CONSUMPTION DRIVEN POPULATION DYNAMICS (CDPD)

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ABSTRACT

Ecologists have long pursued a cohesive mathematical structure describing the interactions between the multitudes of species populating the web of life. Consumption dependence offers a logical approach built upon the mechanism of mass-energy flow necessary to all life processes. Consumption, defined as that fraction of satiation currently enjoyed by a local species population, will affect that population's birth rate, natural death rate, and ability to acquire food. Consumption, a non-linear function of prey population, consuming population, and the environment in which these species live, sets the level of predation forming the primary link between species.

That division of environment comprising all biotic and abiotic elements aside from those directly contributing to consumption, also affects a population's welfare. The inclusion of functions of species within environment variables for other species enables modeling many interactions between species additional to predation. Many environmental elements posses a cyclic nature overlaid by stochasticity. Results generated using cyclic and stochastic variations of environmental variables have produced interesting results that may add to our understanding of persistent competition.

This approach is implemented as the iterated solution to multiple difference equations, one for each included species. Resulting population curves are highly stable, or unstable depending upon conditions impacting predator proficiency, that appear remarkably like real population data recorded over the past century under both natural and laboratory conditions.

Keywords: Ecosystem; consumption; environment; population; model.

INTRODUCTION

Population modeling, as taught and practiced by ecologists over the past century, represents the attempt to understand the forces of nature affecting species populations. To this end, a considerable body of theoretical structure has emerged built upon the concept of constrained exponential growth.

Consumption driven population dynamics (CDPD) begins by assuming that the physiological act of reproduction is predictably dependent upon the consumption of resources to support growth. Likewise, CDPD assumes that mortality, aside from predation, is predictably dependent upon the inverse of consumption. That is, non-predation deaths increase for any active organism experiencing less than optimal consumption. These basic dependencies may be expressed as functions, the characteristics of which may be measured in natural and artificial environments.

The coin of this realm is food. There are relationships with other species where food is not the primary factor, but food, use of other species as food, and competition for food is the predominant theme in the majority of interactions. Benke and Wallace (1997) described a food web reflecting the great variation in linkage strengths for the many predation links between species. No web of life can exist without the complex flow of energy and matter that sustains it. Thus, consumption becomes the foundation upon which CDPD has been constructed, modified by the inclusion of functions for the abiotic environment (Tansley, 1935) and for the broad range of interactions between species, observed and yet to be discovered.

But, those who would consign CDPD to the genre of standard resource-dependent models should first consider the significant structural differences. CDPD gains and losses are both functions of consumption, a term defined in CDPD that is not proportional to the resource population. CDPD mortality, with an inverse dependence upon consumption, captures the observed ability of natural systems to collapse rapidly during times of low consumption or other adverse environmental conditions. CDPD indicates that mortality may dominate the dynamic.

Many population models developed over the past century (*as compiled by Turchin, 2003; Vandermeer and Goldberg, 2003*) set mortality to a constant portion of population, thus constant in good times and in bad. This is not true in nature. Of the remaining models, some come closer to a natural mortality by employing an inverse dependence on the resource, but they do not replicate the natural dynamic at high levels of resource. A few incorporate the hyperbolic simulation of consumption functional response into the term for births but I have not found one that does so properly in inverse form for non-predation mortality. None of these models uses an overlap function to combine predation and non-predation death. And, none of these models use the identical expression of terms in all tropic levels as would be required of a common theoretical framework that could embrace all life.

CDPD meets all these criteria and displays the full dynamic range of natural systems including oscillations and a resilient steady-state that under certain special conditions transitions to collapse, with a plausible and supported explanation for this entire spectrum including single peak events. CDPD does this within a concise mathematical framework.

While CDPD differs in structure, the main departure from classical theory lies in perspective, providing insight that can lead to greater understanding with its own set of unique possibilities. CDPD does not require explicitly building regulation into a model. Regulation is implicit in the finite nature of resources available to an entire modeled ecosystem. CDPD offers simple explanations for biological processes that may be tested and explored by observation and experiment. The path to CDPD has led to a mechanistic model for the full range of consumption functional response dependent upon past consumption by predator and prey, suggested a consumption driven explanation for population movements, offers a demonstration of persistent competition, and has disclosed mechanisms for how absence of predators may generate unstable dynamics.

Physiological mechanisms controlling increase and decrease are the same for all life, so the CDPD mathematical framework should be of similar form for all organisms included in a model. Thus, CDPD provides an easy scaffold on which to model ecosystems using an arbitrary number of species. CDPD should also apply to individuals within individual-based models (IBMs).

In the following description of a simple structure applicable to any species, I attempt to clarify and formalize acknowledged relationships between food supply, reproduction, death, and predation. You will find many places where functions may be substituted for constants, making this approach sufficiently open ended to accommodate a great range of observed biological behavior. But adding functions and parameters for special scenarios is not required to demonstrate a rich dynamic. The few parameters for each species used to generate behavior shown in the figures predict 'bottom-up' population control and a dynamic ranging from equilibrium to single peak events as predation proficiency, a factor in the calculation of consumption, increases and finally exceeds a threshold of instability.

Thus, I propose a model for the underlying mechanisms controlling populations.

CONSUMPTION-DEPENDENT MODEL for a SPECIES

Change over time in the population of a given species in a specific area can be accounted for by the well established simple sum:

$$N_{t+1} = N_t + B - D + IM - EM$$

where N_t is the population aggregate mass (for conceptualization, think of this as the population count) at the beginning of a unit of time and N_{t+1} is the new population mass at the end of that time unit. B denotes births (mass gain) and D denotes deaths (mass loss) during the time increment. IM – EM accounts for immigration and emigration. Initially, I shall examine mechanisms that generate gains and losses for births and deaths.

$$N_{t+1} = N_t + B - D$$

I postulate that births are dependent on consumption C, a number with a range of [0-1] where C=1 denotes consumption at satiation, and upon environment E. CDPD defines E, with a nominal value of E=1, as all biotic and abiotic interactions other than those directly responsible for C. Therefore, I propose the following simple mechanism for births:

$$B = N \cdot Rb \cdot (C \cdot E) \quad ...\text{where } N=N_t \text{ and } Rb=[\text{base birthrate}].$$
$$Rb \text{ would be the rate observed at } [C=1, E=1].$$

I further postulate that deaths, other than predation, are dependent upon the inverse of consumption C and environment E. Therefore, I propose the following simple mechanism for non-predation deaths:

$$Q = N \cdot Rq/(C \cdot E) \quad ...\text{where } N=N_t \text{ and } Rq=[\text{base deathrate}].$$
$$Rq \text{ would be the rate observed at } [C=1, E=1].$$

$$[\text{If } C=0 \text{ or } E(\text{for } Q)=0 \text{ then } N_{t+1}=0]$$

C=0 and E=0 are both possible. While 'divide by zero error' may be one's first thought, biological response to either C=0 or E=0 would be extinction of the population denoted by $N_{t+1}=0$. Therefore, the algorithm contains the conditional [if C=0 or E=0 then $N_{t+1}=0$]. This is legitimate so long as the time increment used in the model is longer than the time to extinction under conditions of C=0 or E=0 for all populations.

Thus, births decline and non-predation deaths increase when a population has less food [C<1] or lives in a less favorable environment [E<1].

Both Rb and Rq should be constant except for scenarios where age or stage distribution may become skewed. In such cases, split population into appropriate age or stage groups.

Death D is a function of predation P and non-predatory mortality Q. P and Q cannot be summed because any predation may remove an individual that would otherwise die a natural death during the time increment.

$$D = (1-Kd) \cdot (P+Q) + Kd \cdot (P+Q+|P-Q|)/2 \quad ...for\ [0 \le Kd \le 1]$$

where Kd=0 means that predator NEVER kills prey that would otherwise die, and Kd=1 means that predator ALWAYS kills prey that would otherwise die.

$$Qn = (D-P) = ((1-Kd) \cdot (P+Q) + Kd \cdot (P+Q+|P-Q|)/2) - P$$

Qn is the number of non-predation deaths a study should disclose for a population in which a measure can be made of both predations P and non-predation deaths Qn. This may be useful to a field or laboratory study.

Every predation link in the food web is subject to its own value for Kd. The closer Kd is to 1, the more P overlaps Q meaning the more likely a predator will choose to kill a weakened prey. Both Kd=1 and Kd=0 are unlikely in nature. If I had to make a guess I would set Kd very close, but not equal to 1 for most animals because their predators tend to select weakened individuals, and I would set Kd very close, but not equal to 0 for vegetation because herbivores prefer the youngest and freshest growth (Price, 1991).

ENVIRONMENT E [Unitless]

Environment E affects births, deaths, and ability to acquire food, often in a manner unique to each category. An environment nominal for one species may not be nominal for another species living in the same ecosystem. Thus, the value of E for a given environment may have to be adjusted individually for each species, then further adjusted to reflect effect on births Eb, deaths Eq, and consumption Ec. E is a parameter with a nominal value of E=1, but E may vary from E=0 to a value of >1. A measured change in births in an alternate environment under conditions of C=1 that is one-half the births expected at Eb=1 requires by definition that Eb=0.5.

For example, the environment Eb for births for a flowering plant that has lost its only insect pollinator to extinction has a rather dim outlook for births (see Janzen, 1979, and Addicott, 1986), but the loss of that insect will likely not change Eq or Ec. Other factors impacting births may be the density of necessary nesting sites and presence of pollutants such as DDT in an affected population's food supply. There are other relationships. Limbaugh (1961) showed that in the absence of "cleaner fish", populations of "customer fish" declined in less than two weeks as a result of skin diseases, making Eq<1.

Certain species kill members of other species that utilize the same prey. Lions kill cheetahs when the opportunity arises. Thus Eq, the environment affecting deaths for a population of cheetahs Ncheetah becomes worse in the presence of lions proportional to the population of lions Nlion, and could be accounted for in the model by a function of the lion population such as EqfactorLION=1/(1+CONSTANT·Nlion) where CONSTANT is a constant of proportionality for lions killing cheetahs.

Environmental factors affecting both Eb and Eq may include waste products such as ethyl alcohol produced by yeast (Gause, 1932). In such cases, both Eb and Eq would include a function of the species producing the substance Eb*f*(Npolluting) and Eq*f*(Npolluting), which in this specific instance is the same as the species being affected.

The environment changes in many ways, some of which are predictable such as night and day, summer and winter, and wet and dry seasons which affect, survivability and nourishment in a known manner. Even for the regular cycles, there is a random nature to the intensity of these changes. I have noted an interesting stabilizing effect on persistence of competition due to environmental cycling of the CDPD model (*see figures 7 - 9*).

Other components of environment are more difficult to predict. Shifting levels of disease and parasitism are good examples. When these factors are known, or one wishes to model the effect of a particular environmental factor, the effect may be incorporated into E.

When an Efactor is entered as a function of the population of another species EfactorX=*f*(NspeciesX), as, for instance, when environmental conditions are improved or degraded by the presence of that other species, this can be used to model mutualisms such as cleaner fish (Limbaugh, 1961), or ants and acacias (Janzen, 1966, and Bronstein, 1998), commensalisms, parasitism (including disease organisms), amensalisms, and competition.

While competition for a common food source involves a reduction in available food for each species competing for the same resource (see Multiple Competitors below), the actual mechanism that prevents one competitor from eliminating the other is usually environmental. Each competitor may be better equipped to deal with a particular set of environmental conditions than the other. Thus, as the environment cycles through its normal range of conditions, first one competitor will fare better, then the other. If the time increment is smaller than the cycle of environmental change, for instance, some division of a year, then E should incorporate a function of time that reflects the impact of climatic cycles upon the species to reflect the manner in which they differ during each time increment.

Ec is a factor in the value of Rp which affects the ability of a population to acquire food, setting the level of consumption C. The greatest effect of Ec may be to reduce Rp to a value that allows a stable predator-prey dynamic.

Increases in predator proficiency Rp, described below, make it easier for a predator to acquire prey. With this model, predator-prey relationships become unstable above a certain value because it becomes too easy for predators to acquire prey (*see Figure 4*). Predator population increases, forcing the prey population to extinction. The predator may follow suit. An environment Ec that contains cracks and crevices, thickets of vegetation, or any other biotic presence or abiotic condition that makes predation more difficult allows populations of predator and prey to find a stable equilibrium.

Thus, the model behavior demonstrated in Figure 4 is in total agreement with the results produced by Huffaker (1958) and Huffaker *et al.* (1963) in their study of a predator-prey relationship between a phytophagous mite and a predatory mite, and with the results of Holyoak and Lawler (1996) who conducted a similar experiment using a protist predator-prey pair.

To more faithfully replicate the actual mechanisms involved in Ec, such as a commensal species or a weather condition providing prey protection from predation, it may be useful to modify the value of Ec by using functions of protecting species populations *f*(Nprotector) and functions of environmental variables *f*(Abiotic protective features).

The grazing or predation environment for all animals that are themselves subject to predation is likely to be negatively affected by the presence of their predators since the need to constantly take actions to avert predation leaves less time and energy for their own predations. Thus, in addition to predation deaths, the simple presence of predators in the prey's environment may very likely reduce a prey population's ability to acquire food. Studies by Beschta, 2003, of cottonwoods, elk, and wolves in Yellowstone led him to conclude that a predatory presence inhibits a prey animal's predations. This could be entered as EcPredatorEffect=1/(1+CONSTANT·Predator) where CONSTANT is a constant of proportionality for predator effect on prey Rp.

Ec is a number that may be greater or lesser than Ec=1, the value that represents an average predation environment. An Ec change from Ec=1 that reduces a predator's consumption C by a factor of 0.95, while predator and prey population levels remain unchanged, represents by definition a change from Ec=1 to 0.95.

CONSUMPTION C [Unitless]

Consumption is the means by which all life continues. But for all populations, within a fixed interval of time, there is a consumption maximum represented by C=1. Maximum consumption, for a population subject to a nominal environment E=1, yields birth rate Rb and natural death rate Rq. Thus, consumption may range from C=0 to C=1. And, consumption C is the fundamental relationship between predator Neater and prey Neaten.

In times of scarcity, predator population Neater consumes the Rp constrained portion of Neaten. This is the value of C for C<1.

$$C = (Rp·Neaten)/(Rc·Neater)$$
$$C = (Rp·Na)/(Rc·N) \qquad [Na=prey, \ N=predator]$$
and...   [if C>1 then C=1]

If Neaten/Neater becomes large enough, the value of C will reach C=1. Population Neater will have all it can consume of population Neaten and further numbers of Neaten will not incur greater predation. C cannot exceed a predator's maximum consumption needs (satiation). Thus, C is conditional.

Cp is predator consumption one step up the food chain.

$$Cp = (Rpp·Neaten)/(Rcp·Neater)$$
$$Cp = (Rpp·N)/(Rcp·Np) \qquad [N=prey, \ Np=predator]$$
[if Cp>1 then Cp=1]

Na is the prey, vegetation, or other resource consumed by N, and Np is the predator or herbivore population consuming population N.

OPTIMAL CONSUMPTION RATIO Rc [UNITS (Nprey · Npredator^{-1} · time^{-1})]

Rc is that ratio of Nprey consumed per Npredator that will provide predator population with maximum consumption C=1 during a specified time interval. Rc, a weighting factor specific to each predator-prey interaction, allows the normalization of C. While Rc may generally be treated as a constant for a predator species or age group, Rc may be dependent on temperature and other abiotic environmental conditions.

Most predators utilize a multiplicity of prey species. Consumption is divided among them in accordance with the relative population number of each prey species, and the difficulty in acquiring each particular prey species' Rp. The value of Rc must be set to reflect each prey species' potential contribution to total consumption. Therefore, the Rc value for each prey species represents that number of prey that would satiate our predator if that prey species were the *only* prey available. Rc is a mass ratio per time.

Rcp is the Rc for the predator, and comes from the next level up in the food chain. It is used to calculate predator consumption Cp and predation deaths P. Rcp passes feedback down one level to the Nprey population.

PREDATOR PROFICIENCY Rp [UNITS (time^{-1})]

Rp is the proficiency with which a predator in a predator-prey relationship is able to acquire and consume prey over the course of a specified time

increment. Rp is analogous to *predator efficiency*, but has been named differently to avoid confusion with where it has been defined elsewhere.

Rp may be thought of as that fraction of the available Nprey that Npredator is actually able to consume within the specified time increment. Thus, the larger the value of Rp, the easier it is for Npredator to acquire Nprey. Rp limits the number of Nprey that Npredator is able to acquire within the specified time increment.

Within a stable predator-prey relationship, predator proficiency Rp will not be sufficient to allow maximum predator consumption C=1, thus effecting population regulation.

Rp may be decomposed into the following factors:

$$Rp = Ec \cdot (Kp/Ka) \cdot Rs \cdot Ri$$

Large values for Rp, which make it easy for a predator to consume prey, lead to collapse of the prey population (*see Figure 4*). Smaller values of Rp, which make it is more difficult for a predator to acquire prey, show great stability (*see Figures 2 and 3*).

Rp is a value specific to a given predator-prey relationship, and in simple approximations may be implemented as a constant for a species or an age group. But, Rp is a function of several factors, each of which may be a function of the presence or absence of other species. Also, Rp may contain time lagged functions of past consumption for both predator and prey.

Rpp is the Rp for the predator, used in the function that generates predation deaths P, a variable that passes feedback down one level to the Nprey population, and comes from the next level up in the food chain.

(Kp/Ka) RATIO – Kp/Ka [Unitless]

The RATIO Kp/Ka represents the current status of the arms race between Neater and Neaten, and is likely to represent a large part of the value of Rp. Note that as the ability of Neater increases, the value of Kp/Ka increases, while as the ability of Neaten increases, the value of Kp/Ka decreases. Kp and Ka may shift with a population's level of nutrition.

    Kp quantifies the skill level, the ability of Neater to consume Neaten.
    Ka quantifies the defense level, the ability of Neaten to survive Neater.

    $Kp = Gp \cdot CP$,   CP represents effect of past predator consumption
    $Ka = Ga \cdot CA$,   CA represents effect of past prey consumption

    $Rk = Gp/Ga$,   the base RATIO of Neater to Neaten ability

The effect of prior consumption on a population's ability to eat or avoid being eaten will depend on the characteristics of predator and prey. For most herbivores, prior consumption Cprior may have only a moderate effect on ability to eat, but more effect on a carnivore that must chase down its prey.

While a carnivore that is truly debilitated by hunger may be at great disadvantage, one that has only missed a few meals may be more desperate and thus try harder than a nearly sated carnivore that is not particularly hungry. By this reasoning, Cprior could affect predation performance far more at the low and high ends than in the midrange.

CPLow, described below, accounts for the reduction in a predator's Rp attributable to low prior consumption. Animals close to satiation, CPHigh, may be less inclined, or simply find it harder to predate on a full belly (referred to as handling time). This decreases the value of Rp as C approaches the limit C=1, generating a *Type II functional response* as described by Solomon (1949) and Holling (1959). CPHigh, detailed below, accounts for this progressive reduction in a predator's Rp attributable to high prior consumption.

The prey's prior consumption may make little difference in ability to avoid predation for a porcupine or turtle, but a great deal of difference to a rabbit or antelope that must run fast to avoid becoming a meal. However, CA has a lower limit, (SKa>0), because even if prey lies dead on the ground, a predator must invest time and effort to find, consume, and digest it.

Prior consumption may be scaled for both predator and prey in each predation link to reflect the effect that prior consumption has on the ability of the predator to predate, and on the ability of the prey to avoid predation. Thus, CDPD provides a plausible derivation of the predation functional response directly from biological mechanism (*see Figure 1*).

CP represents effect of prior consumption on predator's ability Kp.
CP = CPLow · CPHigh

CPLow = $1/(1+SPLow·((1/CpriorNeater_1)-1))$

CPHigh = $SKp+(1-SKp)/(1+SPHigh·((1/(1-CpriorNeater_2/1.000001))-1))$
The 1.000001 term prevents 'divide-by-zero' error at $CpriorNeater_2=1$.

SKp= Neaten[type I]/Neaten[type II]   ...at C=1

SPx represents SCALE factors SPLow or SPHigh for CpriorNeater.
[SPx=0] Cprior has NO effect, CP=1.
[SPx<1] captures the effect of Cprior.

It will likely be found in most instances that SPx<<1.

Prey experiencing low Cprior will increase Rp for the predator.

CA represents effect of prior consumption on prey's survival ability Ka.
CA = SKa+(1−SKa)/(1+SA·((1/CpriorNeaten$_1$)−1))

SKa must be determined by observation.

SA represents SCALE factor for CpriorNeaten$_1$.
[SA=0] Cprior has NO effect, CA=1.
[SA<1] captures the effect of Cprior.

It will likely be found in most instances that SA<<1.

I suspect that these effects do not strongly influence the overall dynamic, but in certain scenarios can cause oscillations. Building on the argument of Keith (1983) in view of Elton and Nicholson's study (1942), a plant may produce a toxin in response to heavy browsing, perhaps due to the higher consumption by the plant population that thinning of that population enables (*predation of a prey population incurs an increase in consumption by prey*). The defense presented by this toxin is accounted for in the value of Ka thus lowering the herbivore's Rp. Herbivore consumption decreases accompanied by a drop in herbivore population, plant mass increases, plant consumption decreases due to limitation by resources, and for this or other reasons, the toxin abates. Herbivore Rp will return to its original value bringing the interaction back to the beginning of the cycle with heavy herbivore browsing and increase in herbivore population numbers. This could produce the cyclic predator-prey oscillations discovered by Charles Elton.

Subject to the affect of time lagged prior consumption on ability to predate and ability to escape predation, oscillations should be a general characteristic of all predator-prey interactions. CDPD shows such oscillations.

FOOD SOURCE Factor – Rs [UNITS (time $^{-1}$)]

If the nutritional value of a food source is high this increases the predator proficiency for that particular source. Conversely, if the effort or time required to find and consume a food source is high then this decreases predator proficiency for that particular source.

Rs = (nutritional VALUE)/(TIME and EFFORT to find and consume)

The effort to find and consume may become very important if Nprey lives in an inaccessible place such as out on the tips of branches, or in other hidden or well protected locations.   If predator access to Nprey becomes disproportionately difficult as Nprey numbers decrease, Rs could become a function of Nprey density.

Predation INTERFERENCE – Ri [Unitless]

If a predator steals a kill from a predator of another species, this increases Rp and corresponding C for Nstealer, and proportionally decreases the Rp and C for Nrobbed. This does not change predations P on the prey population. Predation interference Ri accounts for this change in Rp.

A lion stealing a cheetah's kill is a good example of interference.

    Ristealer = 1+TheftRATE·(Nstealer/Nrobbed)
    Rirobbed = 1−TheftRATE·(Nstealer/Nrobbed)·Rpstealer/Rprobbed
    Ri = 1   ... denotes NO interference

FUNCTIONAL RESPONSES

I have constructed C as a linear function of Neaten and Neater. Simple arithmetic tells us that for any given numbers of predators and prey, the amount of food *available* to each predator will be proportional to Neaten and inversely proportional to Neater.

However, food sources in the physical environment may be scattered thinly, concentrated at discreet locations, or distributed in a manner that affects Rp due to the spatial distribution in Ec. For instance, if Neaten becomes scarce and thinly scattered it may be disproportionately more difficult for Neater to find Neaten. Further, Rp may decrease as the ratio Neaten/Neater decreases due to prey less able to resist attack being killed first leaving more difficult prey (Ives and Murray, 1997). This may be represented in Ec by entering a function where Ecmin represents the minimum value of Ec, and Ecscale is a number used to scale the effect on the predation environment Ec.

    Ec = Ecmin+(1−Ecmin)·(Ecscale·Neaten/(1+Ecscale·Neaten))

Great concentrations of predators may require a similar function of Np to be entered for Predation Interference Ri.

Where past consumption may impact current predator proficiency Rp, it will be necessary to enter time delayed values of Cprior for predator and prey in the calculation of Kp/Ka. Such functions within Rp may be responsible for the different functional responses expressed as *Consumption Rate* per predator versus number of *prey* (Nprey), described by Solomon (1949) and Holling (1959). Exploration in this area continues (Hansson *et al.*, 2001).

    (Consumption Rate) = CR = C·Rc,   C=Rp·Nprey/(Rc·Npredator)
                    CR = Rp·Nprey/Npredator   for C<1
             and...   [if CR>Rc then CR=Rc]   for C=1

REFUGES

Refuges may act to prevent a prey population from being forced to extinction under heavy predation. Calculate predator consumption C replacing prey population N with form (a) for species that are immobile, generally plants, and form (b) for species that are mobile, generally animals. Nwithinrefuge represents that number of immobile Neaten found within the refuge and Refugefraction represents that fraction of mobile Neaten normally found within the refuge.

Replace Neaten in the calculation of C with Neatenavailable.

$$\text{Neatenavailable} = \text{Neaten} - \text{Nwithinrefuge} \hspace{2cm} \text{(a)}$$
$$\text{Neatenavailable} = \text{Neaten} \cdot (1 - \text{Refugefraction}) \hspace{2cm} \text{(b)}$$

CONSUMPTION by PLANTS

Unlike most animals, and carnivores in particular where one prey species is pretty much interchangeable for another in terms of nutritional value per unit of mass, most plants require a variety of non-interchangeable substances plus sunlight. Depending on amounts available and amounts required, one item in the list of necessary nutrients and energy will become the limiting factor for any given population of plants. While temperature and other non-nutritional factors remain within a tolerable range (Shelford's law of tolerance) a plant population will be limited by that specific component which is first exhausted per Justus von Liebig's law of the minimum (Liebig, 1842) (Cargill and Jeffries, 1984).

Therefore, plant consumption must be calculated as follows where Rc_j represents the amount per plant of (Component$_j$) required for primary production by population (Nplant) during the specified time increment.

$$C_1 = Rp_1 \cdot \text{Component}_1/(Rc_1 \cdot \text{Nplant}) \hspace{1cm} [\text{if } C_1 > 1 \text{ then } C_1 = 1]$$
$$C_2 = Rp_2 \cdot \text{Component}_2/(Rc_2 \cdot \text{Nplant}) \hspace{1cm} [\text{if } C_2 > 1 \text{ then } C_2 = 1]$$
$$\vdots$$
$$C_j = Rp_j \cdot \text{Component}_j/(Rc_j \cdot \text{Nplant}) \hspace{1cm} [\text{if } C_j > 1 \text{ then } C_j = 1]$$

Compare series [C1,C2,...Cj] and select Cmin

$$C = \text{Cmin} \quad (\text{C minimum for each plant population}).$$

Just as for animals, each Rp_j represents the plant's proficiency for acquiring some needed nutrient or sunlight, and is likely to be a function of the surrounding biotic and abiotic environment, including concentrations of other items such as water and other compounds that facilitate the needed acquisition, and of life forms that perform a similar service.

MULTIPLE COMPETITORS for a single food source

When a species has competitors for a single food source, and most do, each competitor will have available only a portion of the resource. This weighted portion of Neaten for each competitor will be equal to the weighted portion of Neaten for our predator Neater divided by the sum of the weighted portions for all competitors, including Neater.

$$Lp = \text{(weighted portion of food source for a competitor)}$$
defined as... $Lp = Rp \cdot Neater$

Calculate an Lp for each Neaterj including the focal predator Neater.

Lp $= Rp \cdot Neater$ ...the focal predator
$Lp1 = Rp1 \cdot Neater1$ ...competing predator 1
$Lp2 = Rp2 \cdot Neater2$ ...competing predator 2
:   :
$Lpj = Rpj \cdot Neaterj$ ...competing predator j

$$\text{(portion of Neaten)} = Neaten \cdot Lp/(Lp+Lp1+Lp2+...+Lpj)$$

$$C = Rp \cdot \text{(portion of Neaten)}/(Rc \cdot Neater)$$
$$C = Rp \cdot Rp \cdot Neaten/(Rc \cdot (Lp+Lp1+Lp2+...+Lpj))$$
[if C>1 then C=1]

If C>1 then one should redistribute the excess back among the competitors. Since this could occur with other competitors as well, a simultaneous solution might be necessary. Successive approximation would likely be the easiest approach.

'Multiple competitors' as apportioned above refers to those organisms utilizing exactly the same resource in exactly the same way. For instance, one herbivore may chew a leaf, whereas another's sole mode of consumption is to suck sap. While both modes degrade the plant, and while the amount of plant material removed by one is a portion that is no longer available to the other, the portion available to one does not totally overlap that portion available to the other. Thus, a division of this plant resource between these two competitors may have to reflect this difference in consumption behavior.

MULTIPLE FOOD SOURCES without competition

When a species has multiple resources, calculate C for each source. Use individual Rpj and Rcj rates for each source Neatenj.

$$C_1 = Rp_1 \cdot Neaten_1/(Rc_1 \cdot Neater)$$
$$C_2 = Rp_2 \cdot Neaten_2/(Rc_2 \cdot Neater)$$
$$\vdots$$
$$C_j = Rp_j \cdot Neaten_j/(Rc_j \cdot Neater)$$

$$C = C_1 + C_2 + ... + C_j$$
[if C>1 then C=1]

Scavenger CONSUMPTION

The consumption of many animals, and all decomposers, plant and animal alike, takes the form of scavenging – the consumption of organisms that have already died, either from a natural death, D–P, or predation P. The 'prey' of a scavenger is a function of D–P or P, for each of which C should be calculated separately. Rc will be much higher for a predation due to the smaller quantity of remains following a predator's meal, and Rp for the two types of death may be different also because of the risks inherent in removing 'leftovers' from a predator's kill. Some animals engage in both predation and scavenging. Such consumption should be accounted for in the list of multiple food sources.

$$C = Rp \cdot Da/(Rc \cdot N), \quad \text{where } Da=\{(D–P) \text{ or } (P)\}, \ N=\text{scavenger,}$$
and...   [if C>1 then C=1]

Like predation, each scavenged meal represents a link between Neater and Neaten. But unlike predation, scavenging acts as a commensalism, benefiting Neater while having no effect on the numbers of Neaten.

MULTIPLE FOOD SOURCES with MULTIPLE COMPETITORS

Calculate partial Cj values, as above for multiple competitors, then sum these Cj values as for multiple food sources to obtain a final value for C. With any of these forms, a population can still consume only a fixed maximum.

  So...   [if C>1 then C=1] still applies.

If C>1 then one should redistribute the excess back among the competitors. Since this could occur with other competitors as well, successive approximation might be the fastest way to a solution. Even without such redistribution, the effects of such an error will in most cases be minor compared with other sources of error.

PREDATION

The aggregate mass of individuals killed by predation P in population Neaten equals the mass of prey consumed by the predator Neater. That number will be equal to the predator's consumption Cp times the predator's consumption ratio Rcp times the population mass of predators Np.

$$P = Cp \cdot Rcp \cdot Np$$

Rcp·Np is the number of prey consumed under optimal conditions (Cp=1, E=1), and the fractional part of optimum represented by Cp reduces that number when conditions are less than optimal. Thus, P is a function of Cp, and Cp is conditional. This makes P conditional also.

When the ratio of populations Neaten/Neater is low making Cp<1, P becomes a function of Cp·Rcp·Np.

$$P = Cp \cdot Rcp \cdot Np \quad \text{...with } Cp = Rpp \cdot N/(Rcp \cdot Np)$$
$$\text{so...} \quad P = Rpp \cdot N$$

Thus, P becomes a function only of Rpp·N making it prey-dependent. But, when the ratio of populations Neaten/Neater is high, Cp=1.

$$P = Cp \cdot Rcp \cdot Np \quad \text{...with } Cp = 1$$
$$\text{so...} \quad P = Rcp \cdot Np$$

Thus, P becomes a function of Rcp·Np, making it predator-dependent. And, this serves to show the effect of the non-linearity at Cp=1.

MULTIPLE PREDATORS

Most prey species, including vegetation, have multiple predators, and are accounted for by summing individual predations for each predator.

$$P = P1 + P2 + ... + Pj \quad \text{...where}$$

$$P1 = Cp1 \cdot Rcp1 \cdot Np1$$
$$:$$
$$Pj = Cpj \cdot Rcpj \cdot Npj \quad \text{...so}$$

$$P = Cp1 \cdot Rcp1 \cdot Np1 + Cp2 \cdot Rcp2 \cdot Np2 + ... + Cpj \cdot Rcpj \cdot Npj$$

The Kd value to use for multiple predators is calculated using a weighted average of the individual Kdj values for each predator-prey relationship.

$$Kd = (Kd1 \cdot P1 + Kd2 \cdot P2 + ... + Kdj \cdot Pj)/P$$

Scaling BIRTHS and DEATHS

Births, postulated as $B = N \cdot Rb \cdot (C \cdot E)$ may not be a linear relationship, although the endpoints at $C=0$ and 1 are fixed by definition. If not a more complex relationship, a first-order scaling Cb may be achieved using the following relationship, and scale factor Sb. Removing the dependence of births on consumption, ($Cb=1$), does not qualitatively alter the dynamics.

$$Cb = [C \text{ for BIRTHS}] \quad \begin{cases} [Sb<1] \text{ reduces effect of C} \\ [Sb=1] \ ...Cb=C \ ...\text{NO scaling} \\ [Sb>1] \text{ increases effect of C} \end{cases}$$

$$Cb = 1/(1+Sb \cdot ((1/C)-1)) \quad ...\text{for } C>0, \text{ else } N_{t+1}=0$$

Applying scale factor Sb changes C to Cb making $B=N \cdot Rb \cdot Cb \cdot E$, and $B=N \cdot Rb \cdot Cb \cdot Eb$ where Eb has been tailored to births.

Non-predation deaths, postulated as $Q=N \cdot Rq/(C \cdot E)$ may not be linear either, although, again, the endpoints at $C=0$ and 1 are fixed by definition. If not a more complex relationship, a first-order scaling Cq may be achieved using the following relationship, and scale factor Sq. Natural mortality, together with predator proficiency Rp, appears to have the dominant influence over CDPD dynamics.

$$Cq = [C \text{ for DEATHS}] \quad \begin{cases} [Sq<1] \text{ reduces effect of C} \\ [Sq=1] \ ...Cq=C \ ...\text{NO scaling} \\ [Sq>1] \text{ increases effect of C} \end{cases}$$

$$Cq = 1/(1+Sq \cdot ((1/C)-1)) \quad ...\text{for } C>0, \text{ else } N_{t+1}=0$$

Applying scale factor Sq changes C to Cq making $D=N \cdot Rq/(Cq \cdot E)$, and $D=N \cdot Rq/(Cq \cdot Eq)$ where Eq has been tailored to non-predation deaths.

We now have $P=Cp \cdot Rcp \cdot Np$ and $Q=N \cdot Rq/(Cq \cdot Eq)$ to calculate D.

$$D = (1-Kd) \cdot (P+Q)+Kd \cdot (P+Q+|P-Q|)/2 \quad ... \ [0 \leq Kd \leq 1]$$

SCALING CONSUMPTION

The dynamics of consumption are controlled largely by the dynamic nature of Rp, in particular the effects of past consumption (*see Figure 1*) which may be responsible for the Types I, II, and III functional responses. There may also be dynamics related to the spatial distribution of both predator and prey, and possibly, even 'prey image'.

ASSEMBLING THE POPULATION MODEL difference EQUATION

We can now construct our model for a population living in an isolated area with no gains or losses from immigration and emigration where

N = Population at end of last time increment (mass)
B = Births during current time increment (mass increase)
D = Deaths during current time increment (mass decrease)

E = Environment function (Ec,Eb,Eq),   [Eq>0 else $N_{t+1}=0$]

$$Rp = Ec \cdot (Kp/Ka) \cdot Rs \cdot Ri$$

$$C = (Rp \cdot Na)/(Rc \cdot N)$$
and...   [if C>1 then C=1]   *for a type I functional response*

$$Cb = 1/(1+Sb \cdot ((1/C)-1)) \qquad ...[C>0 \text{ else } N_{t+1}=0]$$
$$Cq = 1/(1+Sq \cdot ((1/C)-1)) \qquad ...[C>0 \text{ else } N_{t+1}=0]$$

$$Cp = (Rpp \cdot N)/(Rcp \cdot Np)$$
and...   [if Cp>1 then Cp=1]

$$B = N \cdot Rb \cdot Cb \cdot Eb$$
$$Q = N \cdot Rq/(Cq \cdot Eq)$$
$$P = Cp \cdot Rcp \cdot Np$$

and... $D = (1-Kd) \cdot (P+Q) + Kd \cdot (P+Q+|P-Q|)/2$

$$N_{t+1} = N_t + B - D$$

This completes the simple model except to note:

   [if $N_{t+1}<0$ then $N_{t+1}=0$]   ...population cannot drop below zero

When using an incremental approach to model continuous activity a negative result does not indicate a flawed model. It means only that the variable has dropped to zero at some point within the time increment, and thus $N_{t+1}=0$.

IMMIGRATION and EMIGRATION

One may use this model to handle immigration and emigration by expanding the basic population equation to the original form.

$$N_{t+1} = N_t + B - D + IM - EM$$

Naturally, there will be individuals moving in while others are moving out. If the model does not require keeping track of both movements, as, for instance, in handling the spread of disease, parasitism, or gene flow, then we may consolidate and calculate net movement [IE=IM−EM].

$$N_{t+1} = N_t + B - D + IE$$

Keeping with CDPD, I propose the testable hypothesis that the primary force moving individuals from one local population to another is the value of C, a population's level of nutrition. First among other competing factors would likely be the search for mates, but I shall not go into that here.

Exogenous forces likely play a large role in the movement of small animals and nearly all plants.   Plankton is carried about by ocean currents. Insects and even birds at times may be spread about by the wind. Animal parasites are moved from place to place by their hosts. The seeds and spores of plants are subject to all these avenues of transport. Whether destination populations persist or not will depend heavily upon available resources C at these destinations. This approach to species movement and persistence may provide insights in the study of metapopulations.

Let Z be a constant set proportional to observed movement between areas x and y after a census of both populations, and a measure of C values in both areas during the movement period with adjustment for Wxy. Let Wxy be a constant proportional to the ease of movement between populations Nx and Ny. Wxy=1 represents an ease of movement equivalent to movement within a local population. If movement is equally easy in both directions then Wxy=Wyx.

$$IMy = Z \cdot Wxy \cdot (Cx - Cy) \cdot Ny \qquad \text{... If } [Cx>Cy] \text{ Else } IMy = 0$$
$$EMy = Z \cdot Wxy \cdot (Cy - Cx) \cdot Nx \qquad \text{... If } [Cy>Cx] \text{ Else } EMy = 0$$

$$IEy = Z \cdot Wxy \cdot (Cx - Cy) \cdot ([Cx>Cy] \cdot Ny + [Cy>Cx] \cdot Nx) \quad \text{... to Nx from Ny}$$

Environment additional to consumption may also be important so one may wish to replace Cx with Cx·Ex and Cy with Cy·Ey.

Adjacent areas from which immigration can originate may differ in consumable resources. These resources may increase or decrease in a pattern that does not coincide with adjacent areas. Thus, populations will shift back and forth with the relative fluctuations in food supply and the consequent change in Cx and Cy within the two populations.

An excessively large population, whether or not living in a fertile area, will include individuals without territory that must travel abroad in search of food. While such animals remain where food is scarce they decrease the value of Cy. When they leave that area, Cy in the original territory increases and Cx in their new territory decreases, like water seeking its own level.

All populations of a species in adjacent areas may be linked to a common area by adding an IE_i for each linked population. Areas do not have to be equal in size or shape. [*example*: $IE=IE_1+IE_2+IE_3+IE_4+...+IE_i$]

Additional movement of animals in both directions beyond net movement should be similar to the diffusion of individual gas molecules of like gases between volumes at equal pressure through a common opening of size W.

RESULTS

Two- and three-trophic level simulations using CDPD are presented below. They illustrate a dynamic ranging from steady-state to collapse. Though not shown here, oscillatory behavior appears in appropriate non-stochastic simulations, but that will be addressed in a later paper.

State variables are Neaten, Neater, and consumption C. Environment has been set to E=1 for all non-stochastic runs. Otherwise, E is varied in a random manner to simulate environmental stochasticity. Parameters Rb, Rq, Rc, and Kd are constants. Rp is varied between simulations to demonstrate the dynamic range.

The number of interactions in living systems can potentially be enormous. Consider a single consumption link between herbivore and plant. The plant may change in its nutritional value with rainfall, sunlight, insect attack, and aging. Predation proficiency Rp of the herbivore for this plant will change accordingly, and in response to how growth of surrounding plants makes the focal plant easier or harder to locate, and of course, to changes in the herbivore's metabolism caused by sickness, thirst, and other factors. But, an average value for these rapid and random variations in the value of Rp, and the underlying predatory relationship it defines, may be used to examine the dynamic over the longer term. It is this fundamental dynamic I attempt to emulate using CDPD.

To this end, modeled species are generic. They do not represent specific organisms. While this mathematical structure may surely be used to model *real* species within a specific ecosystem, the primary purpose of this work is to create a theoretical model that accurately recapitulates the fundamental dynamic generated by structure and mechanism in the natural world. This can serve to answer many questions in ecology while at same time greatly increasing our understanding of the forces that shape living systems.

For simplicity, the modeled dynamics employ a Type I response, capped at C=1 representing satiety (*Figure 1*). However, I have found that inclusion of past consumption in Kp/Ka can produce Types II and III functional responses. High end effects, close to satiety, are responsible for the Type II response. The curve becomes sigmoid when low end effects of past consumption by both predator and prey are prominent. Low end effects

resulting from a very low prey per predator ratio in combination with a disproportionately impaired ability to acquire prey at low densities due to a refuge, suppressing predator consumption of that prey as might occur for a generalist predator subsisting on alternate prey, rather than the time lagged effect of prior consumption, should also produce a Type III functional response.

Figure 1 illustrates the generation of a predominantly Type II functional response resulting from the way in which past consumption of both predator and prey affect the Rp of the predator for this particular predator-prey interaction. You may calculate consumption versus prey for Np predators using C as the independent variable. Plot $N = C \cdot N_1 \cdot CA/(CPlow \cdot CPhigh)$ over the range $[0 \leq C \leq 1]$ while N goes from zero to N_2. $N_1 = Rc \cdot Np/Rp_0$ where Rp_0 is the base Rp before factoring in the effects of prior consumption. Functions offered for scaling CPlow, CPhigh, and CA may be modified in the light of observed data, but endpoints at C=0 and C=1 must hold.

Figure 1 - Scaling Past Consumption in the calculation of Rp
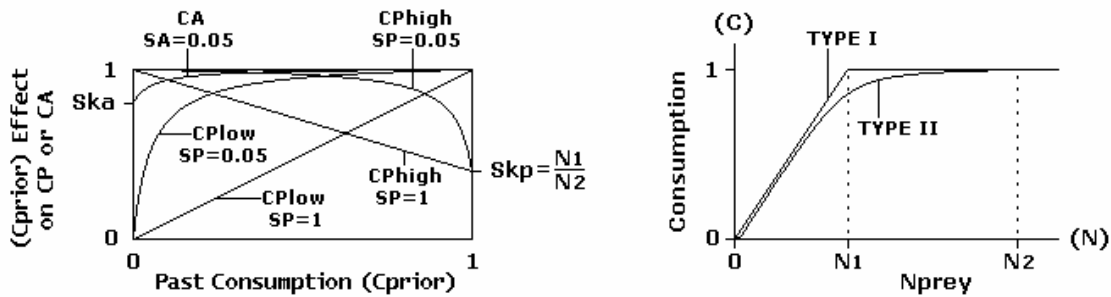
Except where otherwise noted, the population curves in the following demonstrations represent model behavior for a three trophic level system containing a primary producer (Vegetation), an animal that consumes the vegetation (Herbivore), and a second animal that consumes the first (Predator) with no scaling of consumption for either births or deaths.

Starting population numbers N for most of the runs have been set well below the steady-state level so that each population's approach to its 'ecosystem' established carrying capacity K may be observed. Note that while sigmoid, the approach to inflection is not logistic, but geometric while C=1. Inflection will occur only after C<1, where a population becomes subject to resource limitation. Populations N for vegetation, herbivore, and predator have been scaled individually so that their respective curves may be compared. Model generated steady-state values K and consumption C are presented for each tropic level so their relative numeric values may be compared. No attempt was made to fit any data set despite *Figure 6*.

- 21 -

Figure 2 shows stability in a deterministic run and persistence under conditions of environmental stochasticity using a random variation of E. Run length is 50 time increments with Rp=0.1 for both herbivore and predator.

Parameters for Figure 2	VEGETATION	HERBIVORE	PREDATOR
(Rb) Birth Rate	0.5	0.5	0.5
(Rq) Death Rate	0.2	0.2	0.2
(Kd) calculate (D)	0.2	0.8	0.8
(Rc) prey/predator	1	1	1
(Rp) Proficiency	1	0.1	0.1

Note that the convergence of N for each population is due only to the individual graph scale used for each population. This was done to make it easy to observe relative movement during stochastic runs.

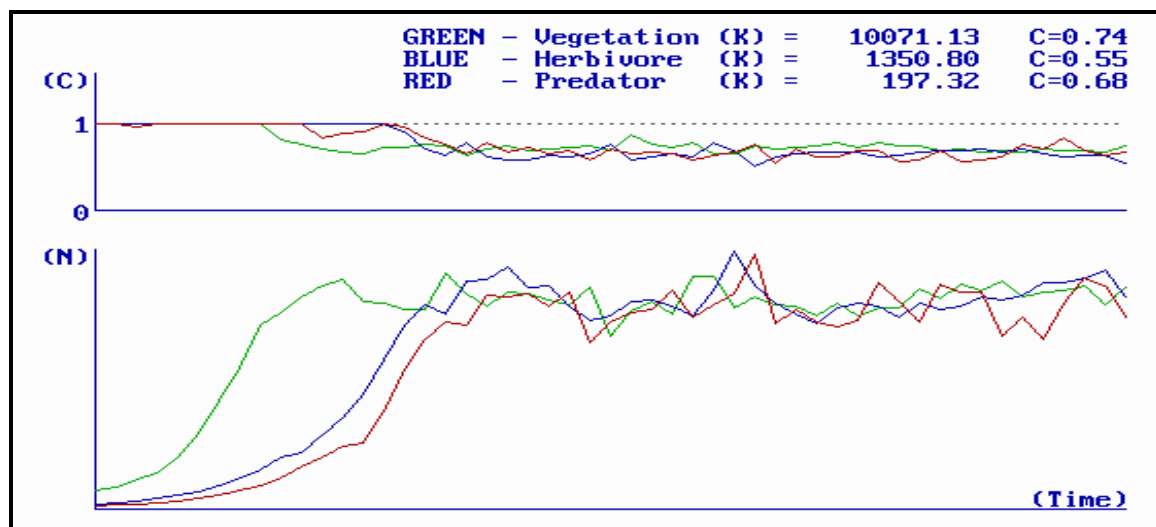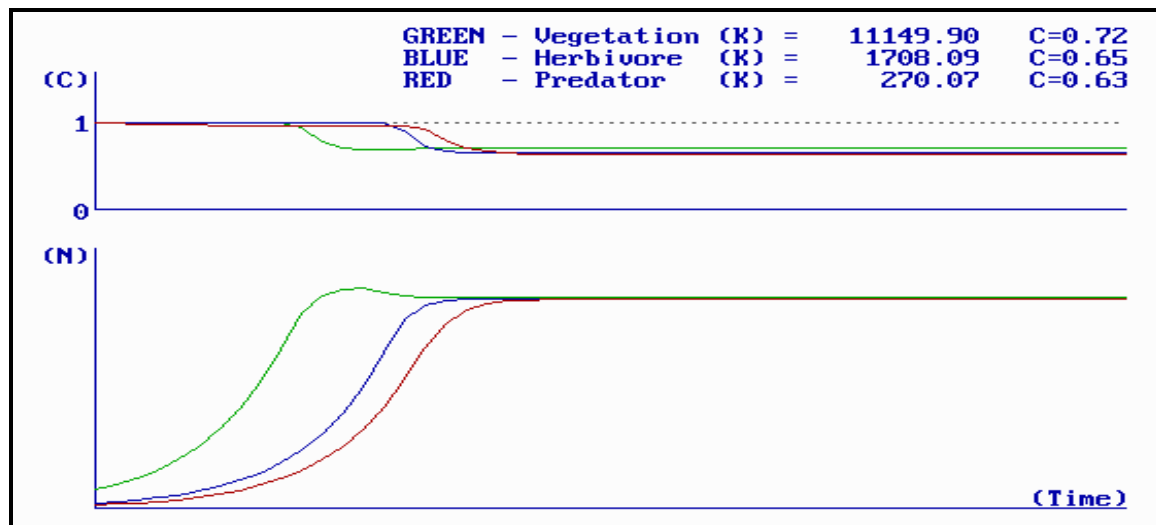**Figure 2 - Stable 3-trophic level system – Low Rp**

Figure 3, run for the same 50 increments but with an increase in Rp for both herbivore and predator to Rp=0.3, also shows excellent persistence, differing only in increased initial overshoot as populations approach the steady-state.

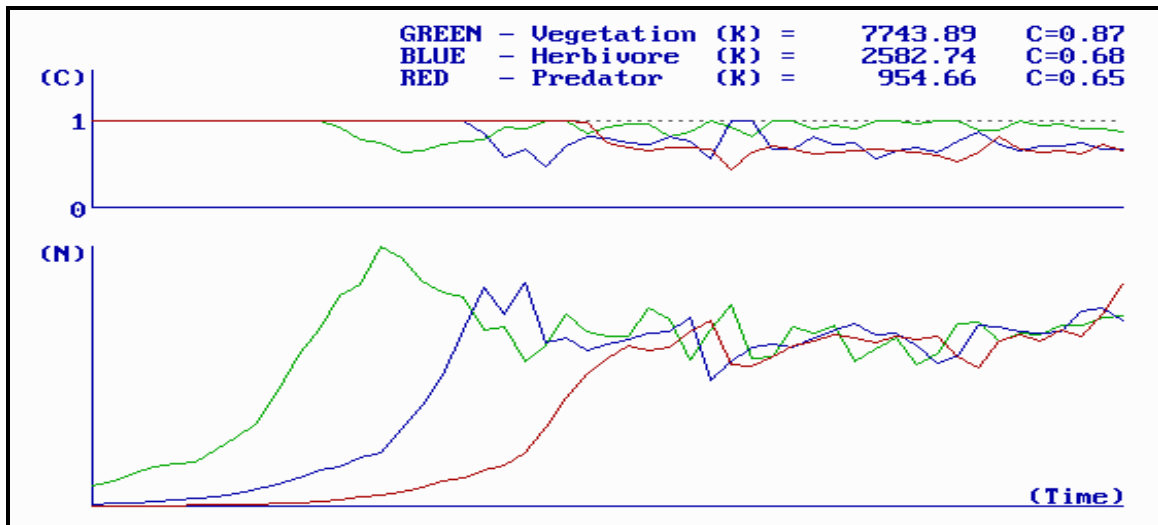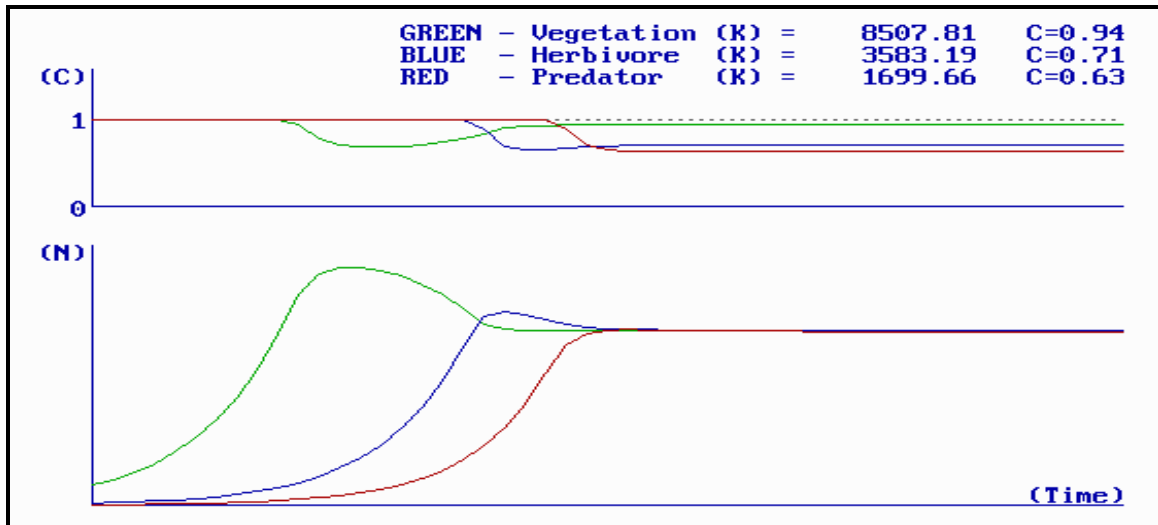**Figure 3 - Stable 3-trophic level system – Intermediate Rp**

Figure 4 has the same parameter values as *Figure 2*, except predator Rp has been changed from Rp=0.1 to Rp=0.98. Proficiency Rp for the predator may be dropped back to 0.55 and the same instability will occur, but it takes about twice as long for populations to drop to zero. Thus, a change in Rp from 0.3 to 0.55 changes stability to collapse.

This system is unstable both deterministically and stochastically in the same manner, and for the same reason, as the predator-prey experiments of Huffaker (1958), Huffaker et al. (1963), and by Holyoak and Lawler (1996), where persistence could not be achieved until sufficient environmental complexity was introduced. This is in full accord with CDPD where adding environmental complexity can lower predator Rp to a level of stability.

Figure 4 - Unstable 3-trophic level system – High Rp
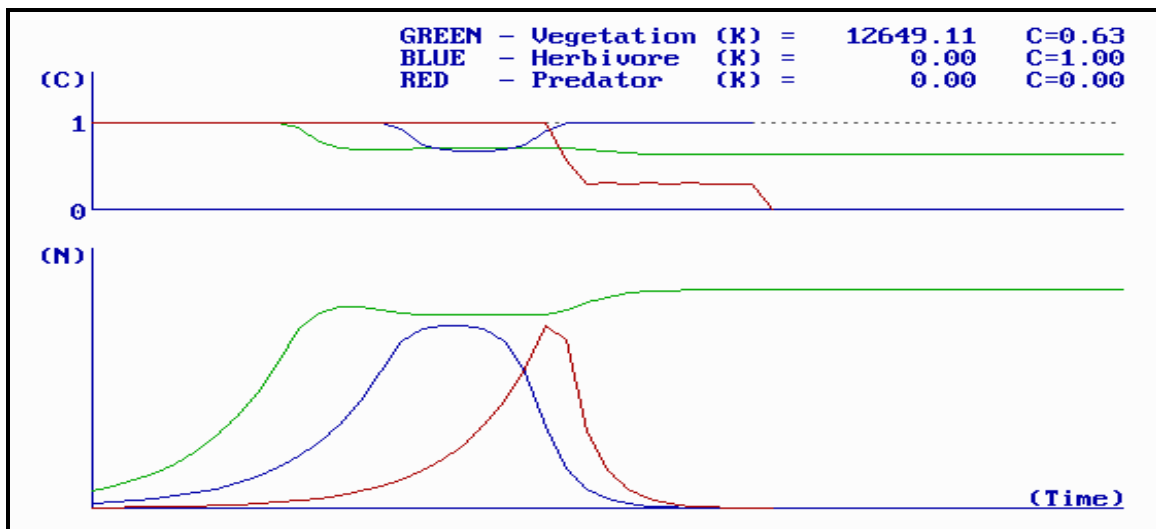
Figure 5 demonstrates maximum sustained yield. Parameters are exactly the same as *Figure 2*. MSY has been determined iteratively by successively cropping a greater number of the herbivore population on each run starting at a point after all populations have arrived at the steady-state. Every cropping run is sustainable until the last which leads to collapse. The cropping level just prior to the last represents MSY. The K values listed are those at MSY=310.

The next two graphs in *Figure 5* demonstrate stochastic runs with MSY reduced by 20 percent [MSY=248]. On the 4th stochastic run, as the odds would have it, a chance sequence of bad environmental conditions leads to collapse. This goes to underscore the risks of pushing the harvesting of a population close to a calculated MSY, and this shows the model in total conformity with what actually happens in nature.

Figure 5 - Maximum Sustained Yield (MSY)

GREEN — Vegetation (K) =   11149.90   C=0.72
BLUE — Herbivore (K) =   1120.21   C=1.00
RED   — Predator   (K) =   177.12   C=0.63

Herbivore MSY =   310

GREEN — Vegetation (K) =   10073.05   C=0.74
BLUE — Herbivore (K) =   1096.10   C=0.73
RED   — Predator   (K) =   160.05   C=0.68

Herbivore MSY =   248

GREEN — Vegetation (K) =   10418.37   C=0.65
BLUE — Herbivore (K) =   0.00   C=1.00
RED   — Predator   (K) =   0.00   C=0.00

Herbivore MSY =   248
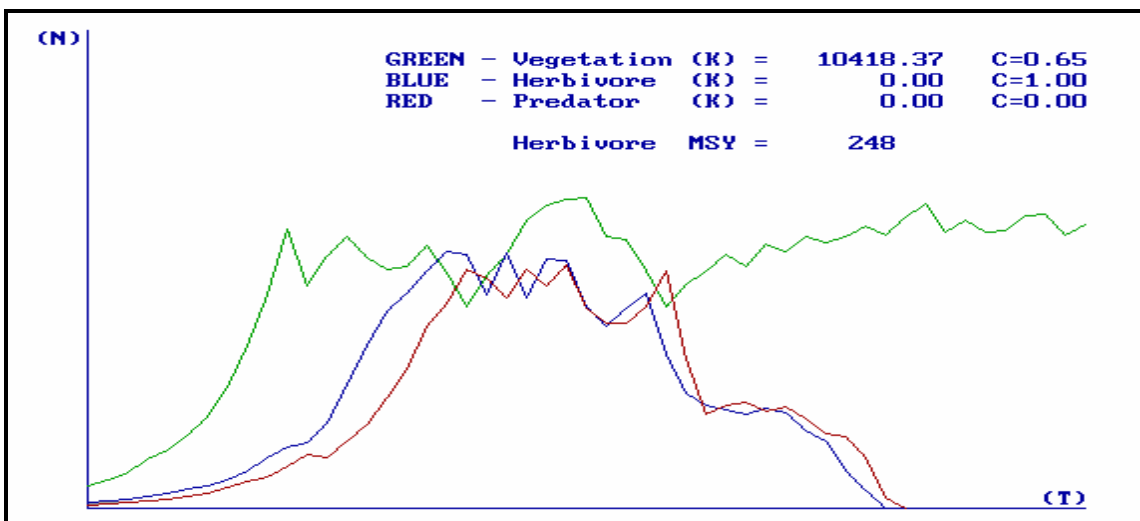
Figure 6 shows instability due to high Rp. Parameters match the standard 50 increment run except Rp value for the herbivore has been increased to 0.7, vegetation starts out at 12650, and there is no predator. The stochastic run demonstrates the same signature. I suggest that an animal's Rp goes up in the absence of predators because the animal spends less time in competition with the herd, less time watching for and running from predators, and more time feeding (Caraco, 1979; Caraco *et al.*, 1980; Beschta, 2003; Ripple and Beschta, 2003).
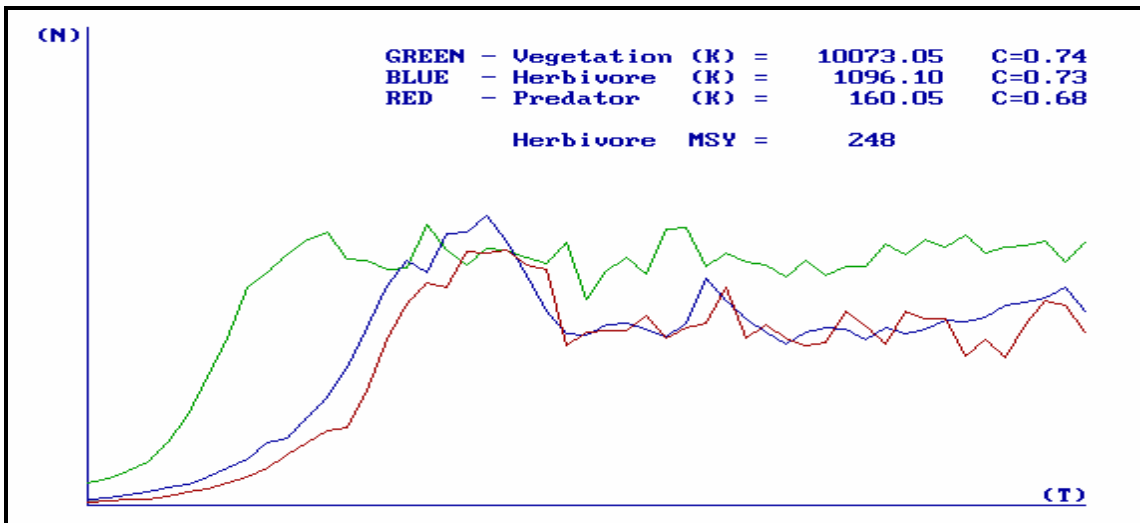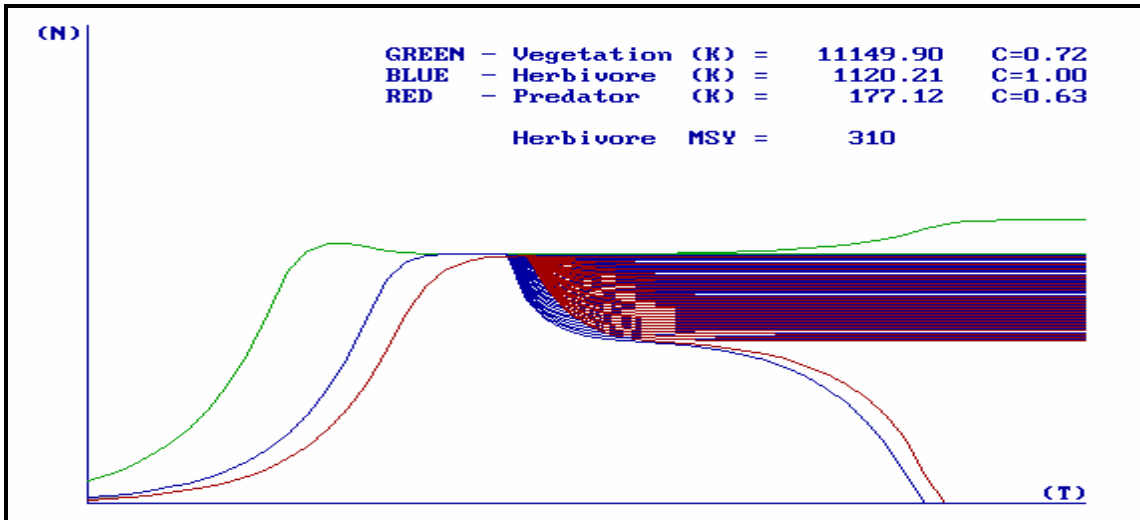
Back in 1911, twenty reindeer were released on St. Paul Island off the coast of Alaska. The reindeer had no predators. The population of reindeer in this classic semi-natural experiment was recorded, and recounted by Scheffer (1951). I include it here for comparison.

Figure 6 - Instability due to High Rp for Herbivore with no Predator

- 26 -
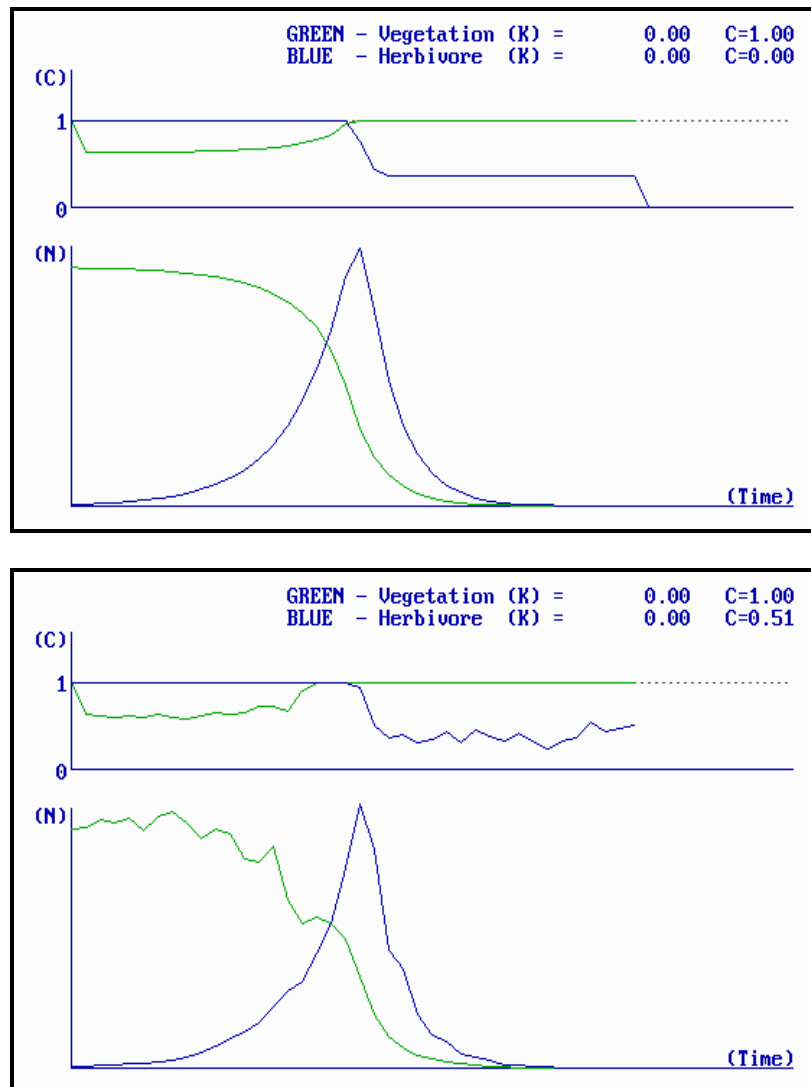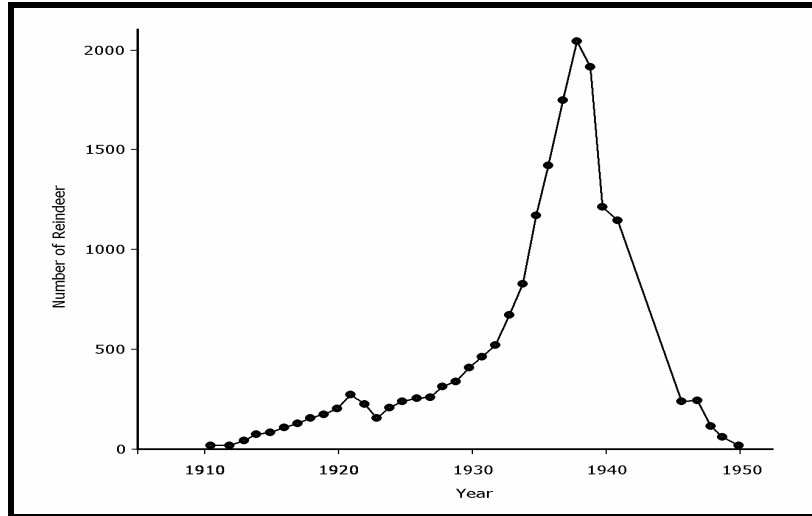
This represents the 'instability' of 'top-down' control. If predator Rp, the predation proficiency of the herbivore in this case, exceeds a certain threshold, the predation rate will exceed the rate of prey increase, the vegetative resource we are observing here. The resource population will begin to drop. As prey decline in numbers, the predator population that has been growing at full consumption C=1 up to now will begin to feel limitation C<1. At this point the resource population is dropping rapidly while the predator population is still climbing. Predation load upon the resource is also climbing. Rather abruptly, in light of too many predators for too few prey, predator consumption drops sharply, and predator population that has recently been climbing begins to drop rapidly. Even while dropping, the predator population with its high Rp continues to drag down prey numbers. This can continue until prey, the vegetation in this case, either goes extinct, or otherwise becomes unavailable in a refuge. The predator population, now at C=0, drops to extinction.

Figure 7 demonstrates competition in a consumption driven environment run for 2000 time increments with parameter values as specified below. With no stochasticity, it shows one competitor prevailing and the other eliminated, consistent with the Lotka-Volterra competition equations (Lotka, 1925; Volterra, 1926).

Parameters for Figs. 7-9	VEGETATION	HERBIVORE	HERBIVORE2
(Rb) Birth Rate	0.5	0.5	0.5
(Rq) Death Rate	0.2	0.2	0.4
(Kd) calculate (D)	0.2	0.8	0.8
(Rc) prey/predator	1	1	0.68
(Rp) Proficiency	1	0.1	0.1

Figure 7 - Two Herbivores in Competition for the Same Resource

Figure 7 caption and chart. Chart legend text:
GREEN – Vegetation (K) =   11149.90   C=0.72
BLUE   – Herbivore   (K) =   0.00   C=0.61
PINK   – Herbivore2 (K) =   1833.23   C=0.89
(C) axis labeled 1, 0; (N) axis; (Time)
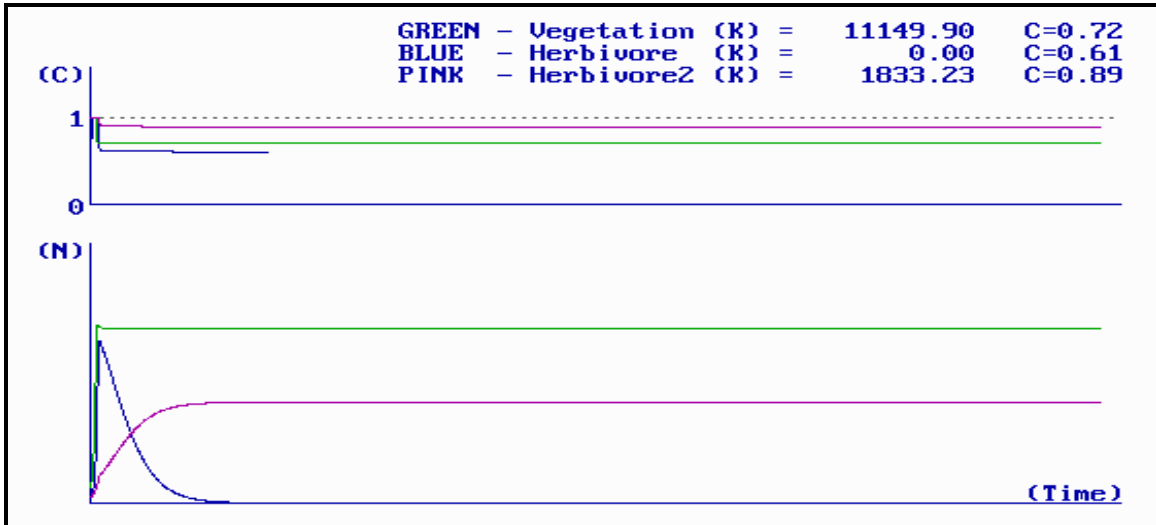
Figure 8 is the same as *figure 7* except for the addition of stochasticity. The behavior changes from that observed in *Figure 7* with neither competitor consistently eliminating the other.

Figure 8 - Stochastic Competition for the Same Resource

Figure 8 caption and chart. Chart legend text:
GREEN – Vegetation (K) =   11062.05   C=0.76
BLUE   – Herbivore   (K) =   1002.49   C=0.72
PINK   – Herbivore2 (K) =   722.34   C=1.00
(C) axis labeled 1, 0; (N) axis; (Time)
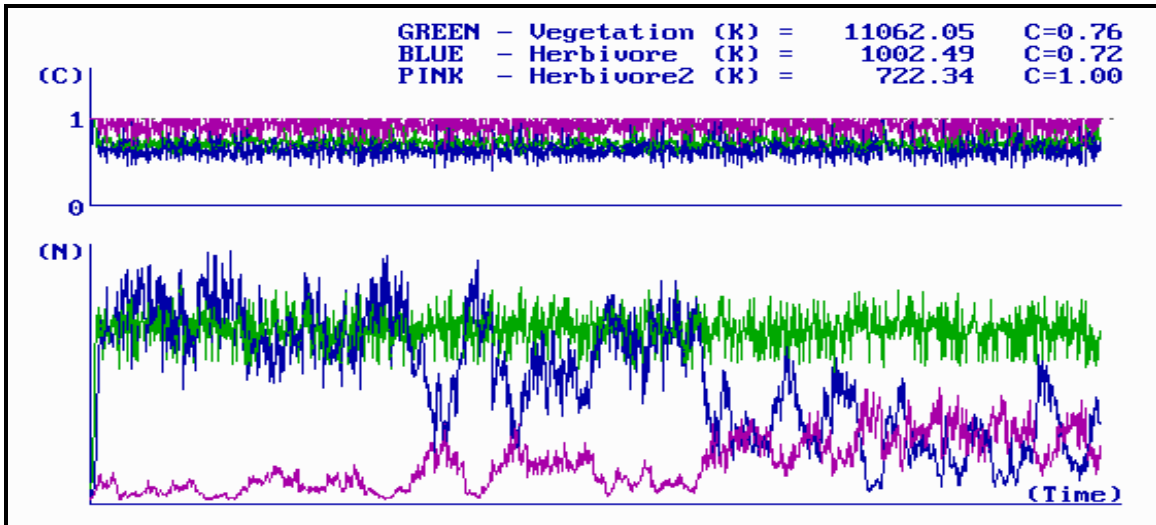
Noting this, I replaced stochasticity with a simple sine wave for the run in *figure 9*. Although oscillating with the environment variable E, both competitors find a stable population range that persists without change beyond 20k time increments, 2k of which are shown.

Once again note that the relative height of each population curve has no significance since each population is scaled independently.

Figure 9 - Competition for the Same Resource in Cyclic Environment
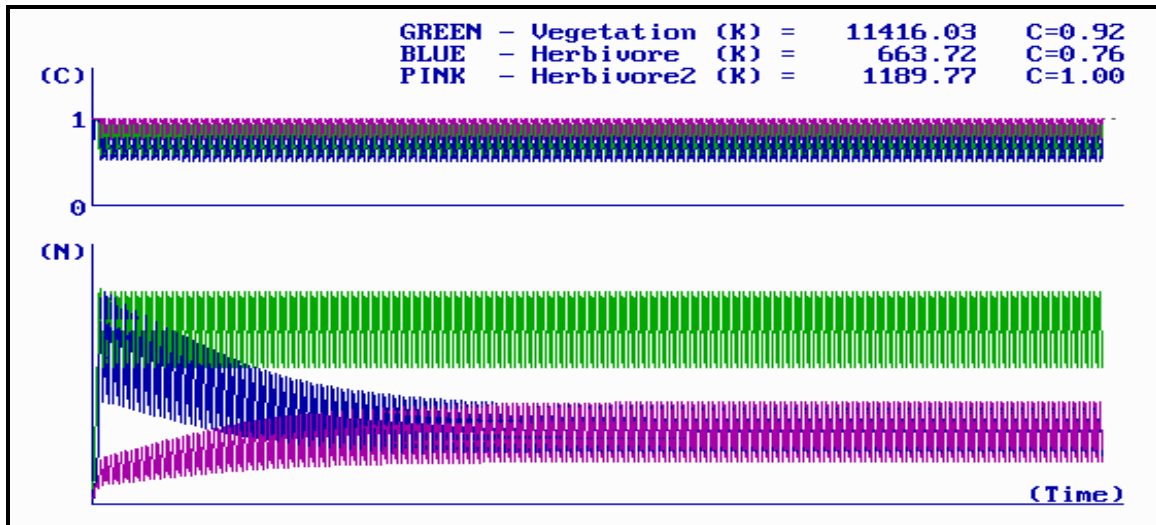
A great many features of environment, both biotic and abiotic, are possessed of a cyclic nature to which stochasticity is added. One competitor may find a particular temperature most comfortable, while another finds peak comfort at a different temperature. As environmental conditions cycle from warmer to cooler, then back, one competitor will do better, then the other. Advantage passes from one species to the other and back again, with neither species able to eliminate the other. Thus, each species, though in competition for the same food supply, flourishes in its own 'niche'.

PROPOSAL of MECHANISM for SINGLE PEAK EVENTS

The dynamics of consumption generates a 'single peak event' signature curve that appears remarkably like the curve of real data recorded for St. Paul Island by Scheffer (1951) (*see Figure 6*). With CDPD, the single peak event occurs when the value of predation proficiency Rp exceeds a threshold. Measured skeletal remains from reindeer that died prior to the similar single peak event on St. Matthew Island show those reindeer grew to a body weight 24 to 61 percent greater than their counterparts on the mainland (Klein, 1968). This is consistent with an increase in Rp, the ability to acquire food.

Why should the value of Rp for reindeer on St. Paul Island or St. Matthew Island be greater than for reindeer living on the mainland when the only notable difference between island and mainland is the absence of predators? Beschta (2003) and Ripple and Beschta (2003) observed browsing of cottonwoods by elk fell substantially when wolves were released in Yellowstone, due not to predation, but to the increased risk of predation. Earlier, Caraco (1979) and Caraco *et al.* (1980), in observations of birds at bird-feeders, found that birds divide their time between eating, quarreling, and looking out for predators. Bird Rp is reduced by the time spent quarreling and looking for predators.

It appears that feeding behavior of many animals responds to the presence of predators in a negative manner. This manifests as a diminished predation environment Ec for these animals with a corresponding reduction of Rp reducing their consumption. Conversely, if these animals find themselves without predators, their Rp can increase. Spending less time looking for and running from predators, and, under less pressure to flock or herd with its attendant competition, they are able to consume more.

DISCUSSION

Ecology has seen the construction of many models for steady-state systems, for example, Sandin and Pacala (2000), and others for single peak events as explored by Huzimura and Matsuyama (1999).

The CDPD model displays this entire dynamic range with the shift from stability to collapse occurring not by design but as an emergent property of the system. Additionally, CDPD demonstrates persistent competition as shown in *Figures 8 and 9*. While such correspondence to nature does not say that CDPD has captured the full truth and subtlety of the natural world, the clearly logical and biologically meaningful construction of the model does suggest that this approach could be a valuable tool to understanding.

A 40 year study of Wildebeest in the Serengeti by Mduma *et al.* (1999) concluded that food supply is the primary limit to population. CDPD agrees with this, and also with Lindeman's (1942) trophic level concept, commonly known as trophodynamics, to the extent that 'bottom-up' forces control populations. But, CDPD suggests that this state of affairs exists because the alternative is inherently unstable. CDPD stands in opposition to the Hairston *et al.* (1960) idea (HSS), that herbivores are limited by their predators. While predation can greatly lower the number of prey creating a heavy top-down force, and predator presence may inhibit a prey's ability to feed, the model shows that if Rp rises to a level where predation becomes *controlling,* the system becomes unstable. Prey population crashes, often taking the predator with it. Thus, 'top-down control' is a self eliminating condition within an ecosystem.

Further evidence for this prediction appears in a study by Basset *et al.* (1997) who investigated the effect of consumer functional response on consumer population stability using the hyperbolic simulation of functional response for consumption $F(X)=a(X^n)/(b^n+X^n)$. Whereas classical population modeling shows a greater range of stability, avoiding the 'paradox of enrichment', for n>1, Basset *et al.* found that a spatially distributed individual-based model (IBM) predicted the opposite. As n increases, ability to consume increases, and their IBM showed population extinction beyond n=1. Their IBM result is consistent with CDPD predation proficiency increase leading to collapse.

This model behavior of stability shifting to collapse with rising predation proficiency Rp offers an explanation for the observed population numbers of moose in the presence of wolves on Isle Royale between 1958 and 1997, tracked early on by Allen and later by Peterson (1999). It was noted that when the wolf population fell for reasons unrelated to availability of prey, moose numbers would jump, then fall sharply due to starvation.

It may be that successful species living in a predation environment have become so because they are able to maintain a strong predation proficiency, and thus healthy population numbers despite the presence of their predators. Consequently, if the population of predators drops for any reason other than lack of prey, the effect upon prey is an increase in Rp that leads to a cycling of population growth followed by a drop. A total absence of predators can raise Rp to the point of a single peak event as discussed earlier.

Thus, the dynamics of consumption pivot on predator proficiency. Rp is not a simple constant, never changing. Rp is dependent upon many factors in the predation environment. Rp may increase or decrease in value depending on prior consumption by predator and prey via mechanisms discussed earlier. Applying these mechanisms in varying amounts to calculation of consumption generates the Types I, II, and III functional response curves observed in nature (Solomon, 1949; Holling, 1959).

Rp is also dependent upon the life strategy of the organism. Many species have stages during which consumption is reduced or halted for long periods. Many single celled organisms can form spores to survive harsh conditions. Many amphibians, reptiles, and mammals may go into hibernation during which body metabolism slows to a point permitting extended intervals of no consumption. Some fish and many insects have a final reproductive stage during which they cease consumption, reproduce, then die. Likewise, plants have a variety of ways for dealing with dry or cold periods during which photosynthesis slows or stops completely. All of this involves change in the value of Rp in response to conditions and as determined by life plan.

CDPD may be further examined in view of previous work published in '*Ecological Modelling*', and in particular, in the context of the current unrest among population theorists.

Awhile back Charles Hall (1988b) wrote a brief summary of a discussion titled, "What Constitutes a Good Model and by Whose Criteria?" The last item in this paper's concluding 'Points of Agreement' states, "There does not yet exist any general theory in ecology that can be universally applied", and there are "...no results of theoretical analysis at this time that could be used to reliably predict any ecological property." That was in 1988. I know I would receive argument from certain quarters, but I contend that one could honestly make the same statement today.

Around that same time Hall (1988a) wrote another paper, "An Assessment of Several of the Historically Most Influential Theoretical Models Used in Ecology...." These are the very models to which I make reference and with which I compare CDPD at the beginning of this paper. In his introduction, Hall comments on his thesis, pointing out "...that if [his] fundamental premise is correct then a large body of teaching and research in ecology is quite unfounded." Hall goes on to argue that the data offered in defense of these models do not, in light of critical examination, support them. Yet there still persists the lingering opinion that these models are "a good place to start" when making more accurate models. If this is true, he asks, then why is there such an absence of data showing these equations to be "good predictors of populations under at least some conditions?"

CDPD demonstrates a complete dynamic range from equilibrium, through oscillations which are not explored in this paper, to collapse. While no real population is parameterized in the content of this paper, stochastic equilibrium and single peak event plots appear remarkably similar to real data, thus indicative of making CDPD a good predictor over a range of conditions especially since this paper offers a supported mechanism for the shift from stability to collapse.

A prior issue of '*Ecological Modelling*' offered a paper by Cale (1988) examining the problems and limitations of mass-balance modeling. His analysis shows that first- and second-order (logistic) mass-balance models cannot, fundamentally, be used to represent real population dynamics. In other words, Cale demonstrates that the mathematical approach of 'standard theory' (first- and second-order power series models) is not valid. Cale suggests that the functional form actually describing population change should contain terms related to ambient conditions: habitat, other populations, and food resources.

CDPD does exactly this, addressing the effects of habitat, other populations, and food resources using Eb, Eq, and Ec which may incorporate functions for other interacting populations, and using C which is a function of all the food resource populations for a particular consuming population within a modeled

ecosystem. This approach is simple and easily understood whether used deterministically or stochastically.

A few years later, Nielsen (1992), examined a strategy for structural-dynamic modeling. The model that Nielsen comments on in his paper is structured in a grid of trophic levels and populations, a structure that is far too simple and regular to represent the random linkages found in real ecosystems. Nielsen comes to a similar conclusion in his 'Discussion', where he states "The lack of generality of this type of model seems to be the most severe criticism of the approach used." Populations do not fall into simple rows and columns. Trophic structure is fine as a concept to understand the relationship between two species where one is the food resource for the other. Beyond that, real ecosystems become far more muddled. Earlier ages or stages of a predator may be preyed upon by the prey of the predator or even by the predator itself. Predator-prey links between populations may go in any direction, between any two populations in an ecosystem and not just in an organized fashion between regularly ordered 'trophic levels'. Additionally, most predators have multiple prey which may occupy positions that would not be interpreted as the same trophic level if observed from the perspective of other prey and predators. Likewise, most prey have multiple predators for which the above statement could be repeated. Thus, any general theoretical model must be capable of handling such a convoluted arrangement of predation links.

CDPD accommodates any configuration of predator-prey linkages, with any number of populations. And populations, where necessary, may be subdivided geographically as well as into age or stage populations.

Moving forward in time, Łomnicki (1999) offers an individual-based approach to population ecology. Łomnicki asserts, and I fully agree with him, that the properties of a system, that is, of a population and its change over time, derive from the properties of their elements. The dynamics of a population is the aggregate of the dynamics of the individuals that make up that population.

The postulates upon which CDPD has been built, namely the dependencies upon consumption within the mechanisms for gains and loses, apply equally well to individuals as to an entire population. But, the CDPD approach is far easier to implement and understand than the IBM approach where a model must keep track of potentially great numbers of individuals, each as a separate entity.

Furthermore, IBMs have been around for some time and in that time these models have yet to inspire the insights into population dynamics that has been the case with CDPD. Until CDPD there has been no convincing mathematical and biological explanation for single peak events. There has also been no mathematical model for the dynamic that Beschta and Ripple, working from the bottom up, call the 'wolf effect', and which this author,

working separately and simultaneously from the top down, calls 'predator effect' - the change in a prey's Rp due to the presence of a predator population. And, IBMs have not inspired a biological mechanism based model for 'Consumption Functional Response'. CDPD has done all of this and more.

CDPD, in the simple form presented in this paper, does not contain elements that implement the mechanism of reserves, the ability of most organisms to continue to engage in life activities without consumption for some period of time, dependent upon the level of accumulated material and energy. Additionally, CDPD as presented above does not provide explicit formulation to represent the great variety of reproductive behavior aside from the ability to model interspecies and other environment interactions using environment variables, although modeling males and females as separate populations with the birth function for each appropriately formulated would be a likely place to start. There are sure to be other elements also important to modeling certain ecological scenarios that are currently not demonstrated in this initial version of CDPD. Nevertheless, it appears that CDPD may well meet the objections to standard models and the criteria for a correct model expressed by the authors quoted above and many others. Thus, CDPD is offered as a foundational candidate for a fundamental theoretical representation of ecology.

And last of all, considering the role of Rp in 'single peak events', implications for *Homo sapiens*, by far the most proficient species on the planet and currently growing exponentially in numbers, should be noted.

APPENDIX A. **COMPUTER SIMULATION**

ITERATIVE SOLUTION to POPULATION DIFFERENCE EQUATION using a computer program or spreadsheet software

FIRST, solve for values of C for each species included in the model. This includes each Cb and Cq if your model includes this level of detail.

SECOND, solve for P for each predator-prey interaction in the model.

THIRD, solve for N(next) for each species included in the model. For every function that includes an N for a modeled species, use the value of N for that species calculated at the last iteration.

If a population is broken down into age groups, solve for each group, make necessary age group transfers based on number of time increments per year, and total to find N(next)=Nage1+Nage2+...+Nagelast for each species contained in age groups.

REPEAT for however many time increments are necessary to model the population behavior being studied.

CALCULATE:

$$C_1 = f(N_0, N_1)$$ `All consumptions`

$$\vdots$$

$$C_n = f(N_{n-1}, N_n)$$

$$P_1 = f(C_2, N_2)$$ `All predations`

$$\vdots$$

$$P_{n-1} = f(C_n, N_n)$$

$$N_1(t+1) = f(N_1(t), C_1, P_1)$$ `All populations`

$$\vdots$$

$$N_n(t+1) = f(N_n(t), C_n, P_n)$$

`{repeat...}`   `for t+2,t+3,...,t+I`   `[I = total time increments]`

Computer programs for the dynamics shown in the figures, plus many more, are available from the author.

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