

**DYNAMIC FOOD WEBS:
MULTISPECIES
ASSEMBLAGES, ECOSYSTEM
DEVELOPMENT, AND
ENVIRONMENTAL CHANGE**

Peter de Ruiter
Utrecht University
Utrecht, The Netherlands

Volkmar Wolters
Justus-Liebig University
Giessen, Germany

John C. Moore
University of Northern Colorado
Greeley, Colorado, USA

Managing Editor
Kimberly Melville-Smith
University of Northern Colorado
Greeley, Colorado, USA

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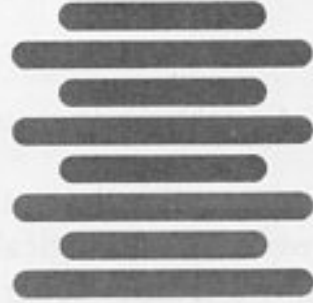


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5.5 | MEASURING THE ABILITY OF FOOD TO FUEL WORK IN ECOSYSTEMS

*Steven H. Cousins, Kathryn V. Bracewell, and
Kevin Attree*

This chapter reports early approaches to developing measurement methods that allow a fundamentally new way of understanding trophic interaction. Measurement has not always had a central place in food web studies; counting organisms and classifying species and their trophic relationships has been more important both recently and in the distant history of our subject. We could probably point to three phases in studying food webs. The initial phase of counting and description, which we might call an 'intelligent natural history' of food webs, led to the development of a number of core concepts including food webs themselves (Elton, 1927). The middle phase, where measurement was paramount, quantified the energy transfers between species using the bomb calorimeter to establish unit mass energy contents (Teal, 1962). The more recent (post-International Biological Programme) phase is one where we have returned to the art of classification and observation in food webs in order to identify pattern and universal properties (Cohen, 1978).

DeAngelis (1992) has classed these phases as contrasting the 'process-functional' school with the 'population-community' school. In recent years the latter approach has tended to dominate but with some innovative work also continuing in the process-functional tradition (DeAngelis, 1992; de Ruiter et al., 1993a). This tradition remains important since if feeding is about anything it is about gaining energy and

nutrients for maintenance, movement, growth, and reproduction. Food webs are structures which only exist such that members of the web gain energy from others, or if they are predated, 'donate' energy and nutrients to their predators. We suggest that additional measurement techniques can clarify the energetics of trophic transfers. Although categories of stored energy can be identified in ecosystems, conventional calorimetry only provides a first law of thermodynamics description suitable for energy accounting in food webs in which energy is neither created nor destroyed. We therefore ask how can we make appropriate measurements for a second law approach to the operation and fuelling of food webs.

EARLY DESCRIPTIVE WEBS

There are some early observations (Elton, 1927), based on body size, which may help structure how these new methods can be applied to food webs. Elton made the very simple point that predators are normally larger than their prey. When this is combined with another observation that there is a limit to both the largest and smallest creatures in an ecosystem, then the number of possible steps in a trophic chain is constrained. The outcome of these feeding relationships is represented by the pyramid of numbers of animals; a distribution with larger numbers of smaller creatures which is fed upon by a progressively fewer number of larger ones. However this simple model does not apply to animals eating plants since this relationship is not directly size structured. Animals of all sizes eat plants although Elton observed that different plant parts had characteristic species of herbivore and that depending on the minimum size of the herbivore then the number of possible steps in a trophic chain was again constrained by size. Finally he noted that all life ultimately relied on energy derived by photosynthesis in the green plant.

This early view of food webs provides us with three distinct cases. First there is the measurement of the properties of *different parts* of the green plant as distinct entry points into the food chain, then the characteristics of the herbivore in linking the plant to carnivores and finally there is size-based measurement for predictive carnivory.

WORK IN ECOSYSTEMS

Work is measured in joules and when one gram of pure water at room temperature is raised by one degree then 4.185 joules are required to do so. For heat to flow there must be a gradient of temperature from hot to

cold and the steepness of the gradient determines the rate at which the heat flow occurs. Importantly therefore, the external conditions affect the rate at which these energy transfers occur. In ecosystem energetics the standard measurement instrument is a bomb calorimeter (Phillipson, 1966; Petruszewitz, 1970). The heat of combustion of a small dried pellet of material burnt in an environment of oxygen is measured by the temperature increase in the mass of water in the water jacket and appropriately converted to Joules. Thus the calorimeter only measures the quantity of heat that is released while the rate of energy transfer is not considered.

What is perhaps surprising is that when materials as different as young leaves and old bark are dried and a unit mass burnt in a calorimeter, the heat output of each is remarkably similar (see Table 1). However, a unit mass of coal can also be burnt in the device and energy content measured but this does not predict the ability of that material to do work in an ecosystem. Similarly why should we believe that the measurement of energy content of bark, rather than coal, is meaningful in terms of fuelling work in the prevailing external conditions of the ecosystem?

SPECIFYING EXTERNAL CONDITIONS

External conditions affect the *rate* at which energy transfers take place by determining the source:sink gradients over which energy flows. One obvious condition is the temperature at which organisms function which is determined by the environment for poikilotherms and held generally at a somewhat higher and more constant value for

Table 1. Data for oak tree parts (*Quercus robur*) showing energy content, nitrogen dry matter, in relation to the rate of energy release W.kg^{-1} by decomposition in soil averaged over the single period from 18–115 days after burial.

Oak tree part	Nitrogen (%dm)	Energy content (MJ/kg)	% mass loss per day	Watts/kg
acorn	1.333	18.6	0.0046	0.99
root	1.011	19.4	0.0009	0.20
bark	0.676	19.4	0.0005	0.11
twig	1.003	20	0.0011	0.25
brown leaf	1.651	20.3	0.0011	0.26
green leaf	2.853	20.2	0.0044	1.02

homeotherms. Another important condition is that the energy in food must transfer to any ingesting organism within the time that the food is present in the gut. Whereas energy transfer in the calorimeter is treated as instantaneous and measured in J.kg^{-1} we are instead interested in $\text{J.kg}^{-1}.\text{sec}^{-1}$ flows under given external (biological) conditions. Since one joule per second is one watt then for ecosystem purposes we are interested in measuring the properties of materials in kW.kg^{-1} rather than the J.kg^{-1} that the calorimeter provides. The problem becomes how do you standardize and make relevant a power measurement when the size or design of the measurement instrument (the external conditions) will determine the power output that is achieved.

The measurement of power per unit mass of biological material entering a food chain (Figure 1) is dependent on the type of material (fuel) is supplied and what specific device (i.e., which organisms) release the energy. A fundamental question is whether there are species of creature evolved to digest bark at the same rate as other organisms might digest seeds? Or, has some irreversible change occurred when the simple sugars produced by photosynthesis are used to make complex long chain and cross-linked molecules such as lignin that affects all species feeding on it? Thus although these bonds can be broken at the temperatures experienced during combustion, what are the implications for biochemical reactions at the temperatures real organisms operate? An intermediate position is provided by plant defense compounds where evolution is known to play a role and an evolved suite of herbivore species can detoxify those compounds, while the bulk of herbivore species cannot do so.

EXPERIMENTS IN POWER MEASUREMENT

We investigated power density measurement in the three aspects of trophic interaction arising from Elton's analysis of food webs; the difference between plant parts, a herbivorous food chain step, and size-based carnivorous food chain step.

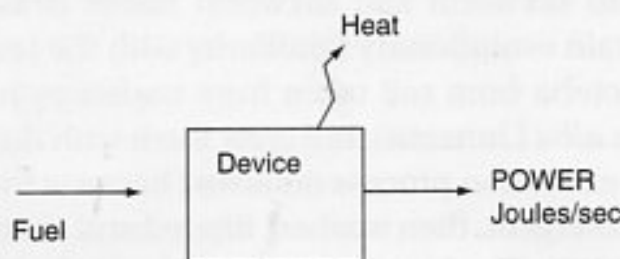


FIGURE 1 | Conceptual diagram showing how power output is dependent on the fuel and the conversion device used.

Comparing Plant Parts

To establish if there is a substantial difference in the properties of different plant parts as food we needed a single 'device' which we could apply to each of the plant parts of a single plant species. A bacterial digester looked appropriate since bacteria are associated with digestion of plants in soil during decomposition and bacteria are also associated with anaerobic digestion of plant material in ruminants. In this case we used soil itself as the physical medium of the digester. We took samples of different parts of the English oak (*Quercus robur* Linnaeus), dried, fragmented them and placed them in nylon bags. These were buried in soil in an ancient oak woodland where by definition the soil faunal community was dependent on that type of food supply (Bracewell, 2000) and could be said to be adapted or evolved to digest oak derived matter. Table 1 shows the energy content of the different materials as measured using a bomb calorimeter. Conventional plant quality measures of plant material composition (Cadisch, 1997) were also made and represented here as percentage mass of Nitrogen in the dry matter. The rate of weight loss was measured over a 115-day period and the loss dimensioned in $\text{kW}\cdot\text{kg}^{-1}$ which was linear after the initial 18-day period when a more rapid loss occurred.

This experiment showed that whereas the energy content of the plant materials differed by only 10%, with bark being more energy dense than acorns for example, the rate at which this energy could be extracted by soil biota in the decomposition bags differed by some 900%. Of these materials the energy in bark was the least available and that in young leaves and acorns the most available. Thus the ability of the plant parts to power activity in the ecosystem were very different and not predictable from energy content analysis.

The Herbivorous Food Step

We investigated the silkworm (*Bombyx mori* Linnaeus) food chain as the reference herbivorous interaction and looked at the transformation of mulberry leaf into silkworm and silkworm faeces (frass). In a similar attempt to maintain evolutionary familiarity with the test substrates we extracted soil bacteria from soil taken from underneath our local mulberry tree (*Morus alba* Linnaeus) and grew them with the test substrates in digesters. The extraction process detached bacteria from soil by sonication in a mild detergent, then washed, filtered and centrifuged them to a pellet (Attree, 1998). The bacteria were re-suspended in a stock solution and added to flasks containing equal masses of powdered materials; leaf, silkworm, and frass plus bacteria-only controls. The respiration of

the soil bacteria was measured over five days by passing carbon dioxide free air into the digester flasks and the CO_2 produced was measured by a precipitation of barium carbonate in the outlet flasks. This experiment has developed some basic techniques to measure the power output per unit mass of the materials in the food chain step and shows that while the energy in the system is conserved, the power density of the materials is not conserved. The power density of the silkworm is raised relative to the leaf and that of the frass lowered relative to both. These are, however, very early results only.

Muthukrishnan (1978) give energy accounting (first law) data for final instar silkworm larvae free-feeding on mulberry leaf and show: 1000 gcal of fresh leaf results in 462 gcal assimilated and 538 gcal frass and a gross conversion efficiency of 16% into silkworm mass. We approximate this to $1\text{g leaf} = 0.16\text{g larva} + 0.54\text{g frass} + 0.3\text{g CO}_2$. The power densities of the materials produced and as measured above have been transformed from; leaf 12.6 W.kg^{-1} (estimated peak 16 W.kg^{-1}) to larvae 13.0 W.kg^{-1} (estimated peak 22.0 W.kg^{-1}) to frass 6 W.kg^{-1} (estimated peak 7.0 W.kg^{-1}) (Attree, 1998). Thus a unit mass of leaf is transformed into a small quantity of material with a higher power density, the silkworm, and a large quantity of low power density material, the frass, while, by the first law, the energy contents are conserved.

The Carnivorous Food Step

Carnivory represents a very different problem compared to the last two cases. The proteins and fats that make up the non-structural components of animals are very similar in all species. If we dry and powder a unit mass of a mammal we would expect the same kW.kg^{-1} output when placed in a bacterial digester regardless of its body size or position in a food chain. Unlike herbivory, where the herbivore has a different chemical make up to the plant, carnivores are similar in their composition to the things that they eat. However, whereas it may be easy for the herbivore to find the plant, the problem for the herbivore is extracting the energy from the plant during digestion. Conversely the problem for carnivores is to find and capture the prey, which is then relatively easily digested and assimilated. The factors which determine the rate at which energy can be supplied to a predator are dependent on foraging rather than digestion and the measure of rate of energy supply in kW.kg^{-1} can be derived via foraging theory rather than microbial reactors.

If we adopt Elton's proposition that carnivorous food webs are size structured then we can take the pyramid of number and turn it through 90 degrees to provide a graph of organism abundance against body

weight (Figure 2B). If this graph represents a real ecosystem and is viewed at successive time intervals, then energy will pass from smaller creatures to the larger ones by process of predation and animal growth. However to model this system, we recognize that any organism can be either prey if it is predated in the next time interval or a predator if it finds prey to eat. To distinguish these trophic roles *of the same organisms* we indicate when we are viewing them as prey, by showing a bar under the variable for the organism (such as weight, w), or when viewing them as a predator we place the bar above the variable e.g. \bar{w} . Unit mass prey handling time, \bar{h} , is a function of both by predator and prey states, so bars are shown above and below the variable concerned.

The process of predation by an individual can be decomposed into a search phase to encounter the prey and a handling phase where time is spent getting the prey into the mouth and swallowing it. For any given predator, the encounter rate p with prey is proportional to prey abundance N_p ; the time between encounters given by $1/pN_p$. Search and handling rates are related since it is not viable to search for prey which cannot be handled and ingested sufficiently quickly per unit mass of prey obtained, represented by a lower limit α and upper limit β on prey size for a given size of predator. Similarly, the time used capturing and handling the prey is a time delay that cannot be spent searching for new prey. Allowing for handling time, encounters occur at $1/hwpN_p$ where h , the unit biomass handling time is multiplied by the mass w of the individual prey of N_p . The handling component is of primary importance in determining predation interactions and is fundamentally constrained by the predator morphology.

If instead of a single predator we take \bar{n} predators at a particular weight, then over the whole distribution of all weights of all individuals n we get (Cousins, 1985)

$$\frac{\partial n}{\partial t} = -n \int_0^{\infty} \frac{\bar{p}\bar{n}d\bar{w}}{1 + \int_{\alpha}^{\beta} \bar{h}\bar{w}\bar{p}\bar{n}d\bar{w}} \quad (1)$$

For a predator organism with an optimal prey size with least handling time h_{min} (see Figure 2A), then smaller prey will by definition, take more time to handle per unit biomass consumed; and similarly for larger individuals. As the width of the diet is expanded more prey individuals will be encountered but there will come a point where the time spent handling very small or very large prey will be so great that the total amount of flesh ingested will decrease. If the predator's demand for food cannot

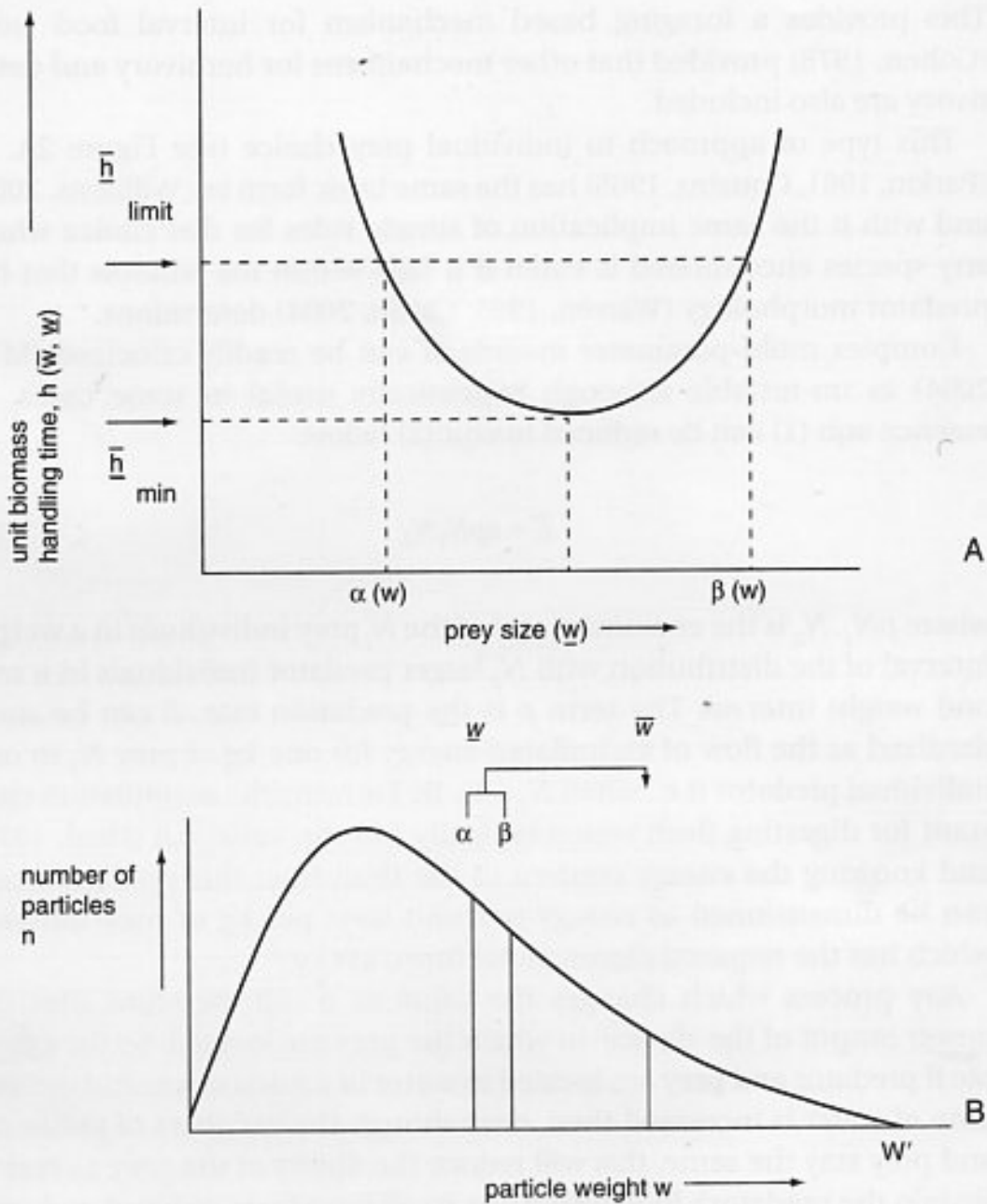


FIGURE 2 | **A**, Foraging window, α - β , for a predator \bar{w} defined by the time to handle one unit of prey biomass \bar{h} for prey w of different sizes (Parkin, 1981; Cousins, 1985). **B**, Number of all particles (organisms) for different weights w up to the maximum size of top predator W' after (Cousins, 1985).

be satisfied within this feeding limit (see Figure 2A) then it will eventually starve; if it can easily be met then it will select food from a narrower range of its possible diet. It is an axiom of this foraging approach (Pulliam, 1974; Charnov, 1976; Silvert, 1980; Cousins, 1985) that any individual of any species which is encountered by the predator and can supply 'flesh' within the current unit biomass handling rate will be eaten.

This provides a foraging based mechanism for interval food webs (Cohen, 1978) provided that other mechanisms for herbivory and detritivory are also included.

This type of approach to individual prey choice (see Figure 2A, B) (Parkin, 1981, Cousins, 1985) has the same basic form as (Williams, 2000) and with it the same implication of simple rules for diet choice where any species encountered is eaten if it falls within the window that the predator morphology (Warren, 1995; Cattin, 2004) determines.

Complex multi-parameter models of can be readily criticized (May, 2004) as un-testable although heuristically useful in some cases. In essence eqn (1) can be reduced to eqn (2) below.

$$E = apN_1N_2 \quad (2)$$

where pN_1 , N_2 is the encounter rate of the N_1 prey individuals in a weight interval of the distribution with N_2 larger predator individuals in a second weight interval. The term p is the predation rate. E can be standardized as the flow of assimilated energy for one kg of prey N_1 to one individual predator (i.e., when $N_2 = 1$). By knowing the assimilation constant for digesting flesh which typically has the value 0.8 (Heal, 1975) and knowing the energy content of the flesh then this predation rate can be dimensioned as energy per unit time per kg of prey biomass which has the required dimensional form, kW.kg⁻¹.

Any process which changes the value of p will therefore alter the power output of the 'device' in which the prey are located. So for example if predator and prey are located in water in a microcosm and the volume of water is increased then, even though the numbers of predators and prey stay the same, this will reduce the ability of the prey as fuel to sustain the predator's food web. Thus p will have been reduced and with it the value of kW.kg⁻¹ of the prey.

ECOSYSTEM AS OBJECT OR DEVICE

We began with the important point that to get an energy flow you need a source:sink gradient, and to measure a flow you need a device of some kind which you can standardize in order to get repeatable values and values which can be meaningfully compared between prey and between systems. Whilst laboratory equipment may provide the standardized measurement of plant parts and of herbivory (and by extension of detritus and detritivory), there is no immediate device that simulates carnivory other than

treating the ecosystem itself as the device (i.e., the set of external conditions under which the trophic interactions occur). The dilution or cryptic location of organisms in an area and the relative abundance of organisms of different sizes found there (the pyramid of number) determines the power output of the system. The pyramid provides a gradient where there is a source of concentrated biomass in large particles versus a progressive sink of diffused material in smaller particles. The notion of the ecosystem as a 'device' is perhaps strengthened by considering the ecosystem as an observable spatial object derived from the food web (Cousins, 1990).

DISCUSSION AND CONCLUSIONS

This chapter has sought to strengthen the case for making direct measurement of the energetics of food webs. In making compatible measurements on plants, herbivores and carnivores we have attempted to move the study of food web energetics from a description of conserved energy balances (first law description) to a non-conserved set of power outputs (second law description). Different plant parts, animals, and by extension detritus, can be treated as materials, distributed in an ecosystem, each with a different potential to fuel organism metabolism and growth. These differences in unit power outputs $\text{kW}\cdot\text{kg}^{-1}$ are seen to be large and therefore have the potential to explain many aspects of feeding interactions. Since energy has also been used as a driver for biodiversity studies then energy availability may also have potential for further exploration of diversity relationships.

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