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Resource Acquisition and Animal Response in Dynamic Landscapes

Keeping the Books

JOHN A. BISSONETTE

Abstract. Quantification in ecology has been the *sine qua non* that has differentiated rigorous science from something less. It is how we have "kept the books." Quantifying the quantifiable to account for population response to resource availability usually has meant that the *quantity* of some resource (e.g., for herbivores, plant biomass, or areal coverage of the plant community or habitat) has been assumed to have some causal effect on some quantitative measure of animal response (e.g., the number or organisms surviving and recruited into the population). As scale effects have been recognized as important, landscape ecologists have followed a similar methodology and have assumed that the habitat area coverage (*quantity*) bears some relation to population and species performance and health. The explanatory power of the spatial amount of habitat elements seems inconsistent, and available metrics to assess the effects of spatial arrangement are problematic. Further, organisms respond to the quality of their food resource. In this chapter, I make the argument that an enhanced understanding of animal response to resource availability may be possible if two elements are added to the standard, single currency quantity approach. The first relates to measuring resource *quality* and requires adding an additional currency to our ecological ledger book. The second element incorporates the idea of temporal discontinuity in resource quantity and quality. I suggest that consideration and a broader incorporation of these two elements into wildlife ecology will enhance our understanding of animal response to resource availability at both small and larger spatial extents.

1.1. Introduction

If habitats can possess a spatial structure relevant to ecology, is it possible that the temporal structure of habitats is also potentially important? Johnson (2000a)

Animal populations, in particular, have often been considered limited by resource *quantity*, but not by the chemical composition of the resource.... Resource *quantity* limitation is a single currency approach.... (italics added) Moe et al. (2005)

ac·count·ing: Pronunciation: ($^{\text{ə}}$ˈka$^{\text{ʊ}}$nt$^{\text{ɪŋ}}$) &-kaun-ti[ng], Function: *noun,* 1 : the system of recording and summarizing business and financial transactions and analyzing, verifying, and reporting the results; *also* : the principles and procedures of accounting, 2 a : work done in accounting or by accountants b : an instance of applied accounting or of the settling or presenting of accounts.

cur·ren·cy: Pronunciation: (ˈk^r$^{\text{ə}}$ns$^{\text{ɪ}}$) ˈk&r-&n(t)-sE, ˈk&-r&n(t)-, Function: *noun*, Inflected Form(s): *plural* –cies; 1 a : circulation as a medium of exchange b : general use, acceptance, or prevalence c : the quality or state of being current: currentness. 2 a : something (as coins, treasury notes, and banknotes) that is in circulation as a medium of exchange b : paper money in circulation c : a common article for bartering d : a medium of verbal or intellectual expression (Merriam-Webster Online Dictionary, www.m-w.com).

Accounting in ecology is accomplished by recording and summarizing data (explanatory and response variable interactions) and by analyzing, verifying, and reporting results. Perhaps insufficiently appreciated is the idea that ecologists use different currencies and accounting to understand ecology, and the differences matter. The term "observation set" (O'Neill et al., 1986) has been used to define and delimit different approaches to science and includes the phenomena of intellectual interest, the nature of the measurements taken (i.e., the currencies), and the statistical and analytical techniques (the accounting) used to derive conclusions (Bissonette, 1997). For example, geneticists, population ecologists, and ecosystem scientists all use different measurements (e.g., gene frequencies, number of animals, or nutrient cycling and energy flow, respectively) to account for the interactions they observe. Quantities of some variable most often represent the currency measured. Given the different observation sets used, accounting in ecology involves ledger books that have fundamentally different currencies that measure "quantity" and often are difficult to reconcile. Quantifying the essentially qualitative nature of nature is arguably more difficult and done less often. However, for behavioral, population, community, and landscape ecologists with an interest in animal response to resource availability, new theoretical developments suggest that single currency approaches, i.e., consumer response to the *quantity* of resources can be informed by addressing temporal differences in resource *quality* as well as quantity. Indeed, net trophic transfer of energy and biomass (both often represented by carbon, C), is often limited by the availability of other key elements such as nitrogen (N), phosphorous (P), and trace elements (Moe et al., 2005). The primary objective of this chapter is to address the idea of basic organisms needs and how spatial and temporal heterogeneity complicate our ecological accounting. To do that, I: (a) examine the idea of temporal explicitness in resource availability (quantity) and quality; (b) discuss the different ways that we keep the books; (c) briefly describe two simple but sometimes neglected distinctions relevant to our understanding of the effects of special complexity, viz., the components of pattern and the differences between fragmentation and habitat loss; (d) suggest that the fragmentation model of conceptualizing landscapes is but one possible way of thinking about heterogeneity and may hinder our accounting and hence our understanding of the effects of varying temporal and spatial variation in resource availability on animal response; and (e) attempt to address the problems inherent in single currency approaches by reference to ecological stoichiometry. Throughout, I place these ideas in the context of temporal explicitness.

1.2. Basic Organism Needs Get Complicated

Basic vertebrate organism needs are surprisingly simple to list. Minimal resource needs include access to food, free or metabolic water, cover from predators and perhaps inclement weather, and to mates, all at variable rates that influence fitness. However, resource acquisition is complicated when resources are distributed heterogeneously. One might get the impression from the current voluminous literature in landscape and population ecology that the complexity stemmed primarily from spatial complications. Indeed, much is promised by an understanding of the effects of spatial scale on animal population response. At one time, panmictic mixing and homogeneous landscapes were common assumptions used in population dynamics (Fisher, 1930) before the broad acceptance that habitat heterogeneity had causal effects and that appropriate scaling of our accounting metrics was essential for a more complete understanding of animal and population response (Wiens, 1989). For ecologists, scale effects or scale complications mean, among other things, that discrete populations exist with different vital rates, i.e., averaging statistics for populations cannot be used as they were traditionally when panmixis was assumed (Ritchie, 1997). The reason is that animal movement in naturally heterogeneous landscapes is often hindered (Merriam, 1998) and panmixis is not commonly possible. Panmixis is probably always a simplifying assumption given mate competition, social hierarchies, as well as individual variation in vagility. Regardless, how organisms fulfil their resource acquisition needs is complicated and often difficult for them to do because individuals need to move across potentially dangerous heterogeneous landscapes in response to temporally discontinuous resource availability. It is not surprising that our ecological accounting is similarly difficult. Both pattern, as well as the dynamics of heterogeneity, need to be accounted for to better understand organism and species responses in space and time.

1.3. Temporal Discontinuities

Temporal resource discontinuities can be regular or pulsed (Ostfeld and Keesing, 2000) or occur stochastically at irregular intervals. They may occur at temporal scales spanning from time of day (e.g., activity patterns, and thus availability of prey), to seasons (primary production) and years (mass seeding events), to decades and even centuries (succession of some desert and forest ecosystems). Temporal resource discontinuities are caused by factors such as seasonality (Norrdahl et al., 2002), phenological events (Kelly, 1994), trophic relationships (Khan and Ghaleb, 2003), or disturbances (White and Pickett, 1985). They can include ephemeral habitats such as ponds (Loman and Claesson, 2003) and “rotting logs, dung, carrion, gravel bars in rivers, and forest openings” (Johnson, 2000b). One of the most obvious discontinuities in resource availability in time is the fruiting of plants. The availability of acorns is a good example of a resource that exhibits strong temporal discontinuities (Abrahamson and Layne, 2003). Wolff (1996) found that rodent densities were positively correlated with oak mast production over a period of 14 years. However, much temporal heterogeneity of resources is gradual; i.e., it concerns variation in resource quality. In this ecological sense, all resources may be considered pulsed or discontinuous to some degree (see Ostfeld and Keesing, Chapter 2, this volume). Most resources appear seasonally in temperate and tropical environments. Additionally, resource quality changes over time as well as over spatial gradients. There is a voluminous literature on the response of species to environment resource gradients. These were largely a result of two papers by Tilman (1980, 1982) who proposed what has come to be known as the resource-ratio theory. The theory essentially describes interactions of competing species through their use and effect on shared resources, and had its antecedents in work by MacArthur (1972), Maguire (1973), and others. Miller et al. (2005) summarized the use of the theory by ecologists, and I will not address that issue here, except to suggest that the idea of "use and effect" would appear to be a multiple currency or bivalent approach at the producer-herbivore trophic interface.

1.4. Temporal Explicitness

The term *spatial explicitness* is common and we have become accustomed to thinking about spatial complications. For population ecologists, the term implies among other things, spatially discontinuous populations, inhibited movement of individuals across heterogeneous landscapes, and processes whose effects are understood only if viewed at the appropriate spatial resolution and extent (Addicott et al., 1987). As a result, vital statistics—viz., birth, death, survivorship, recruitment, and genetic composition may vary in space, and thus, cannot simply be averaged across populations (Ritchie, 1997). Temporal explicitness has been treated far less extensively in those studies that relate animal response to resource availability.

A common temporally explicit approach in ecology is to develop simulation models to explain observed spatial pattern differences caused by ecological processes such as disturbance and succession. For example, Wiegand et al. (1998) explored the impact of disturbances on spatio-temporal shrub land pattern evolution, Franklin and Tolonen (2000) modelled the temporal relationship between fire and vegetation using pollen and charcoal data, and Tian et al. (2002) simulated the spatial and temporal effects of microbial contaminants on grazed farmlands. Because most studies are of relatively short duration, often on the scale of a few years, a space for time substitution is most often used (Hargrove and Pickering, 1992) where landscapes are replicated in space rather than time. The powerful effects of unique historical events on subsequent dynamics, e.g., violent disturbances, are often muted or ignored and lost. System history disappears. Almost... (see With, Chapter 3, this volume). Johnson (2000a, p. 1697) suggested that temporal structure generally "exists when habitat dynamics are defined independently of population density." Thus, temporal variation of processes in landscapes has important implications for metapopulation studies (Holyoak and Ray, 1999). Johnson (2000b, p. 67) considered that “species in successional landscapes may represent the most appropriate examples of classical metapopulations” and explored the idea that species coexistence and metapopulation dynamics can be influenced profoundly by the temporal dynamic of habitat succession (Johnson, 2000a,b). Clearly a major problem lies with the observation that landscapes are changing more rapidly than slower changing animal populations can accommodate (With, Chapter 3, this volume).

The implication of the term “temporal explicitness” is that differences in individual performance (different rates of resource acquisition, and hence presumably fitness) and in vital rates of populations can be caused generally by temporal discontinuities, and specifically, in the present context, by temporal differences in both resource availability and quality. The apparent novelty and general lack of appreciation of this idea points to the problem. There are at least two reasons why temporal dynamics have not been widely addressed explicitly in fragmentation studies of animal response. First, we appear to have lacked a generally accepted conceptual and methodological framework with which to address its effects. Second, the single-currency approach may have limited our ability to measure the important effects of resource quality that vary through time.

One reason that time has not often been addressed explicitly may be because the concept of fragmentation has most often been conceived in a very limited spatial sense. If we think of habitat fragmentation as a *discontinuity* in space and time, and thus in function and process (Lord and Norton, 1990), we then can find a way to address the complexities of time as a variable influencing organism response to habitat fragmentation, and hence to resource availability. For example, a fire regime is a discontinuous process in time. Disturbance regimes are by definition discontinuous. Hurricanes, tornados, and severe weather events occur in some sense predictably, but are discontinuous in time. An important consequence of thinking of resources as not only spatially, but also temporally discontinuous is that quantitative descriptors can be measured using metrics borrowed from disturbance theory. In other words, the currency we have available for ecological accounting is expanded. For example, temporal (as well as spatial) distribution of resources, predictability in the timing that resources are available, differences in amount and quality, and possible concurrent interactions of the availability, quality, and timing of other resources i.e., synergisms, can be measured (See Ostfeld and Keesing, Chapter 2, this volume). Disturbance metrics (White and Pickett, 1985) are well known and lend themselves to measuring resource discontinuities because disturbances themselves are discontinuous. When we are able to consider temporal discontinuities in resource availability (quantity) and resource quality, our understanding of ecological reality is enhanced, because these are the attributes to which animals respond.

1.5. Two Important Distinctions

Words have specific meanings and when we blur definitions, the result is more often than not confusion. I make two important distinctions here. First, landscape pattern has at least two distinct characteristics of importance to those who study fragmentation effects and species response: composition (sometimes given as total amount of habitat (Schiemegelow and Mönkkönen, 2002) and spatial arrangement (Turner, 1989). Both influence and constrain animal response. The colloquial expression might be stated as, "what habitats are present (composition) and where are they (arrangement)?" Given that most organisms need to move to access resources (Merriam, 1998), one should expect different responses from different species to these two characteristics. It is of little consolation that many (but not all) metrics used to quantify landscape heterogeneity confound the effects of composition and arrangement (Gustafson, 1998; Li and Wu, 2004; Neel et al., 2004), i.e., they measure multiple components of spatial pattern and often are correlated, making causal interpretation difficult. Li and Reynolds (1995), Riiters et al. (1995), McGarigal and McComb (1995), and Jaeger (2000), using different methodological approaches, have provided assessments of which landscape metrics appear to be most useful. A priori and clear thinking about species natural history requirements as well as about the processes suspected to be operating, coupled with reasonable hypotheses about pattern composition and arrangement effects would seem to be necessary initial steps in any ecological accounting of species response to fragmentation and resource-related effects.

Second, it is possible that when we think about fragmentation as a process, we make assumptions that seem reasonable but may not hold. Fahrig (2003) provided insight into one of the reasons that fragmentation studies often produce mixed or counter-intuitive results. She suggested that many studies have not differentiated between "fragmentation per se," i.e., the breaking apart of habitat, and habitat loss. The two are not the same, although both are part of the *processes* that occur when landscapes change over time. See Cushman and McGarigal (this volume) for examples of an analysis that distinguishes between the two. When fragmentation is viewed as a process, four effects are implied: (1) a reduction in habitat amount; (2) an increase in the number of habitat patches; (3) a decrease in mean patch size; and (4) an increase in patch isolation. These effects appear logical because we make the tacit assumption that the starting point is an unfragmented landscape. If we relax that assumption, then it is easier to understand that different scenarios may result. Fahrig (2003) provided five possible scenarios where one or more of the expectations were not met, suggesting strongly that we should keep these differences in mind in both the studies we design and the analyses we use. To do otherwise is unhelpful, as Debinski and Holt's (2000) review of 21 experimental fragmentation studies clearly suggests. An additional component relates to the idea that the concept of "habitat" is species-centered and not an arbitrary decision on the part of the observer. This leads to an overt consideration of when "habitat" is really habitat. Additionally, how we conceive "landscape" as a working construct is germane here.

The concept of landscape fragmentation has often been used as if it were a "unitary phenomenon" (Haila, 2002, page 322); the schematic view has its origins in Island Biogeographic theory (MacArthur and Wilson, 1967). However, when translated to terrestrial systems, some of the early assumptions remained: (1) habitat islands were the result of disturbance and breaking apart of once contiguous habitat;

(2) were isolated from one another by an essentially inhospitable matrix that was hostile to a majority of organisms (Haila, 2002); and (3) movement of biota often depended on corridors or long-distance dispersal movement to move between patches (Saunders et al., 1991; McIntyre and Barrett, 1992). This schematic view led to the description of landscapes in terms of patches (usually homogeneous), corridors (usually linear), and matrix (the most connected part of the landscape (Forman, 1995; McIntyre and Hobbs, 1999). Of course, depending upon the degree of disturbance, the matrix can be original habitat or the disturbed area. Observations in Australia in the early 1990s led McIntyre and Barrett (1992) to suggest that the schematic view of landscape did not apply to systems heavily modified by agriculture. They observed that the "intervening areas" were modified versions of the original habitat and were not totally inhospitable to movement; animals moved through these areas. This was a significant finding and implied that habitat modification may result in more than just a binary option of "habitat" vs. "non-habitat" (McIntyre and Hobbs, 1999). A significant conceptual advancement, and one that modifies a significant assumption of the schematic view, is that disturbed habitat is not always inhospitable. McIntyre and Hobbs (1999) presented a modified version of the schematic view where various levels of habitat modification were represented on a continuum of habitat destruction while at the same time considering spatial arrangement, resulting in landscapes ranging from intact ($<10\%$ modified, connectivity high), to relictual ($<10\%$ intact habitat, no connectivity). The schematic view of landscape fragmentation had its "assumption descendants" in the "community-unit theory" (Manning et al., 2006), which holds that plant communities were "homogeneous, discrete, and recognizable units" (Austin, 1985, p. 39). Viewing landscape patches as "habitat" for animals homogenizes them into discrete and recognizable units. The relevant question is: do animals recognize habitat patches in the same manner that we do, i.e., according to the schematic view? Manning et al. (2004) suggested viewing landscapes as evidencing both environmental and spatial continua, i.e., gradients. Indeed, Lindenmayer et al. (2002) found strong gradients in bird assemblages in eucalypt and pine forests in Australia that were governed by a combination of landscape context, and remnant patch size and shape. Manning et al. (2004) suggested that environmental continua occur in abstract ecological space while spatial continua or gradients occur in geographical space. Their concept of "Umwelt" incorporates species response and perception into both environmental and geographical gradients, hence is a significant departure from the schematic or fragmentation model. Finally, Fischer and Lindenmayer (2006) proposed a process based conceptual "continuum" model that provides for individual species response to gradual changes in spatially distributed ecological variables such as food and shelter. It seems to me that the schematic fragmentation model allows assessment of the effects of pattern, while the continuum model (Fischer and Lindenmayer, 2006) may allow linking animal response to ecological processes. The continuum model will be especially valuable if temporal discontinuities in resources can be taken into consideration.

Attention to spatial distinctions is necessary but not sufficient. Note that we essentially are measuring some *quantity* rather than *quality* effect as the explanatory variable. This has been referred to in a general sense as a single currency approach (Moe et al., 2005), where the clear implication is that "currency" refers to either quantitative or qualitative effects, but not both. Regardless, if the objective is to learn how species respond to changing landscapes and hence changing resource availability (quantity) and quality, attention to spatial details gets us only part way there. Attention to temporal effects as well as consideration of the qualitative differences in resources is necessary.

1.6. Resource Quality: Keeping the Books

So then, how might we improve our keeping of the books in ecology? Keeping the books, i.e., accounting in ecology, implies that we are capturing the essence of the interactions so that understanding is enhanced. Specifically, it implies that our observations are buttressed by a conceptual understanding that makes sense. Put another way, the assumption is that the variables we measure, i.e. the currencies, are appropriate and up to the task. Studies of habitat fragmentation that have addressed animal responses to resources availability have used almost exclusively the currency of *quantity* of resource as the explanatory variable. Indeed, many habitat use/preference studies appear to be based on the hypothesis that the *amount* of habitat is more or less directly causally related to response variables such as animal density, growth, reproduction, survivorship, and birth and death rates. Additionally, even though habitat types themselves are often assumed to represent areas of different resource quality, the connection is not at all direct, and begs again the question of when "habitat," arbitrarily defined, is really habitat. In habitat selection studies, habitat quality is inferred by assessing individual performance or by some measure of population performance (Morrison, 2001), rather than by a more direct measure of quality as the explanatory variable.

At larger spatial scales, studies using GIS have used time step analyses of landscape changes that elucidate differences in habitat *composition* and *spatial arrangement* over time to explain, for example, changes in biodiversity. Indeed, a large proportion of habitat fragmentation studies have used landscape composition variables (i.e., how much) to imply or show changes in population abundance or biodiversity (number of species). The literature suggests that ecologists most often simply use quantity over some specific time period as the explanatory variable to explain animal response. However, most ecologists would agree that trophic transfer of energy and biomass can be limited by key elements (Liebig's law of the minimum; but see Muller et al., 2001, for a discussion on multiple and simultaneous limiting factors). For herbivores, nitrogen (N) and phosphorous (P) have been the elements usually measured, although other trace elements have been implicated (White, 1993). Moe et al. (2005) used the convention of referring to carbon (C) as representing energy and biomass, and phosphorous (P) and nitrogen (N) and other elements as nutrients. The idea of limiting resources over a longer time constant can be extended to animal populations. For example, population growth may be limited by the minimum amount of resources available to that population at the time of year of greatest scarcity and not by the total amount of resources available throughout the year. The clear implication is that the single currency of *quantity* of resource that ecologists have used to understand animal response may not be adequate to reflect what ecologists inherently suspect: i.e., dynamic changes in resource quality across heterogeneous landscapes are important determinants of population performance. This begs a need for an appropriate currency with which to measure quality effects.

1.6.1. Ecological Stoichiometry: Another Currency

Ecological stoichiometry, an emerging branch of ecology (Sterner and Elser, 2002; Anderson et al., 2004) has been variously described as "the study of the balance of energy and multiple chemical elements in ecological interactions" (Hessen and Elser, 2005, p. 3), "the study of the balance of elements in ecological processes" (Moe et al., 2005, p. 29), "the study of the balance of energy and materials in living systems" (Kay et al., 2005, p. 6), and "dealing with the balance of energy and chemical elements in ecological interactions and especially in trophic relationships" (Anderson et al., 2004, p. 884). The field developed primarily from pelagic, freshwater studies (Hessen and Elser, 2005). One field of concentration has explored how an imbalance of elements and energy can place strong constraints on individual organism growth and reproduction (Bruning, 1991; Sterner and Schultz, 1998; Aerts and Chapin, 2000). Another approach (Kay et al., 2005) has examined stoichiometry in an evolutionary context across multiple scales, exploring the reciprocal interactions between evolutionary processes and the elemental composition of organisms and their resources, and relating elemental ratios in organisms to phenotypic and genetic variation upon which selection can act. Yet another approach has expanded the ideas of a stoichiometric approach to biogeochemical cycles to address the sustainable acquisition of ecosystem services (Ptacnik et al., 2005). Schade et al. (2005) have provided a conceptual framework for thinking about ecosystem stoichiometry. Importantly for this book, ecological stoichiometry has implications for understanding temporal explicitness in resource quality and its influence on terrestrial populations in fragmented landscapes.

Ecological stoichiometry is well established in aquatic ecology but not yet in terrestrial ecology. Two recent papers on stoichiometry (Anderson et al., 2004, Moe et al., 2005) argue persuasively that ecologists interested in animal population response to resource availability need to consider the currency with which they examine plant-animal interactions. They argue that ecological stoichiometry provides a multiple currency approach to understand the effects of resource *quality*. By multiple currency, they mean that rather than "abstracting populations as aggregations of individuals or biomass," organisms are represented by carbon (C), phosphorous (P), and other trace elements that allow "key feedbacks, such as consumer-driven nutrient recycling" processes (Anderson et al., 2004 p. 884). The argument is that both food quantity and quality can be incorporated into a single framework. The concept of "currency" here has two related parts: one meaning refers to the difference between the effects, or explanatory variables, being measured, viz., quality versus quantity; the other meaning refers to the metrics used. The term “multiple currency,” therefore, can be interpreted to refer to measuring not only *quantitative* but also *qualitative* aspects of the resource using *quantitative* metrics. The message is that measuring only quantity is insufficient; quantification of the qualitative aspects of the resource base is needed. Owen-Smith (2005, p. 613) reinforced this idea when he stated, “the numerical approach to population dynamics is seductive, but potentially misleading through overlooking the material basis for changes in N.” These papers suggest a conceptual basis for some of the observations that ecologists have made concerning plant quality and its importance to herbivore response. An understanding of ecological stoichiometry can be gleaned from these papers as well as from other papers from a workshop called “Woodstoich 2004” sponsored by the Center for Advanced Study at the Norwegian Academy of Sciences and Letters and published in 2005 in volume 109 of Oikos. An additional group of papers appeared in volume 85(5) of Ecology 2004 as a Special Feature edited by D.O. Hessen and called Stoichimetric Ecology.

Box 1.1. What is stoichiometry?

Stoichiometry is the accounting, or math, behind chemistry. Traditional textbooks in chemistry explain that stoichiometry is used to calculate masses, moles, and percents within a chemical equation. While it is beyond the purpose of this chapter to delve into this in detail (readers are encouraged to look at a basic chemistry textbook for a full explanation) the following is given to provide background to understand the developing field of ecological stoichiometry. The balanced chemical equation $8Al + 3Fe_3O_4 \rightarrow 4Al_2O_3 + 9\ Fe$ contains aluminium (Al), iron (Fe), and oxygen (O). The numbers 8, 3, 4, and 9 are coefficients that show the relative amounts (molecules or moles) of each substance present, and can represent either the relative number of molecules, or the relative number of moles. A mole is equal to Avogadro’s number (6.023×10^{23}) of molecules. A mole is simply a term to denote an amount. For example, if have a half dozen apples, you have six of them. If you have a mole of apples, you have 6.023×10^{23} apples. If no coefficient is shown, a one (1) is assumed. Given the equation above, we can tell the number of moles of reactants and products. Hence we have an accounting system to work with chemical formulas. Ecological stoichiometry is extending this basic accounting system to ecological systems. Essentially, the accounting considers both the quantitative as well as the qualitative relationships involved; here the quantity and quality of the resource base are considered important and incorporated into analysis of their influence on heterotroph population response (UNC Chapel Hill Chemistry Fundamental Program 2006).

1.6.2. Resource Quality and Population Response

Anderson et al. (2004, p. 884) have argued that “population dynamics theory forms the quantitative core from which most ecologists have developed their intuition about how species interactions, heterogeneity, and biodiversity play out in time." They show that by using stoichiometric models to examine trophic interface dynamics, one derives qualitatively different predictions (sec. 1.6.3) about the resulting dynamics. A fundamental principle of ecological stoichiometry is that "the requirements of multiple elements vary within and among species, and can cause mismatches between demand and supply at ecological interfaces" (Moe et al., 2005). What this means for herbivores is that plant quality varies over time and space and the conversion of plant biomass into herbivore biomass is often constrained by plant quality and not necessarily plant quantity. The other side of the coin (Anderson et al., 2004) suggests that nutrient cycling back across the trophic interface, e.g., by excretion and elimination, will also be constrained by herbivore nutrient needs relative to what is needed, with the surplus being recycled back. Examining stoichiometric imbalance between carnivores and their prey may be less fruitful because the stoichiometric imbalance in nutrients between food (prey) and consumer (predator) is less for carnivores; the prey themselves are heterotrophs. Hence, the physiological variation between D:N:P ratios is "typically an order of magnitude less" between predator and prey (heterotrophs) than what is encountered between autotrophs (food) and consumer (heterotroph) (Anderson et al., 2004, p. 885). This suggests that predator heterotrophs may be seldomly limited by food quality. More work is evidently needed in this area.

Stoichiometric theory has formalized these constraints (Anderson et al., 2004) by what is known as the threshold elemental ratio (TER). This is the carbon: element threshold where the resource limitation shifts from carbon (C) to nutrient (P, N), that is, where the quality of the plant resource makes a difference. With plant C:element ratios <1, plant quality is always adequate for the herbivore and a single currency approach based on quantity of food will not deviate significantly from a stoichiometrical approach (Urabe and Watanabe, 1992; Urabe and Sterner, 1996). In these cases, ecologists have correctly used quantity to reflect herbivore response. It is when TER ratios >1 that a stoichiometric model approach can be illuminating.

1.6.3. Different Predictions

Perhaps the fundamental key for population ecologists is that because stoichiometric models incorporate *both* food quantity (which ecologists usually measure) and quality, which is inferred but much less frequently incorporated into the measurements, there may appear empirical phenomena that cannot be predicted by single currency models. Examples from laboratory experiments include the observations of a (1) positive density dependence and a shift in the nature of the interaction from competition to facilitation (Sommer, 1992), similar to the Allee effect; (2) coexistence of more than one predator on a single prey item in contrast to predictions based on the single (quantity)-currency theory (Grover, 2003; Hall, 2004; Hall et al., 2005); and (3) the diversity enhancing effects on herbivores of poor food quality (Anderson et al., 2004). Although these results come primarily from aquatic system experiments, terrestrial ecologists may find that similar shifts in predictions may occur if one could take plant quality changes over time into consideration. McNaughton (1985) and Grasman and Hellgren (1993) have shown for African ungulates and for white-tailed deer *(Odocoileus virginianus)* in the United States, respectively, the preference for foods with high nutrient quality. Wildlife ecologists have studied energy and food quality for a long time. Seldom, however, have the results been put into a larger landscape context. Future field studies will demonstrate if different predictions and results obtain.

Food quality may provide a better explanation for vole cycles than the other hypotheses that have been proposed (Ergon et al., 2001). Recent work in Europe (Nolet et al., 2005) on beaver has shown that stoichiometric changes in leaf quality have impacted beaver populations in the Czech Republic and the Netherlands. Nolet et al. (2005) suggest that these qualitative changes may be of greater importance than a shift in food quantity. Likewise, Owen-Smith (2005) has argued that a shift from a numerical currency allows closer modelling of the true dynamics. However, he has argued that placing emphasis on intake responses that determine the capture of resources provides little insight, because population growth is largely fixed by evolutionarily adapted responses; i.e., there is a finite rate of recruitment for any population. He argued (2005, p. 613) that actual realized population growth is an "outcome of environmental restrictions, expressed largely through mortality losses" and that our efforts are better placed there because environmental restrictions include failures to conceive as well as mortality at all life stages. I suggest that focusing on both the intake response, i.e., the influence of forage quality on population response, and on the final outcome, i.e., realized population growth as measured by multiple currencies would appear to provide a nice integration of approaches to inform ecology.

1.6.4. Global Warming: An Added Complication

Temporal differences in resource abundance and quality have been influenced globally by climate change, and have had significant effects on wildlife species. The Normalized Difference Vegetation Index (NDVI) provides a standardized method of comparing vegetation greenness between satellite images. When two or more images are compared over several to many years, it is possible to distinguish changes in vegetation reflectance values that can be represented as a percent change from a long-term average. In this way, trends in the timing of spring bud break and leaf growth, i.e., phenophase, can be detected. In Washington, DC (USA), Abu-Asab et al. (2001) found that 76 of 89 plants whose flowering date was significantly earlier, flowered on average 5.6 days earlier than a 30-year mean Julian date. Flowering dates ranged from 3.2 to 46 days earlier. Numerous other studies have shown similar trends. Changed phenophases mean changed patterns of resource abundance and length of availability. Visser (1998), Visser and Holleman (2001), and Grossman (2004) provided clear examples where global warming and its effects on phenophase have had effects of Great Tit (*Parus major*) demographics. They reported that in the Netherlands, changes in weather patterns have caused oak buds to leaf sooner. Winter moth caterpillars (*Operophtera brumata*), an important food source for great tit chicks, peaked in total biomass 13 days earlier in 2004 than in 1980. However, the date of egg laying has remained the same. For most if not all wildlife species, a primary selection factor on the timing of reproduction is synchrony between offspring energy requirements and food availability (Grossman, 2004). The earlier bud break in oaks and the subsequent earlier increase in winter moth caterpillars have resulted in a mismatch between the availability of food and the needs of the young chicks. Visser (1998) Visser and Holleman (2001) report serious demographic consequences for the Great Tit population near Arnhem, the Netherlands. Clearly, as these studies demonstrate, over larger spatial extents, the timing of resource availability is critical.

1.7. Conclusions: The Truth Is Always Beyond the Perception of Truth

Throughout this chapter, the theme has been to try to find a way to get closer to understanding the true state of nature as it applies to resource availability and animal population response. However, in science generally, and in ecology specifically, the idea of "truth" is an elusive concept. What we know or what we think we know is always based on (often unstated) assumptions; is filtered through our methodological approaches, and is always constrained by the observation set we employ. Put in different terms, "truth" as a science concept is nuanced, and it is so because science is the one enterprise where we continually attempt to falsify our hypotheses and predictions, and examine our premises in order to test what we know. When one thinks about individual animal or population response to the spatial and temporal distribution of required and necessary resources, it seems reasonable that future advances in our understanding of animals that live in dynamical landscapes may be facilitated by diversifying our accounting currency to include measures that do more than just relate the number of individuals (response) with the quantity (area, biomass) of their habitat (explanation). To the extent that we can quantify the qualitative constraints that influence populations, we can at least come a little closer to an ecological "perception of truth."

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