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A PRELIMINARY MODEL FOR CONSUMER

PREDATION

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ABSTRACT

In this paper a generalized multi-species consumer predation model is developed. Predation is seen as a function of kill rate, predator preference, and prey numbers. Consideration is made in the model for predator abundance, predator switching to different prey, prey abundance, and cover conditions. Kill rate also includes information about relative predator and prey advantages. The model is compared with previous models, and some of the matrices are derived from Pawnee Site data to relate the model to a specific example.

INTRODUCTION

The formulation of mathematical abstractions for various biological processes constitutes one of the major efforts of the U.S. IBP Grassland Biome Program. In general, the effort is directed at producing a whole systems model; but this, of course, usually entails an accurate representation of the component subsystems. The consumer/producer, predator/prey relationship is such a subsystem.

The most intensively studied area in the Grassland Biome Program is a portion of the Pawnee National Grassland in northeastern Colorado. Our data acquisition efforts are greatest there, and consequently, we consider it to be the "type specimen" behind our model. Because most of the data on predators and prey from that area concern only vertebrate predators, but both vertebrate and invertebrate prey, such is the orientation of this particular submodel.

Specifically, we were commissioned to draw upon our mutual strengths as biologists and mathematicians to formulate a functioning submodel equation to represent the predation process. That is, we aspired to derive a function which was biologically meaningful and yet suitable for inclusion into various levels of differential equation systems models. It must be kept in mind that this submodel only concerns the process of predation, but that it is designed to operate within a predator-prey population dynamics framework.

Previous Predator-Prey Models

The first models for predator-prey dynamics were developed by Lotka (1923) and Volterra (1926) and are now known as the Lotka-Volterra equations. Their assumption is that the number of prey attacked per predator is directly proportional to prey density. The equations take the form:

$$\frac{dH}{dt} = a_1 H - b_1 HP \tag{1}$$

$$\frac{dP}{dt} = -a_2 P + b_2 HP \tag{2}$$

where H is the number of prey (hosts) and P is the number of predators (parasites); and where a_1 and a_2 are the intrinsic rates of increase or decrease of prey and predator, respectively. An extended version of the Lotka-Volterra equations includes consideration of interspecific competition by incorporating negative $C_1 H^2$ and $C_2 P^2$ terms in equations (1) and (2), respectively.

A model by Kolmogorov (1936) drew upon the following equations:

$$\frac{dH}{dt} = HK_1 (H, P) \tag{3}$$

and

$$\frac{dP}{dt} = PK_2 (H, P) \tag{4}$$

where K_1 and K_2 are general functions satisfying boundary conditions and biologically dictated inequalities. Kolmogorov postulated several forms which the functions K_1 and K_2 might take. These are expanded and explained more fully in a paper by Rescigno and Richardson (1967).

Pearce (1970) developed a model which seems more realistic than the Lotka-Volterra model in that an increase in prey density beyond a certain level does not further increase the number of prey killed, as is the case in the Lotka-Volterra model. His model is less general than the Rescigno-Richardson model, but more meaningful and amenable to practical application.

In the Pearce model, the following relationships develop when prey is very abundant,

$$\frac{dH}{dt} = a_1 H + k_1 P \tag{5)'}$$

$$\frac{dP}{dt} = a_2 P - k_2 \frac{P^2}{H} \tag{6)'}$$

while the following equations hold for less abundant prey populations:

$$\frac{dH}{dt} = \left[a_1 - f_1 \left(\frac{P}{H} \right) \right] H \tag{5}$$

$$\frac{dP}{dt} = \left[a_2 - f_2 \left(\frac{P}{H} \right) \right] P \tag{6}$$

f_1 and f_2 above are monotonically increasing functions of the predator to prey ratio.

Watt (1959) has developed a model which gives the number of prey attacked by predators as a function of the number of vulnerable prey and of the number of predators.

$$\frac{dN_A}{dN_0} = a P^{1-b} (PK - N_A) \tag{7}$$

where N_A = number attacked

N_0 = number vulnerable

P = number predators

a, b, and k = constants

Holling (1965) developed a much more complex and specialized model for mantid predation which includes such complex factors as movement, speeds of predator and prey, hunger levels, eating and digesting times, capture success, pursuit times, etc.

Mott (1969) suggests alterations to the Lotka-Volterra equations which take into consideration the density dependent nature of the birth and death rates, but he does not suggest solutions to his formulation.

All of the models discussed above (except Holling's) are two species models (one predator and one prey species) while Holling allows for several prey species, but only one predator species. What we wish to focus on in this paper is a mathematical model for predator-prey dynamics in a system with many predators and many prey.

Scudo (1970) discussed the extension of the Lotka-Volterra equation to n species,

$$\frac{dN_r}{dt} = (a_r + \frac{1}{\beta_r} \sum_{s=1}^{n} \gamma_{rs} N_s) N_r \tag{8}$$

where the β's are interpreted as the weights or nutritional values of species, and the γ's are the relative part of the diet of predator species s composed of prey species r. This equation only has a stable solution for an even number of species and does not adequately handle the intricacy of the problems in n species. Predation in the dynamics of predator-prey models, it seems to us that only as a constant coefficient, γ_{rs}.

From this short review of predator-prey models, it seems to us that several extensions should be made in order to handle the modelling of the predation process.

(i)   Although the economic entomologists have advanced predator-prey
      models beyond the level of sophistication existant in most areas
      of ecology, their models have dealt mainly with one or two
      predator or prey species (Holling 1959a, 1965; Watt 1959, and
      Huffacker 1958). Yet, the output characteristics of a several-
      species model are undoubtedly different than those of the sum
      of the component parts analyzed individually (Holling 1965).
      Therefore, our initial challenge seemed to be that of working
      with a matrix of several predator and prey species simultaneously.

(ii) Similarly, since our formulation was to represent a mid latitude
      field situation, we felt that seasonal dynamics were an integral
      part of any model. To substantiate this claim, we simply need
      to point out that the migration and hibernation phenomena cause
      nearly complete changes in the winter and summer species arrays.

(iii) Our third line of divergence from the published predator-prey
      models is that of a "switching function" (Murdoch 1969). From
      the above discussion, it seems essential that if a predator were
      to remain in the area year-round it would likely need to "switch"
      its diet in accordance with prey abundance. Equally important,
      but possibly more subtle "switches" are necessary for predators
      to have any homeorhetic or controlling effect on the subsystem
      (Holling 1961).

(iv) Although the question of how much detail should be incorporated
      into a model may be debatable (Pielou 1969), surely the model
      structure is dictated by the objectives. Our main objective was
      that of describing, in a mechanistic sense, certain of the complex

predator-prey interactions. We could not, therefore, consider only large groups of species without destroying the mechanistic nature of the process. Indeed, our "functional array" was defined as one of two age categories for each of the major species present.

Other biological phenomena included herein consist of "thresholds-of-security," vulnerability, and saturation densities. Some of the highly specific variables cited earlier (e.g., searching, identifying, and handling times, mean hunger level, and angles of approach) (Holling 1965), are not included explicitly, but may be implicit in several of the more general functions.

As alluded to earlier, the model is site-specific insofar as it draws upon an array of shortgrass prairie species densities. Changing this array, along with other modifications will allow the adaptation of the model to other situations.

To date, the model has not been coded, punched, and exercised for want of a suitable population dynamics model to drive the mechanisms.

MODEL CONSTRUCTS

Types of Predation

Different authors have implicitly and/or explicitly defined a number of different types of predation (Leopold 1933; Errington 1946; Ricker 1954; Holling 1959b). In general, these categorizations reflect differences in the type of response exhibited by predators to varying levels of prey densities. Even Errington's compensatory versus noncompensatory predation (Errington 1946, 1963) can seemingly be described by the degree of

depressant effect upon the prey population. For example, his noncompensatory

effect of canids on ungulates can be expressed as a compensatory effect by

simply lowering the "threshold-of-security" to the point of near extirpation

of the prey. Consequently, we do not consider predation to be of distinctly

different types, but rather, a matter of degree-of-effect. This can be fully

resolved by varying the functional and numerical responses of specific

predators to changes in prey density.

Factors of Predation

As long ago as 1933, Leopold (1933) postulated five basic factors which

determined the degree of predation upon a particular prey population:

(i)   Predator food preference,

(ii) Prey density,

(iii) Predator density,

(iv) Prey species condition and environmental quality, and

(v)   Abundance of "buffer" species.

Although there has been considerable exploration into the mechanisms

underlying these, no distinctly different factors have since been

elucidated. It is with these five variables then, that we will embark

upon our analysis of predator-prey dynamics.

General Model Notation

We wish now to present a mathematical framework within which to couch

the harvest model. The harvest rate of prey species j by predator species i

is determined by an intrinsic kill rate as modified by the vulnerability of

prey species j to predator species i, and the preference of species i for

species j relative to the other available prey.

First, we present our notation:

Consider a situation where the community consists of m prey species (or functional groups) and n predator species. Now let,

h_i = the total harvest of prey by predator species i per unit time

h_{ij} = the harvest rate of predator species i of prey species j per unit time

such that

$$h_i = \sum_{j=1}^{m} h_{ij}$$

Let k_{ij} = the kill rate in g/cm^2/day of individuals of predator species i on prey species j

pr_{ij} = preference of predator species i for prey species j under "normal" conditions and no consideration of availability

The total harvest rate (h_i) of predator species i (summed over all prey) is expressed by the following relationship:

$$h_i = \sum_{j=1}^{m} h_{ij} = \sum_{j=1}^{m} k_{ij} pr_{ij} \qquad (9)$$

Each of the two factors which contribute to predation in this model will now be treated in some detail with emphasis on how they are related to the five factors of predation presented by Leopold (1933).

Predator Preference pr_{ij}

Since a fundamental property of natural communities is the multi-species array of organisms within a tropic level, it is only natural that a mechanistic

community model should include several categories of predators and prey. For the purposes of this endeavor, the predominant species of each major functional group (e.g., mammal predator or diurnal raptor) are considered individually. Only when the numbers or biomass density are so low as to provide little influence on the model behavior are species lumped into an "other" (functional group) category (Table 1).

Elements of the seasonal food preference matrices (see Fig. 1) represent the proportion of the predator diet contributed by an age-specific prey group under "normal" conditions. "Normal" in this case refers to the averaging out of the confounded "preference" and "availability" values obtained from a broad spectrum of literature. We believe that by utilizing values collected from a range of habitat types and other conditions, the availability component largely cancels out, and the elements do represent a reasonable estimate of preferences under normal availability conditions.

This dietary composition changes, of course, as other factors impinge; and thus these matrices really only provide an initial condition from which the model starts operating. The fact that the dietary composition values do not always sum to 1.0 is a reflection of the predator's consumption of items not included in the matrix (e.g., vegetation, carrion, drug). Thus, the matrix composed of the preference factor pr_{ij} is actually of a submatrix showing all eating and eaten elements, including vegetation and carrion among the eaten and herbivores and microbes among the eaters.

We have chosen to represent the seasonal changes in diet (largely caused by presence-absence phenomena) as a discrete time variable as opposed to a continuous one. First, we are cognizant that abiotic conditions most likely

Table 1. Important predator and prey species densities known to inhabit the shortgrass prairie of Pawnee National Grassland in northeastern Colorado.

Species	Average Annual Density	Wet Weight Biomass $(g \times 10^{-6}/cm^2)$	Source
Pronghorn antelope	$3/mi^2$	5.40	Nagy and Hoover (1971)
White-tailed jackrabbit	$4.8/mi^2$	0.55	Flinders and Hansen (1971)
Black-tailed jackrabbit	$13.2/mi^2$	1.47	Flinders and Hansen (1971)
Cottontail rabbit	$6.4/mi^2$	0.25	Flinders and Hansen (1971)
Ground squirrel	1.0/ha	1.33	Flake (1971)
Kangaroo rat	0.3/ha	no data	
Grasshopper mouse	1.75/ha	1.00	Flake (1971)
Deer mouse	1.25/ha	no data	Flake (1971)
Other small herbivorous mammals	no data	2.00	
Horned larks	1 pr./4 acres	0.407	Giezentanner (1970)
Lark buntings	1 pr./6 acres	0.267	Giezentanner (1970)
Meadowlarks	1 pr./14 acres	0.421	Giezentanner (1970)
Other birds		0.220	
Frogs and toads		0.200	Bauerle (Personal communication)
Grasshoppers	$1/m^2$	5.000	Van Horn (Personal communication)
Coyote	$1.5/mi^2$	0.54	
Skunk			
Badger	$0.5/mi^2$	0.19	
Weasel			
Other mammal predators			
Eagles		0.014	Ryder (1969)
Rough-legged hawk		0.002	Ryder (1969)
Ferruginous hawk		0.001	Ryder (1969)
Marsh hawk		0.001	Ryder (1969)
Other hawks	$1.0 \text{ kg}/56 \text{ mi}^2$	0.001	Ryder (1969)
Owls	40% total diurnal	0.004	Ryder (Personal communication)
Snakes		0.080	Bauerle (Personal communication)

Prey spp. \ Predator spp.	Ground Squirrel	Deer mouse	Grasshopper Mouse	Other Small Mammals	Horned Lark	Lark Bunting	Meadowlark	Other Birds	Coyote	Skunk	Weasel	Eagle	Rough-legged hawk	Ferruginous hawk	Marsh Hawk	Other Hawks	Owls	Snakes
Pronghorn									.05			.05	.00	.02	.00	.00	.00	.00
W-t. Jackrabbit									.15			.07	.04	.02	.01	.02	.00	.00
B-t. jackrabbit									.15			.10	.05	.04	.02	.02	.00	.00
Cottontail									.15	.02		.15	.04	.02	.01	.05	.05	.02
Ground squirrel									.10	.00		.05	.08	.20	.05	.10	.05	.10
Kangaroo rat	.02		.02						.04	.01		.00	.10	.08	.10	.15	.15	.10
Grasshopper mouse	.02		.00						.04	.01		.00	.15	.08	.10	.15	.15	.10
Deer mouse	.02		.02						.04	.01		.00	.15	.08	.10	.15	.15	.10
Other mammal	.02		.02						.10	.01		.10	.15	.08	.10	.15	.15	.10
Horned lark	.02		.02						.01	.01		.01	.00	.05	.08	.01	.02	.04
Lark buntings	.02		.02						.01	.01		.01	.00	.05	.08	.01	.02	.04
Meadowlark	.02		.02						.01	.01		.01	.00	.08	.08	.01	.02	.04
Other birds	.02		.02						.01	.01		.01	.00	.08	.08	.01	.02	.04
Herps			.02						.04	.03		.05	.05	.05	.10	.05	.05	.15
Grasshoppers	.14	.25	.30	.15	.15	.35	.20	.15	.00	.25		.00	.05	.00	.00	.00	.02	.05
Other insects	.18	.25	.40	.15	.15	.35	.50	.35	.00	.25		.00	.02	.00	.00	.00	.02	.05
Snakes	.02		.02						.01	.02		.05	.02	.05	.05	.05	.05	.00
Skunks												.02	.02	.02	.01	.01		.00
Weasels																		

Fig. 1. A generalized Predator preference matrix. Each element of the matrix is an estimate of the proportion of the ith predator species' diet constituted by the jth prey species under "normal" conditions. For example, kangaroo rats (of all ages) are believed to constitute about 2% of the annual average ground squirrel diet. Three important changes need to be made before these data would correspond to those described in the text. (i) This generalized annual diet matrix needs to be replaced by the two seasonal matrices (i.e., summer = past migrant ingress, premigrant egress, and winter). (ii) The species should be substituted for by young and adult age classes. For example, it is unlikely that ground squirrels eat any adult kangaroo rats, but it is probable that they do eat 2% baby kangaroo rats. (iii) Weasels, badgers, and harvester ants should be added in appropriate places as it is now believed all three of these are important species.

stimulate migration and hibernation. But we feel the information presently available about the effects of these conditions is not substantially better than time of year alone as a predictor of these events. Secondly, since our knowledge of exactly when these activities occur is deficient, we felt that describing preference at discrete times (e.g., "before migration" and "after migration") would be adequate for this effort. We look forward to modifying the model to utilize abiotic driving variables as more information becomes available.

Age Classes

Although the rationale for considering at least two age classes (immature and adult) per species was briefly mentioned in the introduction, we will be more explicit here. Evidence suggests that, in many cases, the infant and juvenile age classes suffer much higher mortality rates than do adults. Much of this is mediated through selective predation (Errington 1943, 1946; Crisler 1956; Schaller 1967; Hornocker 1970). Other justifications include the sometimes striking differences in food habits, energy budgets, habitat requirements, and behavioral attributes, all of which affect the predator-prey relationships (Holling 1965).

Although it has also been observed on several occasions that predation is sex- as well as age-selective, we feel it is infeasible to include separate sex classes at this time.

Prey Switching and Buffer Species

Although the net worth of "buffer species" is frequently puzzling to resource managers (Leopold 1933), their value in providing alternative food

sources for existing predator populations has long been understood. Thus, in the context used here, a buffer species is any prey species which may be utilized for sustenance by predators whose "normal" or "more preferred" prey has become unavailable. The act of changing diets from largely one prey species to another constitutes a "switch." Thus, switching from one prey species to another plays an important role in areas where prey hibernation and migration are important phenomena.

Murdoch (1969) uses a slightly more rigorous definition for "switch" and concludes that, "in the weak-preference case no switch would occur in nature except where there is an opportunity for predators to become trained to the abundant species." Nonetheless, it is the case that predators frequently reflect greater percentages of an item in their diet than would be predicted from simple abundance relationships. To allow for this, we have incorporated a dual-faceted switching function into our harvest model. First, switching from a dietary item is assumed to occur if the relative density of a particular prey species falls below some threshold level. Thus, if the biomass density (b_j) of prey species j, relative to the sum of all other prey species, falls below the threshold value t_{ij}^1, the preference for species j is immediately set at .01. If

$$\frac{b_j}{\sum\limits_{j=1}^{m} b_j} < t_{ij}^1$$

then $\quad pr_{ij} = .01 \quad$ and $\quad pr_{ik} = pr_{ik} + pr_{ij} \times \dfrac{b_k}{\sum\limits_{j=1}^{m} b_j}$

for all $k \neq j$ with $pr_{ik} > 0$.

In the above case, t_{ij}^1 represents a lower threshold value for switching away from a prey species and, in a sense approximates Errington's "threshold of security." The preference pr_{ij} is seen to be distributed among the other m-1 prey species in proportion to their biomass densities b_j.

Similarly, if one species' density should rise above some level t_{ij}^2, relative to all other species, the predator with the highest preference value for it will switch almost completely to it. Thus, if

$$\frac{b_j}{\sum\limits_{j=1}^{m} b_j} > t_{ij}^2$$

and $\quad pr_{ij} > .01 \quad$ then pr_{ij} becomes .95 and $\quad pr_{ik} = \frac{.05(b_k)}{(\Sigma b_j - b_j)}$

for all $k \neq j$ for which $pr_{ij} > .01$. It will be seen that, in this case, the remaining 5% of the predator's diet is distributed among the extant species according to their relative biomass densities. In this case, t_{ij}^2 is analogous to a saturation density above which predators switch almost exclusively to the high density prey item.

Predator Kill Rate k_{ij} as a Function of Prey Density

It is commonly observed that individuals of a predator species may change their consumption rates as a function of prey density. Although it is conceivable that certain predators might consume less per unit time as the prey density increases, in general, individual predators increase the amount consumed per unit time as a function of increased prey density. Solomon (1949) coined the term "functional response" for this phenomenon, and it

has since been a topic of considerable interest (Hassell 1966; Holling 1959b, 1961, 1965).

Conceptually different, but mechanistically similar, is the excessive killing response of many raptors and mustelid mammals (the weasel family). Birds of prey have often been reported to kill more than could be immediately eaten (Craighead and Craighead 1956, Tordoff 1955), and not infrequently, raptors have been reported to catch or hoard prey items (Wallace 1950; Sparrow 1970). Similarly, the proverbial fox-in-the-chicken-coop phenomenon apparently carries over into natural mammal populations, at least in mustelids (Errington 1943; G. Heidt, personal communication). Of course, this response is common to parasites, and Holling (1959b) cites several examples of it occurring with invertebrate predators.

Holling (1961) has pursued this topic in depth. He describes three general forms of response curves of predator kill rate to prey density, one of which is applicable to vertebrate predators. The form of this curve is very similar to the classic sigmoid growth curve. Leopold (1933) also predicted the response curve would be of this general form, and other workers have alluded to a similar function (Hornocker 1970).

We interpret the mechanisms underlying the functional response as follows: at low prey densities a number of factors may limit the kill rate. For example, the individual prey may be so secure in their environment that the predators simply cannot capture a substantial number of them. Similarly, at low densities, the prey may be so scarce that the predators cannot afford to hunt for them per se (because of time and energy constraints). Therefore, predation becomes a function of random encounter, and when the density of prey is low, the number of encounters is also low. There are other plausible interpretations as well.

As the prey density increases, a number of phenomena probably occur: (i) the number of random encounters between predator and prey most likely increases; (ii) the prey may be less secure in their environment and thus be forced to move about more than normal; and (iii) they may have access to less protective cover.

The number of prey killed continues to increase as a function of prey density until a number of factors mitigate against further increase: (i) a level of satiety must be attained by most predators, above which they will kill few if any prey. That is, they simply stop hunting; (ii) similarly, there is only so much hunting and so much handling that can be done within normal time and energy limitations. This provides the upper limit above which no increased prey density can have an effect; and (iii) finally, even those predators which continue to kill prey above some level of satiety can only kill so many prey per unit time under natural conditions. It, therefore, seems that, under no conditions, can predators continue to increase the rate of killing indefinitely.

Holling (1961) considers five factors to be important components of the functional response curve, i.e., time of exposure, searching rate, handling time, hunger level, and group stimulation. Although we do not believe that all must be operative in all cases, there is little evidence to negate the validity of the overall response curve form.

Prey Vulnerability vu_{ij}

For a number of reasons, it seems that an "effective" prey density exists which is greatly affected by the amount and type of cover as well as prey density per se. Thus, a number of writers have employed the term

"vulnerability" to express the combined effect of density and several other
factors which reduce the security of prey populations (Errington 1943, 1946;
Leopold 1933; Hornocker 1970; Craighead and Craighead 1956). We denote this
vulnerability function by vu_{ij}. Craighead and Craighead (1956) concluded
that the "vulnerability" of a species was approximately 70% determined by
prey density and about 30% determined by prey "risk." We believe there is
merit in this philosophy. Although the only factors we explicitly consider
under prey "risk" are cover density, others, such as climatic conditions,
are undoubtedly involved.

For lack of better information, we have let 70% of our vulnerability
function be determined by prey density per se, and the remaining 30% by
habitat conditions (i.e., standing crop, species composition, and spatial
heterogeneity). Further, we have tacitly equated our vulnerability function
with the more renowned "functional response" as it incorporates the five
factors considered important by Holling (1961). Thus, we have functionally
related kill rates to vulnerability rather than to prey density. This was
done because it was felt that the predator's functional response was to
what he could catch, not necessarily how many were there. Since vulnerability
is largely a function of prey density, kill rate was indirectly related to
prey density in the model.

Let $vu_{ij} = vu^1_{ij} \times vu^2_{ij}$, where vu^1_{ij} is a function of prey density (see Fig.
2) and vu^2_{ij} is a function of cover. The population density of prey species j
is given by b_j and appears on the x axis in Fig. 2.

vu^3_{ij} is an arc tangent function of b_j. Two threshold points, b_j^a and b_j^b,
depending upon prey species j (and predator species i), are chosen to reflect
the prey levels for 5% density above minimum vulnerability and 95% vulnerability,
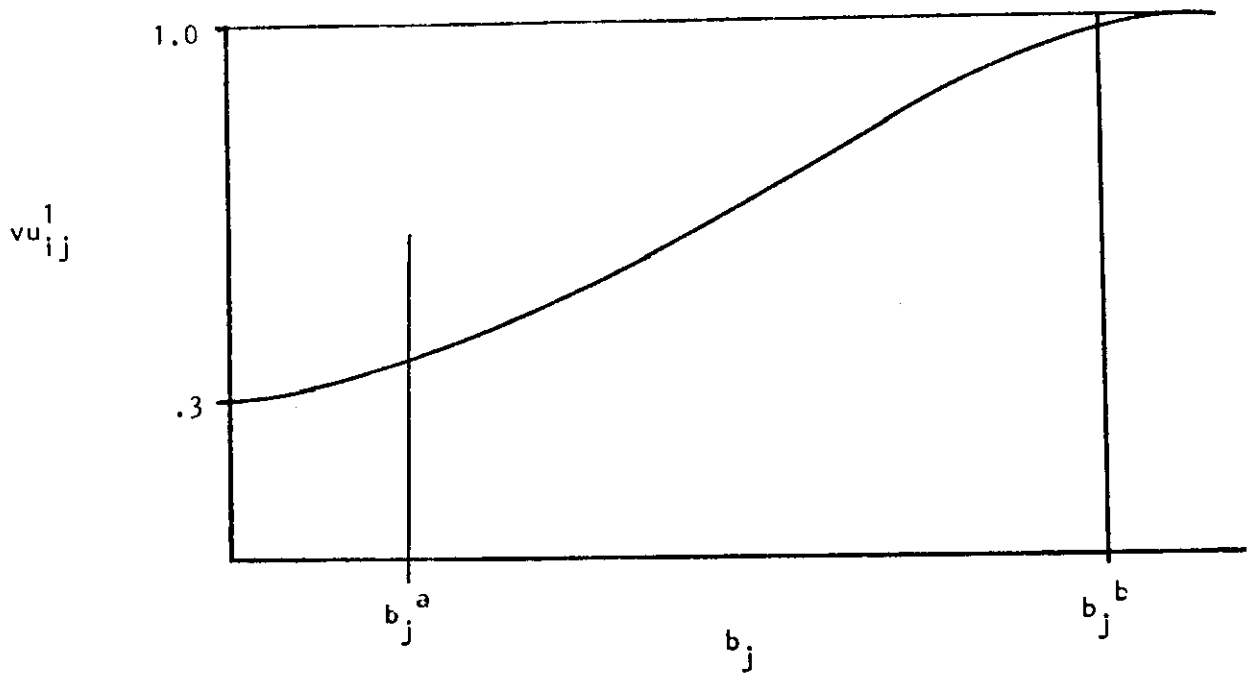
Fig. 2. Prey vulnerability (vu^1_{ij}) as a function of prey density (b_j).

respectively. Minimum vulnerability is .3 so that 70% of total vulnerability vu_{ij} is mediated through prey density. These values, b_j^a and b_j^b, control the shape of the curve for vu_{ij}^1.

vu_{ij}^2 is a function of cover given by a cover index C (Fig. 3). Fig. 3 is also an arc tangent curve, the shape being determined by the vulnerability at threshold levels of cover C^a and C^b. vu_{ij}^2 varies between .7 and 1.

As mentioned earlier, approximately 30% of the total vulnerability of a species to a particular predator (vu_{ij}) is due to cover conditions, while approximately 70% of vu_{ij} is due to prey density.

vu_{ij} takes values between .21 and 1. This value for minimum vulnerability is somewhat arbitrary. It is greater than zero because it was felt that, even under low densities and good cover, the prey is somewhat vulnerable. They are difficult to catch, however, and this is reflected in the preference matrix where scarce species are very low in preference.

In examining Fig. 2 and 3, it will be noticed that prey vulnerability increases with prey density and decreases with cover density. As mentioned above, the shapes of the curves depend on the values for vu_{ij}^1 chosen at b_j^a and b_j^b and the values of vu_{ij}^2 chosen at C^a and C^b. These depend upon the *relative abilities* of predator i to capture prey j under varying cover conditions and varying prey densities.

Kill Rates and Vulnerability

Let us divide kill rate k_{ij} into two parts: k_{ij}^1 will be the functional response to prey density through prey vulnerability vu_{ij}; and k_{ij}^2 will be the part responding to predator density. Then
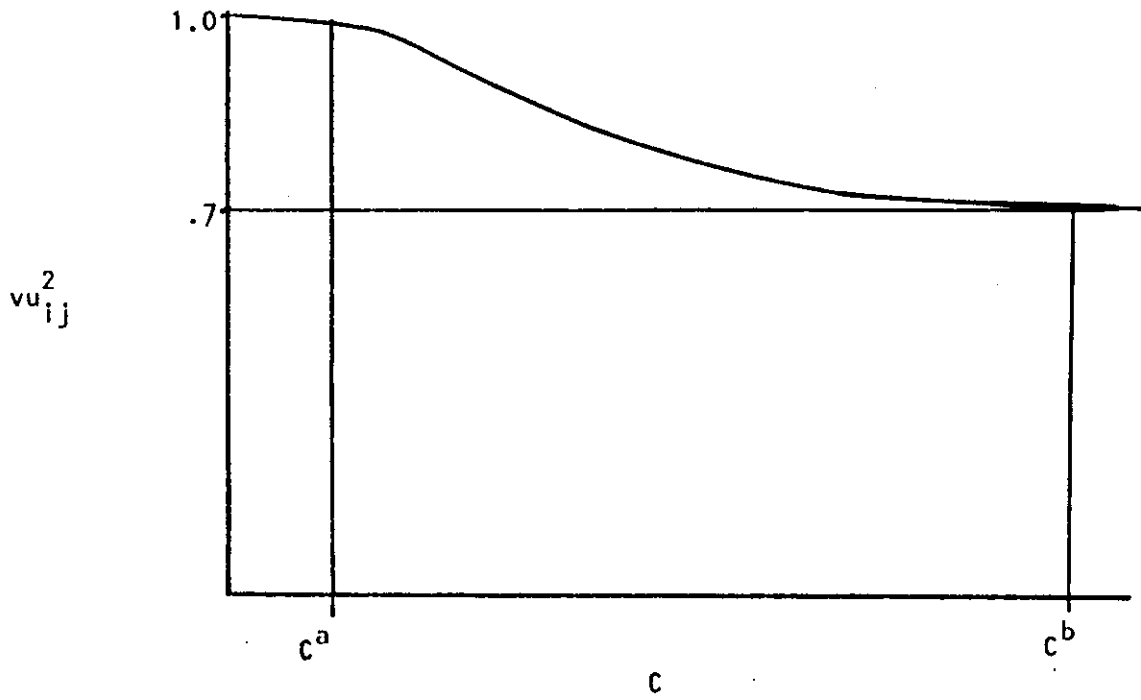
Fig. 3. Prey vulnerability (vu^2_{ij}) as a function of cover (C).

$$k_{ij} = k_{ij}^1 \times k_{ij}^2$$

k_{ij}^1, as a function of prey vulnerability vu_{ij}, is given in Fig. 4.

The relationship in Fig. 4 may be represented by an arc tangent function, truncated at $vu_{ij} = 1$ so that the maximum possible kill rate $k_{ij}(max)$ occurs when the prey is completely vulnerable (i.e., $k_{ij}(max)$ occurs when $vu_{ij} = 1$).

At $vu_{ij} = .2$, the minimum value of vu_{ij} in the present model, the minimum kill rate $k_{ij}(min)$ is obtained.

Predator Density and Kill Rate k_{ij}^2

Although there is relatively little field data regarding the effect of predator density upon the individual kill rate, Holling (1961) summarizes what is known and postulates a general form for the function. Since we have no evidence to the contrary, we have incorporated a predator-density dependent predation function of similar form.

k_{ij}^2, the predator density factor, will be a number between .9 and 1. This constrains predator density to have an effect on no more than 10% of the total kill rate. The relationship is shown in Fig. 5. Here, b_i represents the population density of predator i.

The shape of this curve in Fig. 5 is influenced by threshold values b_i^a and b_i^b. b_i^a is the predator density level below which predator density effectively does not affect kill rates, and b_i^b is the predator density above which further density increase no longer reduces total kill.

Total kill rate k_{ij} may take values between $k_{ij}(max)$ and $.9\ k_{ij}(min)$, depending upon the values of k_{ij}^1 and k_{ij}^2.
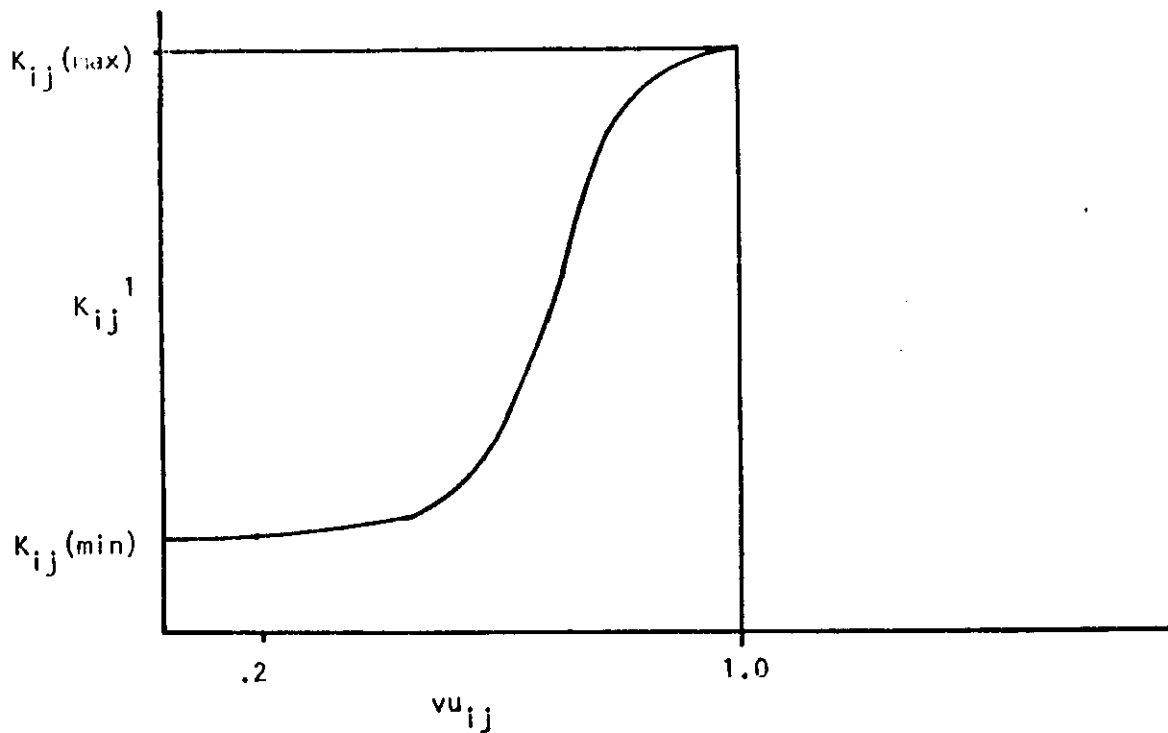
Fig. 4. Relationship between kill rate (k^1_{ij}) and vulnerability (vu_{ij}).
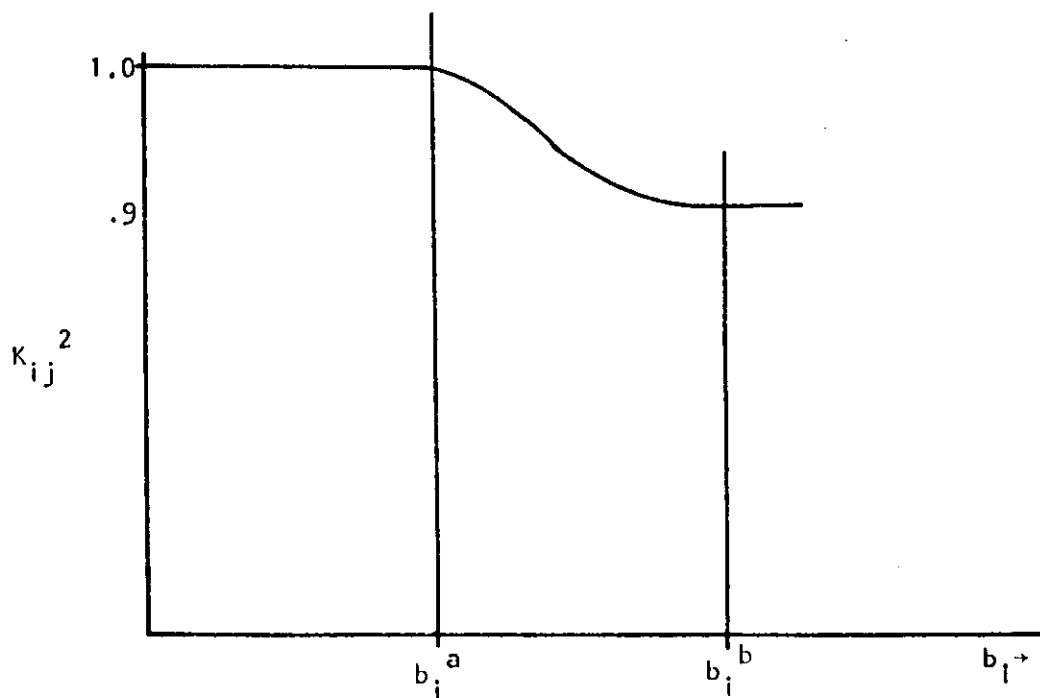

Fig. 5. Relationship between predator density b_i and k^2_{ij}.

We recognize that kill rates also depend a great deal upon predator voracity. However, consideration of this factor would lead to complex considerations of predator energy dynamics as was done in the model of Lassiter and Hayne (1971). We feel that this would lead us too far afield from our predation model and therefore have considered animals of average hunger level, satiation occurring only in cases of high prey densities.

Predator Density Related to Prey Density

Although this is not necessarily the case, predator density is frequently greatly affected by prey density. The sometimes rapid changes in predator density following prey outbreaks, or even more mild prey density increases, have been termed the "numerical response" to prey density (Solomon 1949). This response can only be mediated through one or more of three basic mechanisms: (i) a relatively rapid ingress of predators onto the area, (ii) a somewhat slower increase as a result of decreased mortality rates, and (iii) a yet slower response resulting from increased reproduction. There is good evidence to indicate that all three mechanisms are operative under natural conditions.

It appears from a broad spectrum of literature that there are frequently two classes of predators: (i) the resident or territorial, and (ii) the errant or transient individuals. Thus, Sanders and Knight (1968) report on resident and errant predators controlling aphid populations; Pitelka, Tomich, and Treickel (1955) describe the temporary presence of jaegers on the arctic tundra, and Schaller (1967) and Hornocker (1970) describe territorial vs. transient tigers and African and American lions, respectively. From this it seems that, in many cases, there is a reserve of predators which can move onto

an area of prey abundance and provide a rather quick response to increases in

prey density. But the longer-term response of increasing predator numbers by

enhanced birth and death rates may also provide an essential mechanism. Thus,

Pearson (1966) recorded a 47-fold increase in mammalian predators as the

density of prey increased, and Clark and Wagner (1969) concluded that both the

mean litter size and fecundity of female coyotes increased concurrently with

increased jackrabbit densities. A copious literature indicates that, not

only is the clutch size of arctic raptors significantly greater during years

of high lemming density, but that in some cases breeding is completely deferred

until a lemming "high" (Pitelka et al. 1955).

All three of these mechanisms are feedback responses to the underlying

population dynamics model and need not be considered further here. Suffice

it to say, all three are triggered by prey density and involve varying degrees

of lag time. For example, the shortest lag involved with the mammalian birth

response is several months, from fall to the following spring.

Factors Not Considered in This Model

As mentioned earlier, energy dynamics of both predator and prey are not

considered here as average animals are chosen. For example, all prey density

values fall below the level t_{ij}^1 to make hunting of them worthwhile and if no

alternate food is abundant, starvation will set in. This would be added

through the animal death rates.

Interaction effects between predator species and between prey species

was not considered, but would be incorporated into birth and death rates.

Cover density C might be expanded to include type of cover, including snow

cover. The kill rate function might be further explored and expanded to

include predator energetics considerations.

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