed choices regarding response traits, formal recognition of the multivariate nature of life histories, and situating experiments and outcomes within the context of ecological and evolutionary constraints. Ultimately, the integrated synthesis of NE and BE will result in more robust answers to how and why animals regulate their resource intake and balance their life histories to maximize fitness under natural conditions (top row).

Coogan, Raubenheimer, Stenhouse, & Nielsen, 2014; Lihoreau et al., 2017; Lurz, Garson, & Wauters, 2000; Senior et al., 2015; Simpson, Sword, Lorch, & Couzin, 2006). Studies of nutritional balancing are therefore most meaningful when based on ecologically relevant nutritional landscapes. However, many historical nutritional ecology studies investigating nutritional balancing utilized artificial foods and lab-based settings in which nutritional availabilities only loosely approximated field conditions. And indeed, for many animals, we have only rudimentary understanding of the nutritional environments they encounter in the wild, and consequently little knowledge of how their feeding behaviors in the lab correspond to real outcomes in the field. An exciting development in nutritional ecology in the last decade has been to bridge this lab-field gap using studies of the dietary decisions of freely foraging animals (e.g., Coogan et al., 2014; Felton et al., 2009; Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2015; Johnson, Raubenheimer, Rothman, Clarke, & Swedell, 2013; Raubenheimer, 2011; Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015; Rothman, Raubenheimer, & Chapman, 2011). These studies are providing compelling insights into how animals, vertebrates and invertebrates alike, engage in dynamic nutritional balancing in an ecological context, and increasingly in an evolutionary context (e.g., Cui, Wang, Shao, Raubenheimer, & Lu, 2018; Nie et al., 2019). More work on this front is an essential task that requires both nutritional ecology and behavioral ecology approaches.

Finally, it is important to consider variation in phenotypic plasticity of both behavior and nutrition. The recent emphasis in behavioral ecology on behavioral syndromes has highlighted that behavioral plasticity may often be limited, leading to individual differences that cross behavioral contexts (Sih et al., 2004). By linking behavioral phenotypes across an organism's lifestyle, behavioral syndromes are likely to drive differences in the underlying nutritional requirements of individuals (e.g., individuals that are more active than their conspecifics are likely to require more carbohydrates in their diets to fuel this higher level of activity, Biro & Stamps, 2010). Support for this comes from the relatively extreme case of locust phase changes (Simpson, Raubenheimer, Behmer, Whitworth, & Wright, 2002). Conversely, reduced plasticity in nutritional regulation may limit the ability of organisms to acquire the resources necessary to supply certain behaviors, which could in turn link behavioral phenotypes across contexts (Biro & Stamps, 2008). Integrating nutritional ecology and behavioral ecology thus offers excellent opportunities to better understand phenotypic plasticity, and its causative links between nutrition and behavior (Fig. 2, middle row, left and center panels). We note that for nutritional ecology research, such considerations of phenotypic plasticity (or the lack thereof), motivated by advances in behavioral ecology, may help to not only explain the population mean of a nutritional balancing phenotype, but also the biological basis for its variance.

4. Integrating nutritional ecology and behavioral ecology to better understand reproduction

What might greater integration of behavioral ecology and nutritional ecology look like, and why might it be valuable? Below we describe how increased integration of these fields promises to generate novel insights at the interface between nutrition and reproduction. We focus our attention on nutrition and reproduction for largely logistic reasons: our expertise allows us to more rapidly survey this topic, and proper treatment of the full overlap between nutritional and behavioral ecology is beyond the scope of a single chapter. However, by doing so, we acknowledge that we are leaving out many exciting intersections between these two fields that we hope others will take the time to explore in the future.

We approach this large topic by focusing first on females, then males, followed by consideration of differences in male and female interests that give rise to sexual conflict. In general, we argue that the best integration of behavioral ecology and nutritional ecology leverages the strengths of each—behavioral ecology's evolutionarily holistic framework for investigating behavior and nutritional ecology's increasingly sophisticated approach to unraveling how animals interact with food—to provide robust insights into how organisms pursue fitness over evolutionary time (Fig. 2).

4.1 Female reproduction

Research in nutritional ecology has have often investigated nutrient effects on female reproduction, traditionally characterizing female reproductive investment by measuring fecundity. However, while offspring production is clearly resource-intensive, other female reproductive traits may also rely heavily on nutritional currencies, and would thus benefit from the application of a multivariate nutritional perspective. These include the nutritional bases of female choice, sexual cannibalism, and the value of nuptial feeding and nuptial gifts. In addition, nutritional ecology studies would benefit from considering female nutritional decisions in the context of their reproductive state, life history priorities, and interactions with prospective mates and rivals. This more holistic perspective of female reproduction, motivated by insights from behavioral ecology, would better ground nutritional ecology findings in their broader adaptive context. Below, we review current evidence and highlight key opportunities for how an integrated behavioral and nutritional ecology would benefit our understanding of female reproduction.

The costs of female mate choice have remained understudied from a nutritional ecology perspective, despite figuring as a pivotal parameter in behavioral ecology's theoretical development of Fisherian and so-called "indicator" or "handicap" hypotheses of sexual selection (e.g., Day, 2000; Iwasa, Pomiankowski, & Nee, 1991; Pomiankowski, 1987; Pomiankowski, Iwasa, & Nee, 1991), as well as models of speciation via sexual selection (Kopp & Hermisson, 2008). Reviews over the last few decades have highlighted that mate choice is variable and often dependent on individual state (Ah-King & Gowaty, 2016; Cotton, Small, & Pomiankowski, 2006; Jennions & Petrie, 1997; Kelly, 2018; Widemo & Sæther, 1999). However, our understanding of the material basis for this variation is still rudimentary.

Female mate choice is a product of female choosiness (i.e., willingness to invest in mate sampling and selection, Jennions & Petrie, 1997) and the shape of female preference functions. Both choosiness and preference functions exhibit intra- and interspecific variation (Cotton, Small, & Pomiankowski, 2006; Dakin & Montgomerie, 2014; Jennions & Petrie, 1997; Widemo & Sæther, 1999), but the extent to which each are responsive to environmental and/or genetic perturbations remains poorly understood (Ah-King & Gowaty, 2016; Kelly, 2018; but see Rodríguez, Rebar, & Fowler-Finn, 2013 for links between social environment and mate choice plasticity). Nutrient-specific manipulations of female phenotypic state offer one means of probing costs specific to choosiness vs preference and instances where these costs overlap. For example, choosiness may often be energetically costly to females due to the locomotory requirements of increased mate sampling and/or copulation resistance (e.g., Dakin & Montgomerie, 2014). If the costs of mate choice arise largely in these contexts, then dietary reductions in energy-rich substrates (i.e. carbohydrates and lipids) should lead to decreases in female choosiness (Harrison, 2018). Alternatively, choosy females may require longer periods of time to select a suitable mate, resulting in higher somatic maintenance costs (e.g., muscle repair, enzymatic turnover in tissues) which may be more challenging to meet for individuals whose access to protein is limited (Harrison, 2018). Thus, manipulations of multiple nutritional currencies (e.g., carbohydrates, proteins) may allow us to tease apart the specific costs associated with female choosiness.

Female preference functions may also impose material costs on females through required investments in sensory systems and/or cognitive abilities that enable discrimination between potential mates (Bateson & Healy, 2005; Riebel, 2011; Ronald, Fernández-Juricic, & Lucas, 2012; Ryan, 2011). Development and maintenance of these sensory and neural tissues requires inputs of specific nutritional currencies (Laughlin, de Ruyter van Steveninck, & Anderson, 1998; Ronald et al., 2012). Experimental manipulations of female nutritional state should help to characterize the aspects of female cognitive and sensory systems most sensitive to resource perturbations (Doria, 2019; Ronald et al., 2012; Ronald, Ensminger, Shawkey, Lucas, & Fernández-Juricic, 2017). Evidence is sparse but growing for such relationships between dietary stress on female sensory systems, cognition and associated female preference characteristics. For instance, in stalk-eyed flies, females prefer males with larger eyespans (Wilkinson, Kahler, & Baker, 1998). The strength of this preference has been linked to female eyespan in two species of stalk-eyed flies (*Diasemopsis meigenii* and *Cyrtodiopsis dalmanni*, Cotton, Rogers, Small, Pomiankowski, & Fowler, 2006; Hingle, Fowler, & Pomiankowski, 2001), a condition-dependent effect that has been attributed to associated differences in female visual acuity and thus ability to assess male eyespan (Cotton, Rogers, et al., 2006). Similar insights are also emerging in vertebrate systems. For example, recent work on zebra finches has revealed that cognitive traits associated with song evaluation are sensitive to developmental conditions, suggesting that dietary stress during development may have long-lasting effects on female choice for male song characteristics (Holveck, Gerberzahn & Riebel, 2011; Holveck & Riebel, 2010; Riebel, Naguib, & Gil, 2009; Woodgate, Bennett, Leitner, Catchpole, & Buchanan, 2010; but see Woodgate et al., 2011). More research into the effect of nutritional stress on female cognitive function is needed, but this preliminary research suggests that sensory and/or cognitive abilities related to female preferences may be impaired by restricted access to key dietary resources.

Perhaps the most compelling evidence for a nutritional basis of both choosiness and female preference functions comes from work by Hunt, Brooks, and Jennions (2005) on the black field cricket, *Teleogryllus commodus*. Females fed a higher protein diet during development reached sexual maturity faster, were larger as adults, had longer lifespans and exhibited stronger preferences for male song characteristics (Hunt et al., 2005). Intriguingly, within high- and low-protein treatments, individuals that developed more rapidly emerged as smaller adults and were less choosy than larger, more slowly developing females. This suggests that growth rate and somatic investment may dynamically trade off against female choice behaviors even when access to dietary resources is similar among individuals, thus underscoring the need to consider these traits within the context of individual life history variation. In contrast, female choosiness was not responsive to a large qualitative shift in diet in the house cricket, *Acheta domesticus* (Gray, 1999), although older females were much less choosy than their younger conspecifics. Clearly, specific manipulations of key resources, a key step toward integrating nutritional ecology into behavioral ecology (e.g., Fig. 2), should allow us to disentangle the effects of age and resource availability on allocation to female choice within a broader life history context (e.g., Harrison, 2018; Hosking, Raubenheimer, Charleston, Simpson, & Senior, 2019).

While quantification of the costs of female choice is an important agenda for sexual selection research, female preferences themselves can only evolve when these costs are outweighed by the benefits associated with choice. The extent to which these benefits are direct (i.e., material) vs indirect (i.e., genetic) remains an area of active investigation (Hill, 2018; Kokko, Jennions, & Brooks, 2006; Svensson, 2019). However, even in instances where females receive material contributions from males, the benefits to females remain controversial. For example, the extent to which females benefit nutritionally from nuptial gifts is still unresolved in many taxa (Gwynne, 2007; Lewis et al., 2014; Meslin et al., 2015; Meslin et al., 2017; Rapkin et al., 2016; South & Lewis, 2011). Researchers have argued that polyandrous females in gift-giving species choose to remate as a foraging strategy to gain key resources (Kaitala & Wiklund, 1994) or alternatively that nuptial gifts are a form of sensory exploitation by males that offers little nutritional benefit (Rapkin et al., 2016; Vahed, 2007; Warwick, Vahed, Raubenheimer, & Simpson, 2009). The key question is not whether male nuptial gifts contain nutritive substances, but whether such resources correspond to important nutritional needs on the part of females, especially in relation to female reproductive output. Manipulations of female nutritional state offer a powerful empirical tool for understanding the nature of potential benefits arising from male nuptial contributions.

One means to evaluate the nutritional benefit of nuptial gifts is to consider how female mating rates respond under resource limitation.

Evidence for increases in female mating rate under resource restrictions has been reported for bruchid beetles (Fox & Moya-Laraño, 2009; Takakura, 2004; Ursprung, den Hollander, & Gwynne, 2009), sagebrush crickets (Judge, De Luca, & Morris, 2011), katydids (Gwynne, 1990; Simmons & Gwynne, 1991) and nursery-web spiders (Bilde, Tuni, Elsayed, Pekar, & Toft, 2007). These results stand in contrast to findings in nongift giving species where food deprivation induces no effect (e.g., wolf spiders, Wilder & Rypstra, 2008) or even lowers mating rate (e.g., water striders, Ortigosa & Rowe, 2002). In nearly all of these studies, female state has been manipulated by qualitative or gross quantitative restrictions of dietary intake. However, more convincing evidence that females gain nutritional benefits from nuptial gifts has come from nutritionally explicit work on the bruchid beetle *Callosobruchus maculatus*. Researchers found that female longevity and fecundity were most strongly influenced by access to sugar, whereas access to water had a smaller affect, and access to yeast produced no positive effect on either lifespan or reproductive output (Fox & Moya-Laraño, 2009; Ursprung et al., 2009). This nutritional rank order was mirrored by the response to dietary restrictions of female choice traits (Fox & Moya-Laraño, 2009). Females provided access to sugar and water were the least likely to remate, followed by females with only access to water. Unfed females were the most likely to remate. Interestingly, Fox and Moya-Laraño (2009) also found evidence for a diet effect on female preference functions. Well-fed females exhibited a preference for larger males, but this preference disappeared in unfed conspecifics (see also Ortigosa & Rowe, 2002 for a similar result in the water strider, *Gerris buenoi*). Taken together, these studies illustrate that female choice decisions relate to the state-dependent value of male-contributed nutritional resources. Research that leverages multivariate manipulations of female nutritional state thus offers an important step forward in understanding the costs and benefits associated with female mate choice.

While adopting new approaches from nutritional ecology should benefit behavioral ecology's understanding of a number of aspects of female reproduction, the reverse is also likely to be true. For example, to our knowledge nutritional ecologists have yet to evaluate how major resource inputs during mating (i.e., in the form of seminal fluid proteins or nuptial gifts) influence foraging and nutritional regulation of females. Indeed, many male seminal contributions are known to dramatically reshape female physiology by increasing female egg laying rate, decreasing female lifespan, and changing female feeding rates (see extensive work in *Drosophila*, for example Billeter &

Wolfner, 2018; Camus, Huang, Reuter, & Fowler, 2018; Ribeiro & Dickson, 2010; Rubinstein & Wolfner, 2013; Vargas, Luo, Yamaguchi, & Kapahi, 2010; Wolfner, 1977, 2002). Thus, mating may not only influence female resource state, but also female allocation to resource intensive processes (e.g., Levin, Mitra, & Davidowitz, 2016). Investigating how female nutritional regulation changes following mating (e.g., Ng, Simpson, & Simmons, 2019; Ribeiro & Dickson, 2010; Vargas et al., 2010) thus offers an important opportunity to understand how shifts in nutritional balancing are controlled physiologically (e.g., by hormones of either female or male origin). This could be used to expand growing evidence of critical changes in female nutritional regulation during pregnancy and lactation (Dufour & Sauther, 2002; Emery Thompson, 2013).

Insights from behavioral ecology may also help nutritional studies to compare patterns of female nutritional regulation observed in lab settings to those realized by free-living females in the field. A number of mating systems are likely to influence female access to nutritional optima as a result of male defense of resources, or excessive male harassment in habitat areas that would otherwise be optimal for female foraging. For example, excessive male harassment is thought to drive female distributions across the landscape in damselflies and butterflies (Darden & Croft, 2008; Gilchrist & Rutowski, 1986; Koch, 2006; Odendaal, Turchin, & Stermitz, 1989; Severns & Breed, 2018; Sirot & Brockmann, 2001). The influence of such altered female movement has not been explored from an explicitly nutritional perspective but may reveal that female nutritional optima are often inaccessible when population densities and/or male harassment are high. Whether this results in the evolution of female resource needs (and associated nutritional regulation) in populations with persistent male harassment remains an exciting but unexplored possibility at the interface between nutritional and behavioral ecology.

4.2 Male reproduction

In contrast to female reproduction, which has often served as a dependent variable in nutritional ecology studies, male reproduction has only recently become the focus of nutritional ecology research. However, adoption of a multivariate perspective on nutrition will benefit our understanding of male reproduction in a number of ways, including uncovering how nutrition drives male investment in costly sexual ornaments, how nutrient demands influence alternative reproductive strategies, and how resources influence trade-offs between pre- and postcopulatory sexual traits. Similarly, consideration of male investments in reproduction will help nutritional ecologists to better predict and understand variation among males within focal populations.

A multivariate approach to nutrition may help behavioral ecology researchers better situate connections between reproductive traits and specific nutritional resources. It is no surprise that male reproductive investments are costly in nutritional terms. Researchers working in single nutrient paradigms have repeatedly found significant effects of specific nutrients (e.g., carbohydrates, proteins, phosphorus, carotenoids, or amino acids) on male reproductive behaviors. Interestingly, however, some of these effects are substantially reduced or even disappear once researchers move to a multiple nutrient framework. Consider, for example, cricket mate attraction signaling. Male crickets signal more often for mates when they are fed foods rich in protein (e.g., Hunt et al., 2004; Judge, Ting, & Gwynne, 2008; Simmons et al., 1992; Wagner & Hoback, 1999; Zajitschek, Hunt, Jennions, Hall, & Brooks, 2009). However, research by Maklakov et al. (2008) and Reifer et al. (2018) revealed that cricket mate attraction signaling is more strongly influenced by carbohydrate availability than by protein availability when both currencies are considered together. Further, while Bertram, Schade, and Elser (2006); Bertram, Whattam, Visanuvimol, Bennett, and Lauzon (2009) revealed that male crickets signal more often when fed phosphorus-rich foods (Bertram et al., 2006, 2009), recent work by this research team revealed that phosphorus does not affect mate attraction signaling relative to the influence of protein and carbohydrates (Harrison et al., 2014). These studies highlight how working in a single nutrient paradigm can mislead researchers into pursuing less important nutrients, whereas working with multiple nutritional currencies can help to clarify those nutrients with the strongest leverage on reproductive trait expression.

Working with multiple nutritional currencies can also inform the evolution of alternative reproductive strategies by revealing the different nutritional demands imposed by alternative tactics. For example, in the dung beetle *Onthophagus acuminatus*, females provision each offspring with a ball of dung that serves as the sole source of nutrition during larval development (Emlen, 1994). Males provisioned with large dung balls develop into large adults with sizeable horns used for physical competition over access to females (Moczek & Emlen, 2000). However, males provisioned with small dung balls develop into small, hornless adults. Unable to physically compete with horned males, small males adopt a sneaker mating strategy, attempting to access females by digging burrows that bypass horned males defending the female's burrow (Moczek & Emlen, 2000). Interestingly, males raised on similarly sized but "lower quality" dung balls developed into smaller adults but with proportionately larger horns (Emlen, 1997), suggesting a complex set of interactions between diet, developmental allometry and the evolution of alternative reproductive morphologies. In these studies, differences in diet quality were created by adding "lower quality" ungulate dung to typical howler monkey dung, leaving open the question of which nutrient(s) drive these phenotypic responses (Emlen, 1997). Independent manipulation of multiple nutrients could extend this intriguing result to more precisely characterize phenotypic responses of different aspects of each alternative reproductive phenotype, thereby revealing the potential costs and benefits associated with each reproductive tactic as well as the consequences of maternal dung selection on offspring success. Such a nutritionally explicit approach has been adopted in recent investigations of sexually selected weapon growth in broad-horned beetles (e.g., House et al., 2016) and sexually selected aggression in field crickets (e.g., Harrison, Godin, & Bertram, 2017).

Our discussion above has centered on precopulatory male sexual traits, largely because this is where most nutritionally explicit studies have focused. However, nutrient balance can also affect postcopulatory male sexual traits, the subject of a string of recent studies (e.g., Bunning et al., 2015; Fricke, Bretman, & Chapman, 2008; Jensen, McClure, Priest, & Hunt, 2015; Rapkin et al., 2016; Reddiex, Gosden, Bonduriansky, & Chenoweth, 2013). These and other studies highlight that males must balance the nutritional requirements of both pre- and postcopulatory traits to maximize their reproductive success (Mehlis et al., 2015; Morimoto & Wigby, 2016). This view raises a number of interesting questions. For example, are the nutritional inputs of individuals balanced to allow maximization of both pre- and postcopulatory sexual traits? Conversely, do nutritional constraints or competing nutritional requirements force compromises in the expression of pre- vs postcopulatory sexual traits? Morimoto and Wigby (2016), for example, used a Geometric Framework approach to address these questions. When male *Drosophila melanogaster* were given the opportunity to balance their macronutrient intake, they regulated their intake toward carbohydrates, at a protein-to-carbohydrate (P:C) ratio of 1:1.5. However, there was a mismatch between dietary choice and their requirements for pre- and postcopulatory sexual traits.

The P:C ratio required to maximize attractiveness to females was 1:1, whereas the P:C ratio required to maximize offspring production through postcopulatory sexually selected traits was 1:9. These findings suggest that a single diet that maximizes pre- and postcopulatory sexually selected traits may often not exist. Instead, males may need to select dietary compromises that improve fitness on balance. Considering both pre- and postcopulatory sexually selected traits thus allows researchers to better understand why observed dietary choices may not align with nutrient requirements needed to maximize only pre- (or post)copulatory sexually selected traits.

Nutritional ecology studies can also benefit from adopting behavioral ecology perspectives by expanding traditional metrics of reproductive investment beyond female fecundity to also include male reproductive investment (e.g., Camus et al., 2018). Males often expend significant amounts of energy in territory defense, mate attraction, mate defense, and material investments during mating or offspring production (Gwynne, 2007; Prestwich, 1994). Recent work has highlighted how integrating both male and female perspectives can lead to new insights in nutritional ecology studies. For example, Maklakov et al. (2008) revealed that male and female crickets (*T. commodus*) differ in their nutritional optima as a result of divergent nutritional demands imposed by differences in their reproductive traits. Interestingly, when they tested for sex differences in nutritional regulation, they found that males and females pursued nearly identical intake targets, suggesting that the sexes may be genetically constrained in their ability to pursue independent nutritional optima. Thus, nutrition may be a source of intralocus sexual conflict between males and females, a subject ripe for further study (see below).

Consideration of the mating history of focal individuals would offer further opportunities for understanding links between nutritional regulation and reproduction. For example, use of both mated and nonmated individuals will help to develop more accurate nutritional budgets, especially given the transfer of nutrients that can occur during mating (e.g., nuptial gifts, seminal fluid proteins), and the major energy expenditures of males and females during mate searching and courtship. The resulting changes in nutritional status in mated vs unmated individuals are likely to impact subsequent nutrient regulation in ways that may potentially differ between males and females. Although there is mounting evidence that such postmating changes to nutritional regulation exist for both females (e.g., Lee, Kim, & Min, 2013; Ng et al., 2019; Tsukamoto, Kataoka, Nagasawa, & Nagata, 2014) and males (e.g., Camus et al., 2018; Jensen & Silverman, 2018), less is known about whether they are transient, persistent, and/or under the control of one partner or the other. Attention to this topic is likely to improve nutritional ecology's understanding of nutritional regulation across adulthood in many animals.

4.3 Sexual conflict

Because males and females realize fitness in distinct and often contrary ways, evolutionary conflict between the sexes is thought to be a pervasive feature of sexually-reproducing organisms (Arnqvist & Rowe, 2005). Researchers have highlighted the various ways in which sex-specific interests may diverge, both for single traits/genes (intralocus sexual conflict) and for the outcomes of male-female interactions (interlocus sexual conflict) (Arnqvist, 2006; Bonduriansky & Chenoweth, 2009; Chapman, Arnqvist, Bangham, & Rowe, 2003; Wedell, Kvarnemo, Lessells, & Tregenza, 2006). These evolutionary conflicts are an area ripe for investigations that integrate nutritional and behavioral ecology.

Intralocus sexual conflict, the evolutionary tug-of-war resulting from sexually antagonistic selection acting on traits shared by the sexes, should often be a signature of traits related to resource acquisition and allocation. This is because male and female phenotypes are often morphologically and energetically distinct (as the result of divergence under sexual selection), leading to differences in the resources required to build and maintain them (Camus, Piper, & Reuter, 2019; Morehouse et al., 2010; Piper et al., 2017). These divergent resource needs should impose disruptive selection, particularly on traits related to resource acquisition. In response to such sexually antagonistic selection, associated trait loci are predicted to evolve higher levels of sex-linkage and sex-biased gene expression (Connallon & Clark, 2011; Ellegren & Parsch, 2007; Perry, Harrison, & Mank, 2014). The processes that resolve intralocus sexual conflict are expected to often move more slowly than those that generate it (Bonduriansky & Chenoweth, 2009). Thus, in many instances, males and females may remain constrained to compromise positions that reduce their individual fitness maxima. Such constraints may persist for traits related to resource acquisition even when resource allocation has evolved independently in the sexes to enable sexual dimorphism (Bunning et al., 2015; Bonduriansky & Chenoweth, 2009; Jensen et al., 2015; Maklakov et al., 2008; but see Ng et al., 2019; Rapkin et al., 2017).

The study on sex-specific nutrient balancing in crickets by Maklakov et al. (2008), highlighted above, presents such a case for nutritional regulation. In this study, males and females maximized their reproductive effort when fed foods of divergent nutritional composition. However, when allowed to self-select their diet, both males and females regulated intake to the same target composition representing foods that fell in between the two "optimal" food compositions in terms of sex-specific fitness. This result suggests that intralocus sexual conflict over nutritional regulation has yet to be resolved in this species. However, while this is perhaps the most intuitive explanation for their results, modeling of the role that sex-specific nutrition plays in population dynamics suggests that the situation may be more complex. Morehouse et al. (2010) found that while equilibrium population sizes were generally maximized when the sexes were allowed to pursue independent nutritional optima, this was not always the case. When intersexual competition was included in models, equilibration population sizes were sometimes maximized when both sexes shared a common nutritional substrate even in the absence of constraints on their ability to pursue their own nutritional optima. Thus, nutritional "compromises" may arise even in the absence of genetic constraints. The key here is whether average population fitness is reduced by nutritional compromises resulting from shared nutritional regulatory traits. Nevertheless, Maklakov et al.'s (2008) study represents a promising area for further research on intralocus sexual conflict. Combining their approach with organisms for which we have high-quality, annotated genome assemblies could be highly productive for probing the evolution of sex-linkage mechanisms under intralocus sexual conflict.

While traits related to nutritional intake may often be subject to intralocus sexual conflict, nutrition should also strongly influence the strength and nature of interlocus sexual conflict via effects on the costs of reproduction in each sex. Research on interlocus sexual conflict has often focused on sex differences in optimal mating frequency (Arnqvist & Rowe, 2005; Wedell et al., 2006). Although not always the case, optimal mating rates should typically be higher for males due to lower investment in offspring. This common inequality in optimal mating frequency creates conflict that can lead to male traits which increase remating rate (e.g., sexual coercion and forced copulation) and female traits which reduce remating rate (e.g., evasion or resistance; Arnqvist & Rowe, 2005). Coevolutionary dynamics in these situations should often be modulated by resource availability. For example, as discussed above, a female's nutritional state can influence her willingness to remate and her ability to bias partner identity based on mate preferences. The costs of resisting male coercive mating tactics may also be dependent on female nutritional state, with females in poor nutritional condition unable to successfully deter male copulation attempts. Similarly, male remating frequency may be limited by the ability to energetically fund coercive behaviors and/or rapidly mobilize the resources required for ejaculate production. The latter should be particularly true in species that contribute large spermatophores or nuptial gifts during matings.

Similar considerations apply to control of partner remating frequency. In polygamous species, males benefit from monopolizing the reproductive output of female partners. Females, on the other hand, are best able to optimize their reproductive success if they retain control over their remating decisions. A variety of male traits appear to function as mechanisms for reducing female remating rate, including genital damage from barbs on the male intromittent organs in *Callosobruchus maculatus* (Eady, Hamilton, & Lyons, 2007) and biochemical constituents of ejaculates in *Drosophila melanogaster* and other insect species (Avila, Sirot, LaFlamme, Rubinstein, & Wolfner, 2011; Meslin et al., 2017; Rapkin et al., 2016). The extent to which these male traits reduce female remating frequency will depend in part on female nutritional state. For example, the rate at which females are able to heal genital damage in *C. maculatus* should depend on her ability to devote resources to her immune response. Clearly, nutrition should play a key role in the ability for each sex to realize their optimal (re)mating frequency, both over ecological and evolutionary timescales.

How such dynamics play out in field populations where food resources may often vary seasonally or stochastically remains an open question. However, evidence for the role of nutrition in driving sex roles and the strength of sexual conflict is beginning to accrue. For instance, Hall, Bussière, and Brooks (2008) found that male Australian ground crickets (*Pteronemobius* sp.) reared on low protein diets evolved shorter lifespans over the course of 7 generations (Hall et al., 2008). The observed decrease in male lifespan was not the result of evolutionary modification of male investment in reproduction vs somatic maintenance, but rather the evolution of increased mating costs imposed by females in the form of increased female nuptial feeding on male tissues during copulation (Hall, Bussière, & Brooks, 2009). Thus, experimental evolution using nutritional manipulations resulted in a rapid, detectable increase in interlocus sexual conflict. Restrictions in dietary protein availability have also been shown to induce sex role reversal in katydids (Gwynne & Simmons, 1990), which may lead to rearrangement of the costs and benefits of sexually antagonistic traits in this and similar species (Gwynne, 2004).

A number of researchers have called for increased attention to the functional traits that underlie interlocus sexual conflict (Arnqvist & Rowe, 2005; Chapman et al., 2003; Gwynne, 2007), as well as a broader view of sexual conflict across life histories (Wedell et al., 2006). Thus, work on sexually antagonistic traits that leverage both explicit univariate and more robust multivariate methodologies like the Geometric Framework should produce timely contributions to this growing body of research. Likewise, a better understanding of the dynamics of intra- and interlocus sexual conflict in focal species should help to inform why the sexes exhibit shared or divergent nutritional optimal and realized intake targets (e.g., Bunning et al., 2015; Jensen et al., 2015; Maklakov et al., 2008), thereby deepening nutritional ecology's grasp of the adaptive bases for sex-specific nutritional balancing.

5. Conclusions and future directions

The discussion above sets a broad and ambitious agenda for integrating the study of behavioral tradeoffs and synergies that are central to modern behavioral ecology with the study of dietary component interactions emphasized in modern nutritional ecology. However, our coverage only scratches the surface. Productive interstices within other areas of behavioral ecology and nutritional ecology are ripe for the integration of insights from behavioral and nutritional research. For example, predation risk can increase forager vigilance, affect habitat/patch use behavior, and reduce foraging time (Bednekoff, 2007). While these responses exhibit fitness performance costs, the role nutrition plays has received limited attention. Nevertheless, recent work highlights the potential importance of an integrated behavioral ecology-nutritional ecology perspective. Take Hawlena and Schmitz's (2010) study, which showed that the generalist grasshopper, *Melanoplus femurrubrum*, had 32–40% higher metabolic rate and consumed a lower P:C diet under predation risk than in control conditions, suggesting that physiological stress induced by predation risk had a particularly large effect on energy demands (Hawlena & Schmitz, 2010). Such studies of the influence of predation risk on nutritional balancing should be a fertile area for future research. Moreover, integrating the effects of competitors and predation risks into nutritional ecology research should help to identify how ecological factors affect the evolution of nutritional balancing, food selection, assimilation, and digestion.

The emerging fields of eco-immunology and behavioral genomics also present a number of opportunities where precise nutritional manipulations could be used to reveal underlying mechanisms, trade-offs and pathways of interest (e.g., Cotter, Simpson, Raubenheimer, & Wilson, 2011; Ponton, Wilson, Cotter, Raubenheimer, & Simpson, 2011; Rapkin et al., 2018). For example, sex differences in immune function may often relate to the divergent nutritional economics of each sex (Rapkin et al., 2018; Stoehr & Kokko, 2006). Conversely, nutrient balance can affect the nature and extent of immune responses (Lee, Simpson, & Wilson, 2008; Ponton et al., 2011; Povey, Cotter, Simpson, & Wilson, 2013; Smith & Holt, 1996), suggesting that scarcity of particular dietary components should influence the relative fitness costs of different mechanisms promoting immune function (Cotter et al., 2011; Simpson & Raubenheimer, 2012). Although such interactive effects are well-documented in solitary organisms (e.g., Cotter et al., 2011; Lee, Simpson, & Wilson, 2008; Povey et al., 2013; reviewed in Ponton et al., 2011) recent work on ants suggests that "social immunity" (disease resistance mechanisms enhanced by cooperative exchanges) can also depend on dietary nutrient balance (Kay et al., 2014). Such results reveal how nutritional optima may be influenced by the nature and magnitude of immune challenges, and how nutrient access may affect susceptibility to disease.

In behavioral genomics, researchers have recently uncovered candidate genes with pleiotropic influences on both nutrition and behavior. For instance, the gene *foraging* is responsible for both a behavioral polymorphism in *Drosophila* larvae and differences in carbohydrate uptake and transport (Kaun et al., 2007; Kaun, Chakaborty-Chatterjee, & Sokolowski, 2008). Genomic connections between nutrition and behavior may thus be even more direct than previously appreciated. New technologies and high-throughput techniques arising from contemporary metabolomics and transcriptomic research should allow for more rapid screening and identification of important genetic mechanisms and physiological pathways that underlay many of the phenomena described above (e.g., Camus et al., 2018, 2019; Perry et al., 2014; Piper et al., 2017; Ribeiro & Dickson, 2010; Vargas et al., 2010). Much exploratory research remains to lay foundational information in this area, but we see ample opportunity for crosstalk between nutritional ecology and behavioral ecology to provide critical insights.

Anthropogenic concerns likewise warrant careful consideration from this perspective (e.g., Cease, Capps, Gates, McCrackin, & Nidzgorski, 2015; Snell-Rood et al., 2015). The contemporary challenges resulting from imbalanced dietary intakes in humans are currently felt throughout the world. Attention not only to food intake and the underlying determinants of appetite but also human behavioral and psychological patterns is already beginning to reveal important insights into obesity and food-based illness (Gluckman, Hanson, Beedle, & Raubenheimer, 2008; Power & Schulkin, 2008; Simpson & Raubenheimer, 2005). Human alteration of habitats and climate at local, regional and global scales continues at unprecedented rates and has important consequences for nutrient cycling, trophic interactions, sexual selection, and behavioral movements of animals (Espeset et al., 2019; Snell-Rood et al., 2015). The value of addressing these concerns using integrated perspectives such as the one described above should not be underestimated.

The first step in such an integration simply requires increased crosstalk and sharing between behavioral ecology and nutritional ecology. Clearly, behavioral ecologists have long been interested in the nutritional basis of behavior, and nutritional ecologists regularly consider the behavioral basis of nutrition. Nevertheless, we see clear benefits to a deeper and more pervasive integration of these two research fields. We hope that the points described here motivate conversations that lead to increased collaboration at this critical interface.

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