SPATIAL HETEROGENEITY AND THE STABILITY OF A PREDATOR-PREY LINK

A Dissertation
for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
Philip Haney Crowley
1975

This is to certify that the

thesis entitled

SPATIAL HETEROGENEITY AND THE STABILITY

OF A PREDATOR-PREY LINK

presented by

Philip Haney Crowley

has been accepted towards fulfillment
of the requirements for

Ph. D. degree in Zoology

Donald J Hall
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Date May 23, 1975

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S → 065

W → 357

ABSTRACT

SPATIAL HETEROGENEITY AND THE STABILITY OF A PREDATOR-PREY LINK

By

Philip Haney Crowley

Heterogeneity of spatial structure can stabilize a predator-prey link: Let the stability of an ecosystem or of a predator-prey interaction be its ability to absorb perturbations without extinction or escape of the prey population. Then the presence of saturable refuge space in the system makes stable, predator-limited prey equilibria possible by displacing the functional response curve toward higher prey densities. And if the time scale of prey increase is less than or about equal to the time scale of the predator's numerical response, then stability can be operationalized and calculated directly from parameter values of a mathematical model.

An analysis of the effects of stability of adjusting the model's parameters shows that reducing the chance of prey extinction and the chance of escape from predator regulation are often incompatible goals. For example, increasing the amount of refuge space in a system decreases the chance of prey extinction but increases the chance of their escape; similarly, increasing intraspecific interference among predators decreases the chance of extinction and increases the chance of escape. These results and those for other parameters can be quantified for specific environmental conditions and control measures, providing a means of predicting and policing the behavior of spatially-distributed ecosystems in stochastic environments.

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1975

ACKNOWLEDGMENTS

I thank the members of my Guidance Committee, D. J. Hall, Chairman, D. L. Beaver, W. E. Cooper, and E. D. Goodman for advice and encouragement during this project. J. E. Breck and J. A. Van Sickle contributed several helpful suggestions; D. M. Johnson, supplied some data and an unpublished graph; and Bodil Burke, who sustained a tender fingertip, exhibited flawless predatory behavior.

I gratefully acknowledge financial support from NSF-RANN Grant GI-20 to H. E. Koenig and W. E. Cooper and from a Zoology Department Teaching Assistantship.

All other essential forms of sustenance came from my wife Lillie: as typist, bread-winner, mathematical consultant, and counselor, she is here on every page.

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LIST OF SYMBOLS

Functions and variables are capitalized (except t); parameters are lower case.

a	rate of successful attack (outside), volume)predator-time)$^{-1}$
$\underline{a}$	rate of successful attack inside, volume(predator-time)$^{-1}$
a*	rate of encountering predators, volume(predator-time)$^{-1}$
b	handling time (outside), predator-time prey^{-1}
$\underline{b}$	handling time inside, predator-time prey^{-1}
b*	interference time, time
C	conformability, an ordered pair of differences between the magnitudes of a parameter and each of the boundaries of the conformable region
$\mathcal{C}$	conformable region, the interval of parameter magnitudes within which a stable, predator-limied prey density equilibrium can exist
c	Allee coefficient, the prey density above which the per capita prey increase rate becomes positive, prey volume^{-1}
d	radius of the large discs used in the disc experiments, cm
d'	radius of the small discs used in the disc experiments, cm
E	elasticity, an ordered pair of differences between the magnitudes of the stable (predator-limited) prey density and escape and extinction thresholds, prey volume^{-1}
$\mathcal{E}$	elastic region, the interval of prey densities within which a stable, predator-limited prey density equilibrium can exist, prey volume^{-1}
e	exchange rate of prey between inside and outside, time^{-1}
F	functional response (outside), prey (predator-time)$^{-1}$

$\underline{\mathrm{F}}$	functional response inside, prey $(\text{predator-time})^{-1}$
F*	predators encountered per predator-time, time^{-1}
f	effective fingertip radius from the disc experiments, cm
G	dummy variable for prey density, prey volume^{-1}
g	tap rate in the disc experiments, taps min^{-1}
H	prey density, prey volume^{-1}
$\underline{\underline{\mathrm{H}}}$	positive prey density at which inside and outside functional response curves intersect, prey volume^{-1}
$\underset{\sim}{\mathrm{H}}$	minimum prey density just above which a stable, predator-limited prey density equilibrium can exist, prey volume^{-1}
$\tilde{\mathrm{H}}$	maximum prey density just below which a stable, predator-limited prey density equilibrium can exist, prey volume^{-1}
$\underline{\mathrm{H}}$	prey density inside, prey volume^{-1}
$\bar{\mathrm{H}}$	prey density outside, prey volume^{-1}
H	equilibrium prey density, prey volume^{-1}
$\check{H}$	stable equilibrium prey density, prey volume^{-1}
$\overleftarrow{H}$	extinction threshold, lower unstable prey density equilibrium, prey volume^{-1}
$\overrightarrow{H}$	escape threshold, upper unstable prey density equilibrium, prey volume^{-1}
h	refuge capacity, prey volume^{-1}
i	an index, dimensionless
j	an index, dimensionless
k,k',k"	carrying capacity of a universe, prey volume^{-1}
m	an index, dimensionless
N	time scale of the numerical response, time
n	number of prey populations in the system

p	predator density, predators volume^{-1}
$\bar{p}$	number of predators minus one, divided by the universe volume, predators volume^{-1}
Q	refuge occupancy quotient, a function of the exchange and per capita increase rates, dimensionless
q	refuge occupancy quotient (when the exchange rate greatly exceeds the per capita increase rate), dimensionless
R	per capita increase rate of prey excluding predation effects, a function of prey density, time^{-1}
$\mathcal{R}$	time scale of prey increase, time
r	maximum per capita increase rate of prey, time^{-1}
$\overleftarrow{r/p}$	minimum r/p just above which a stable, predator-limited equilibrium prey density can exist, volume (predator-time)$^{-1}$
$\overrightarrow{r/p}$	maximum r/p just above which a stable, predator-limited equilibrium prey density can exist, volume (predator-time)$^{-1}$
s	sigmoid coefficient (outside), prey volume^{-1}
$\underline{s}$	sigmoid coefficient inside, prey volume^{-1}
T	stability topography, a function of prey density, prey^{2}volume^{-2}time^{-1}
t	time
u	volume (area) of the universe
v	universe volume: outside volume, dimensionless
$\underline{v}$	universe volume: inside volume, dimensionless

It may be that, in some way at present unknown, the heterogeneity of environments in space and time can independently bring about natural control, but I cannot see a logical basis for this and shall remain unconvinced unless someone can demonstrate how it works out (or at least, for a start, how it could do so).

M. E. Solomon, 1957

INTRODUCTION

Densities of predator and prey populations in a flask or on a tray of oranges fluctuate violently (Gause, 1934; Huffaker, 1958), but densities of the same populations in natural ecosystems may remain relatively constant. Such observations have suggested to many ecologists that trophic complexity is somehow responsible for the stability of ecological systems, a view currently being challenged by some rather elegant theory. According to May (1973), Maynard Smith (1974), and others, biologically complex systems should be *less* stable than simpler ones, often strikingly so. The question has now become, "Where is all that natural stability coming from?"

Smith (1972) catalogued major stability-related influences on ecosystems and demonstrated the critical stabilizing role of *spatial heterogeneity* (patchiness in space) (also see Holling, 1968). Unfortunately, however, little progress has been made in *quantifying* spatial heterogeneity, though Smith's work and that of Levin and Paine (1974) appear promising. And even stability itself has yet to be quantified in an ecologically general and empirically useful way, as attested by the disparate stability notions of MacArthur (1955), Margalef (1969), Lewontin (1969), Smith (1972), Holling (1973), and many others.

This paper presents an attempt to operationalize the concepts of stability and spatial heterogeneity in order to help explain and

measure the behavior of ecosystems distributed in space. Three concepts central to this analysis are introduced first: stability, spatial heterogeneity, and the responses of predators to prey and predator densities. Next, the effects of one kind of spatial heterogeneity on the stability of a predator-prey link are analyzed theoretically, and the theory is extended to two more complex cases. The discussion then focuses briefly on three case studies from the literature, considers stabilizing responses of predators, and outlines applications to pest and game management. Finally, an appendix presents some empirical support for a theoretical result.

Stability

In this paper, stability is taken to be an *inherent property* of an ecosystem and of its constituent populations (i.e., a tendency in response to perturbation), rather than an "*emergent property*" at the ecosystem level of organization or the *observed behavior* of the system through time (i.e., persistence or constancy). It is assumed that ecosystem-level stability simply integrates the characteristics of the constituent population-level predator-prey interactions (Smith, 1972; May, 1973; Maynard Smith, 1974). From this perspective, stability can initially be analyzed within single predator-prey links, with biologically and spatially complex cases elaborated later. Interspecific competition and multispecies predator-prey interactions are deferred for consideration elsewhere.

Following a suggestion by May (1974a) and a similar approach in Anderson (1974), I distinguish two fundamental kinds of stability: elasticity and conformability. *Elasticity* is a measure of the tendency for perturbations of state variables (functions of time reflecting the system's history, such as prey density) to be damped (cf. "Lyapunov stability" in Rosen, 1970). Conformability is a measure of the tendency for elasticity to be maintained in the face of perturbations of parameters (coefficients independent of the system's dynamics, such as maximum prey per capita increase rate). Quick but drastic changes of environment can "shock" the state variables directly, whereas more subtle but longer-lasting changes of environment will "shift" the parameters of the system (see Takahashi, 1964). If the elasticity and the conformability of an ecosystem are operationally defined and appropriately quantified, then the response of that system to "shocks" and "shifts" can be predicted.

Spatial Heterogeneity (SH)

Biological populations almost always assume clumped (under-dispersed) distributions in physical space in response to one or both of two kinds of spatial heterogeneity:

1. stochastic SH, in which patchiness arises from environmental or demographic stochasticity, and
2. structural SH, in which patchiness is imposed on the organisms by the deterministic structure of the environment (cf. Levin, 1974).

The rocky intertidal zone along the coast of Washington State studied by Paine (1966, 1969) and his students nicely exemplifies stochastic SH (though structural SH is certainly also present): barnacles, mussels, starfish, and other invertebrates occupy the tidal rocks in transient patterns that slowly shift in response to competition, predation, and

the gouging action of logs and waves. At any given place within the intertidal, the abundance of each population depends much more strongly on such stochastic events than on local physical structure. Other systems featuring predominantly stochastic SH include those in Huffaker (1958), Huffaker et al. (1963), Pimentel et al. (1963), Luckinbill (1973, 1974), Hardman and Turnbull (1974), and several in Levin and Paine (1974).

The most familiar example of structural SH must be the *Paramecium*-*Didinium* flask systems of Gause (1934), in which the oatmeal sediment at the flask bottoms protected the paramecium from its predator. Other structural SH-dominated systems are found in Errington (1946), Smith (1972), van den Ende (1973), Crombie (1946), Huffaker and Kennett (1956), and Johnson (1973); the last three of these provide the case studies considered later in this paper. Structural SH, with physical structure of paramount biological importance, is the major focus of this analysis; in particular, the implications of including *refuges* in a predator-prey universe are examined in detail.

The term "refuge" is used here in a broad sense to designate structurally definable regions of space within which predators harvest prey less effectively (cf. "relative refuge" of Huffaker, 1958 and Smith, 1972). In turn, this reduced effectiveness of predators must generate a strong selection pressure for prey to occupy such regions preferentially (Tullock, 1970; Smith, 1972). In Errington's mink-muskrat system, for example, muskrats with lodges established in ponds or marshes are nearly (not completely) invulnerable to mink predators (Errington, 1946). Similarly, in van den Ende's chemostat, bacteria

attached to the vessel walls largely (but not entirely) escaped the swimming Tetrahymena population and avoided the outflow; moreover, after only a few days the bacteria in the reactor had adapted to the refuge by failing to synthesize polysaccharide capsules, facilitating adherence to solid surfaces (van den Ende, 1973). Demonstrating the stability effects of such refuges in predator-prey interactions depends on an understanding of the responses of predators.

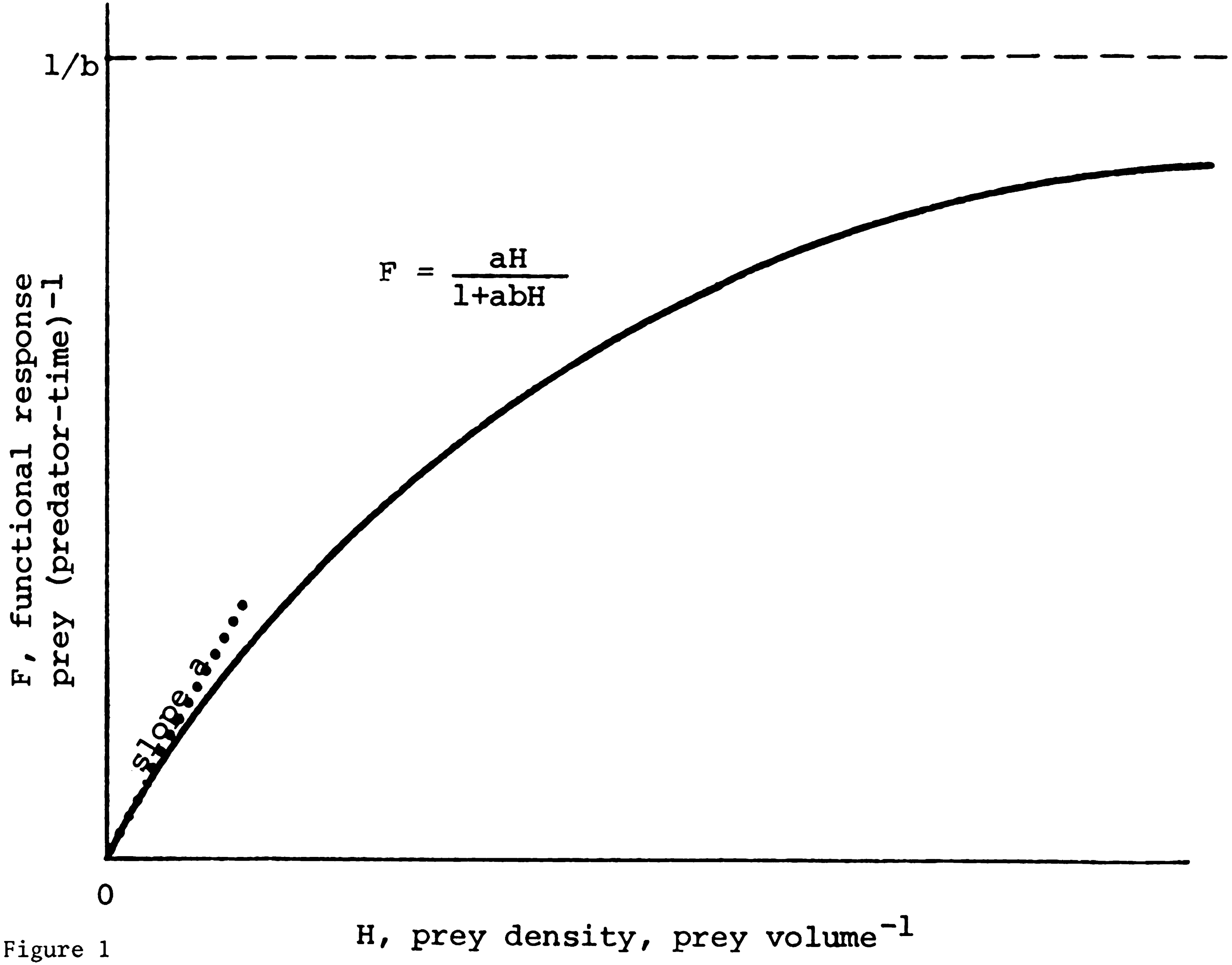
Responses to Predators to Prey and Predator Densities

"Predator" is another term broadly applied here, denoting at least carnivores, insect parasitoids, and some herbivores (e.g., seed eaters). Since this analysis emphasizes instantaneous responses and the prediction of dynamics from the magnitudes of equilibria, many important distinctions between parasitoids and classical predators (see Royama, 1971) can be ignored to preserve "perspective" (Huffaker, 1971).

Predators can respond to changes in the density of their prey by changing their own density, a numerical response, or by changing the rate at which they kill prey, a functional response (Solomon, 1949). The numerical response of predators to prey increase may include reproduction or aggregation or both, but such numerical changes can be expressed only after a time lag. Although the (behavioral) lag in aggregation is probably often negligible (e.g., hawks vs. field mice), the (physiological-developmental) reproductive lag can be quite long (e.g., fish vs. zooplankton); the stability properties of models that track predator density without a reproductive lag, such as the "pathologically simple" Lotka-Volterra equations, are probably only mathematical artifacts (see May, 1973; Nicholson, 1955). Furthermore, the relation in nature between prey density and the resulting predator density is invariably quite complex and lacks a truly general form (Readshaw, 1973). So both mathematical intractability and biological complexity impede the development of a sufficiently broad, quantitative model incorporating the reproductive numerical response.

Many predators either have negligibly small or extremely slow numerical responses relative to the increase rates of their prey (e.g., planktivorous fish, insectivorous birds), or they are limited by other resources (e.g., some territorial birds and mammals). The stability of these interactions and others considered below depends on the functional response (Takahashi, 1964; Solomon, 1964), a phenomenon thoroughly investigated both theoretically and experimentally by Holling (1959a, 1959b, 1961, 1965, 1966). Holling classifies the functional response to prey density--the killing rate per predator as a function of prey density--into three main types: *type 1,* a linear rise of the functional response with prey density to a plateau; *type 2,* a negatively accelerated, monotonically increasing response, rising asymptotically to a maximum; and *type 3,* a sigmoid functional response, featuring initial positive acceleration and an asymptotic rise to a plateau. Type 1 has never been convincingly demonstrated empirically and is at best uncommon. The vast majority of laboratory functional response data resemble type 2 and fit the theoretical curve in Figure 1, particularly data from invertebrate predators and parasitoids and from vertebrates in the absence of alternate prey (Holling, 1965). There are also considerable data resembling type 3 for both vertebrates (e.g., Holling, 1959a) and invertebrates (e.g., Lawton et al., 1974), usually but not invariably

Figure 1. The type 2 functional response. "a" is the rate of successful attack, volume (predator-time)$^{-1}$; "H" is prey density, prey volume^{-1}; and "F" is the functional response, prey (predator-time)$^{-1}$. In deriving an equation analogous to (1), Holling (1959a) first reasoned that if the predator searches randomly, the rate of encountering prey should be proportional to prey density; that is, $F = aH$. But for each prey actually pursued and captured, an increment of time b is no longer available for search, reducing the effective rate of successful attack by the factor $(1-bF)$. Thus if "a" and "b" are independent of prey density, then $F = a(1-bF)H$, or $F = aH/(1+abH)$. Any possible social interactions, hunger, learning, or prey exploitation effects are ignored.



$$F = \frac{aH}{1+abH} \qquad (1)$$

Figure 1

with alternate prey present, yet no simple analytical expression is available in the literature to fit them. An equation derived for this purpose from the type 2 equation is illustrated in Figure 2; but since the new equation does not explicitly incorporate the dynamics of learning or of any of the other behavioral factors commonly supposed to cause this sigmoid shape (see Krebs, 1973), it will only be used to suggest the general stability implications of the type 3 functional response.

Thus, in striking contrast to the numerical response, the functional response of predators exhibits little or no time lag and occurs mainly in one or two characteristic forms. Furthermore, all parameters of the equation describing the most common form can be obtained independently of the functional response data themselves. Whenever the functional response dominates predator-prey dynamics, these important features can greatly facilitate an _a_ _priori_ stability analysis of the interaction.

Predators may also exhibit a functional response to _predator_ density. Though social facilitation may be significant in some cases, the predominant non-linear consequence of increasing predator densities is interference. The theoretical derivation below includes a cursory analysis of the impact of interference on stability in a spatially heterogeneous universe.

The developmental reponse of predators (Murdoch, 1971), a largely unexplored phenomenon of possible limited importance for stability, is ignored in this paper.

Figure 2. The type 3 functional response. "s" is the sigmoid coefficient, prey volume^{-1}. If the rate of successful attack "a" from equation (1) is expanded into an increasing asymptotic function of prey density, then the new equation mimics the effects of learning (and forgetting) on the functional response; that is, let $a' = aH/(s+H)$, where "s" is the prey density at which the rate of successful attack is half its maximum value, an analogue of the Michaelis constant in enzyme kinetics. Now substituting back into equation (1), $F = a'H/(1+a'bH) = aH^2/(s+H+abH^2)$, equation (2). Notice that when $s = 0$, equation (1) is recovered.

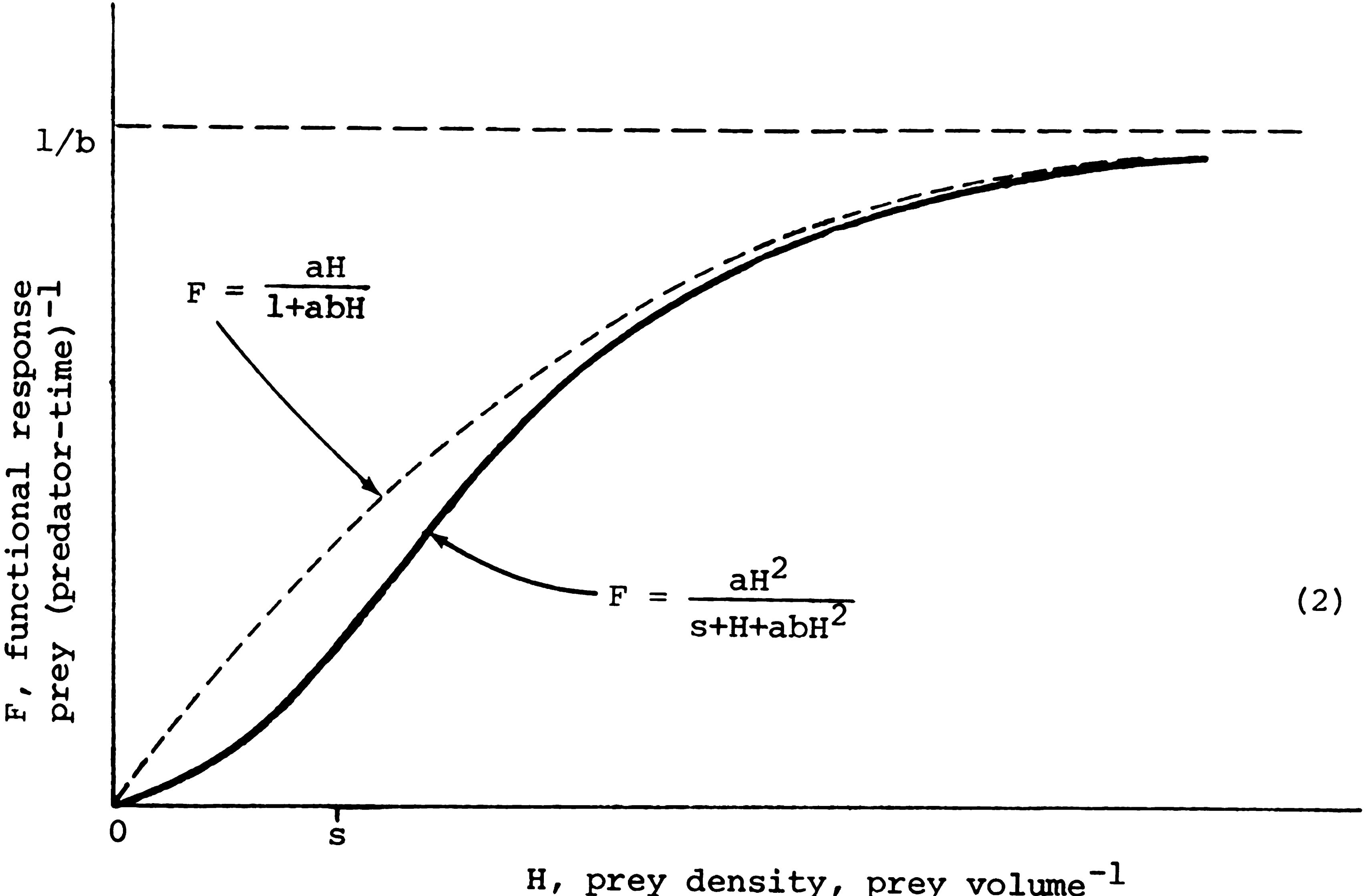

1/b
F, functional response
prey (predator-time)$^{-1}$
$F = \frac{aH}{1+abH}$
$F = \frac{aH^2}{s+H+abH^2}$
(2)
0
s
H, prey density, prey volume^{-1}

Figure 2

STRUCTURAL SPATIAL HETEROGENEITY AND STABILITY:
DERIVATION AND ANALYSIS

The Functional Response in a Universe Containing Refuge Space

Consider a conceptual universe composed of two types of space: refuge space ("inside") and non-refuge space ("outside"). Ignore temporarily the question of how these spaces are distributed--as many small patches of refuge and non-refuge or as a few larger patches. And suppose initially that the refuge space is a "perfect refuge," that is, that (1) predators cannot kill prey inside and (2) prey stay inside if there is room for them. Now if the perfect refuge has a capacity of h prey density units, then the functional response of predators in this universe (but outside the refuge space) must be displaced h units to the right along the prey density axis from its corresponding values in a refuge-free universe. For type 2 predators in particular, Figure 3 replaces Figure 1.

Now the two restrictions that made the refuge "perfect" can be relaxed: Distinguish "$\underline{a}$", the rate of successful attack for predators hunting inside, from "a", here restricted to the rate of successful attack for predators hunting outside, such that $0 \le \underline{a} \le a$; and let "q" represent the refuge occupancy quotient, the fraction of prey occupying the refuge space when $H \ll h$, with the restriction that $0 \le q \le 1$. (Thus for a perfect refuge, $\underline{a} = 0$ and $q = 1$.) Then in the general case, with

Figure 3. The type 2 functional response of predators hunting outside the refuge space in a universe containing a perfect refuge. "a" is now the rate of successful attack outside, volume (predator-time)$^{-1}$; "b" is now the handling time outside, predator-time prey^{-1}; "h" is refuge capacity, prey volume^{-1}; and "v" is the dimensionless ratio universe volume:outside volume, transforming overall prey densities into prey densities outside the refuge space.

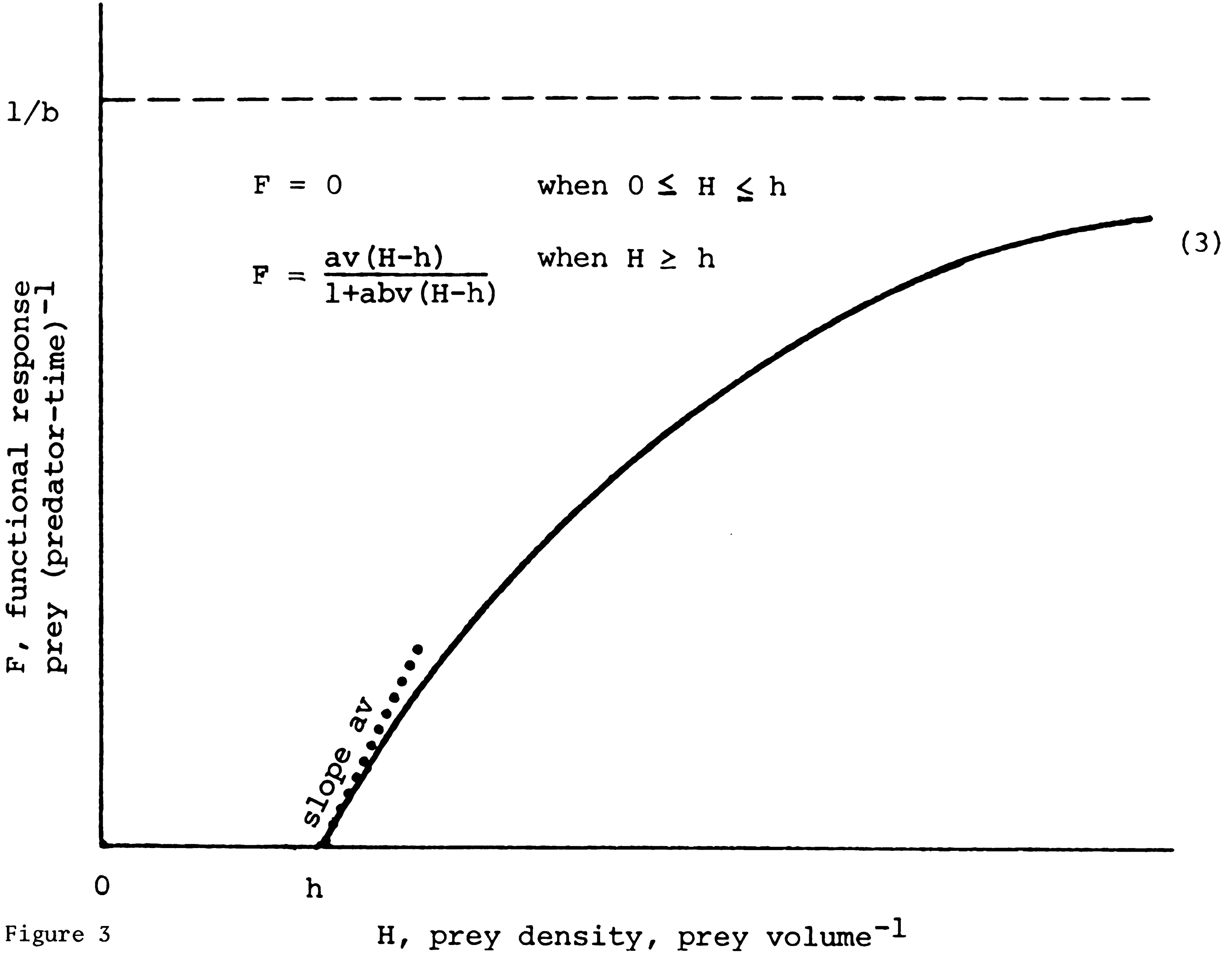

1/b
$F = 0$ when $0 \leq H \leq h$
$F = \frac{av(H-h)}{1+abv(H-h)}$ when $H \geq h$
(3)
F, functional response prey (predator-time)$^{-1}$
slope av
0
h
H, prey density, prey volume^{-1}

Figure 3

$0 < \underline{a} < a$ and $0 < q < 1$, functional responses of predators hunting inside and outside the refuge space may differ strikingly (see Figures 4 and 5): Predators hunting *inside* encounter prey at densities reflecting the prey occupancy quotient q and the volume ratio $\underline{v}$, but at some critical density of prey in the universe, $\underset{\sim}{H}$, the refuge space is just saturated and cannot admit additional prey; equating the functional response when $H \leq \underset{\sim}{H}$ with the functional response with $H \geq \underset{\sim}{H}$ and solving for prey density shows that $\underset{\sim}{H}$ equals h/q for both predator types. So the functional response curves of predators inside rise from the origin--in the typical hyperbola for type 2 or in the sigmoid-shape for type 3--bending sharply to a plateau at prey density h/q. Predators hunting *outside* exhibit a functional response similar in shape to the inside curve at prey densities below h/q; the prey density outside depends directly on v and on $1-q$, the fraction of prey occupying *non*-refuge space at low densities. Since the initial curves reach the original displaced curves (e.g., Figure 3) at h/q--the saturation density, above which the refuge space is indistinguishable from a perfect refuge--the displaced curves specify the functional response at prey densities greater than h/q. In sum, predators inside encounter prey at a density of $\underline{v}qH$ when $0 \leq H \leq h/q$ and at $\underline{v}h$ when $H \geq h/q$; predators outside encounter prey at a density of $v(1-q)H$ when $0 \leq H \leq h/q$ and at $v(H-h)$ when $H \geq h/q$. And for both type 2 and type 3 predators, the functional response curve has a slope discontinuity at h/q, above which it remains constant for predators inside and rises to an asymptote at $1/b$ for predators outside.

Figure 4. The type 2 functional response inside and outside the refuge space. "*a*" is the rate of successful attack inside, volume (predator-time)$^{-1}$; "*b*" is handling time inside, predator-time prey^{-1}; "q" is the refuge occupancy quotient, dimensionless; "*v*" is the dimensionless ratio universe volume:inside volume; "***H***" is the prey density at which inside and outside curves intersect; "F" is now the functional response outside, prey (predator-time)$^{-1}$; and "F" is the functional response inside, prey (predator-time)$^{-1}$.

$$\begin{array}{l|ll} \underline{\text{inside}} & \underline{\text{outside}} & \\ \underline{F}= \dfrac{\underline{\underline{av}}qH}{1+\underline{abv}qH} & F= \dfrac{av(1-q)H}{1+abv(1-q)H} & \text{when } 0 \leq H \leq \dfrac{h}{q} \\ \hline \underline{F}= \dfrac{\underline{\underline{av}}h}{1+\underline{abv}h} & F= \dfrac{av(H-h)}{1+abv(H-h)} & \text{when } H \geq \dfrac{h}{q} \end{array} \qquad (4)$$

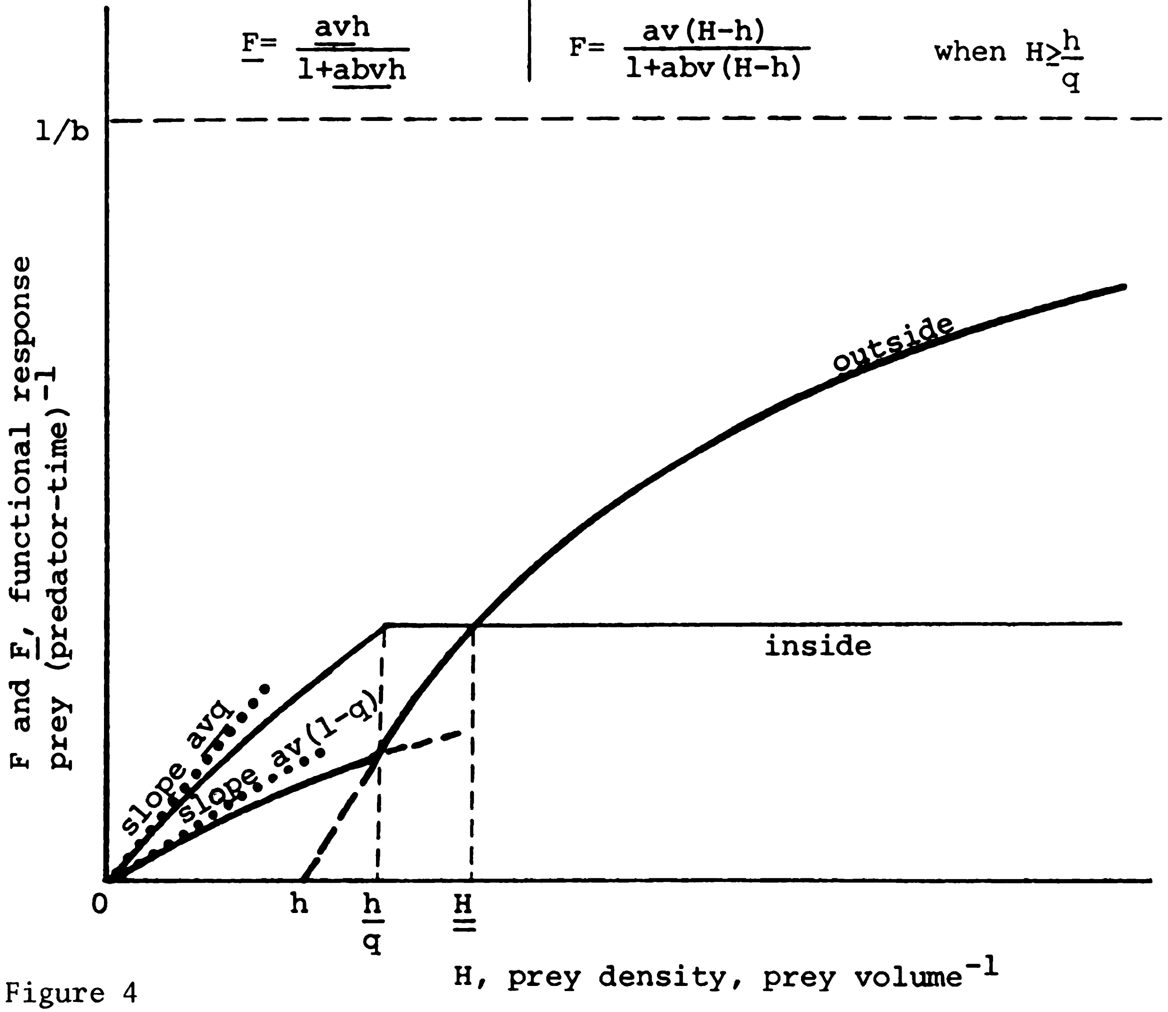


Figure 4

Figure 5. The type 3 functional response inside and outside the refuge space. "s" is now the sigmoid coefficient outside, prey volume^{-1}; and "_s_" is the sigmoid coefficient inside, prey volume^{-1}.

$$
\begin{array}{c|cl}
\underline{\text{inside}} & \underline{\text{outside}} & \\
\underline{F}=\dfrac{\underline{av}qH^2}{\underline{s}+H+\underline{ab}vqH^2} & F=\dfrac{av(1-q)H^2}{s+H+abv(1-q)H^2} & \text{when } 0\leq H\leq \dfrac{h}{q} \\
\hline
\underline{F}=\dfrac{\underline{av}h^2}{\underline{s}+h+\underline{ab}vh^2} & F=\dfrac{av(H-h)^2}{s+H-h+abv(H-h)^2} & \text{when } H\geq \dfrac{h}{q}
\end{array}
\qquad (5)
$$

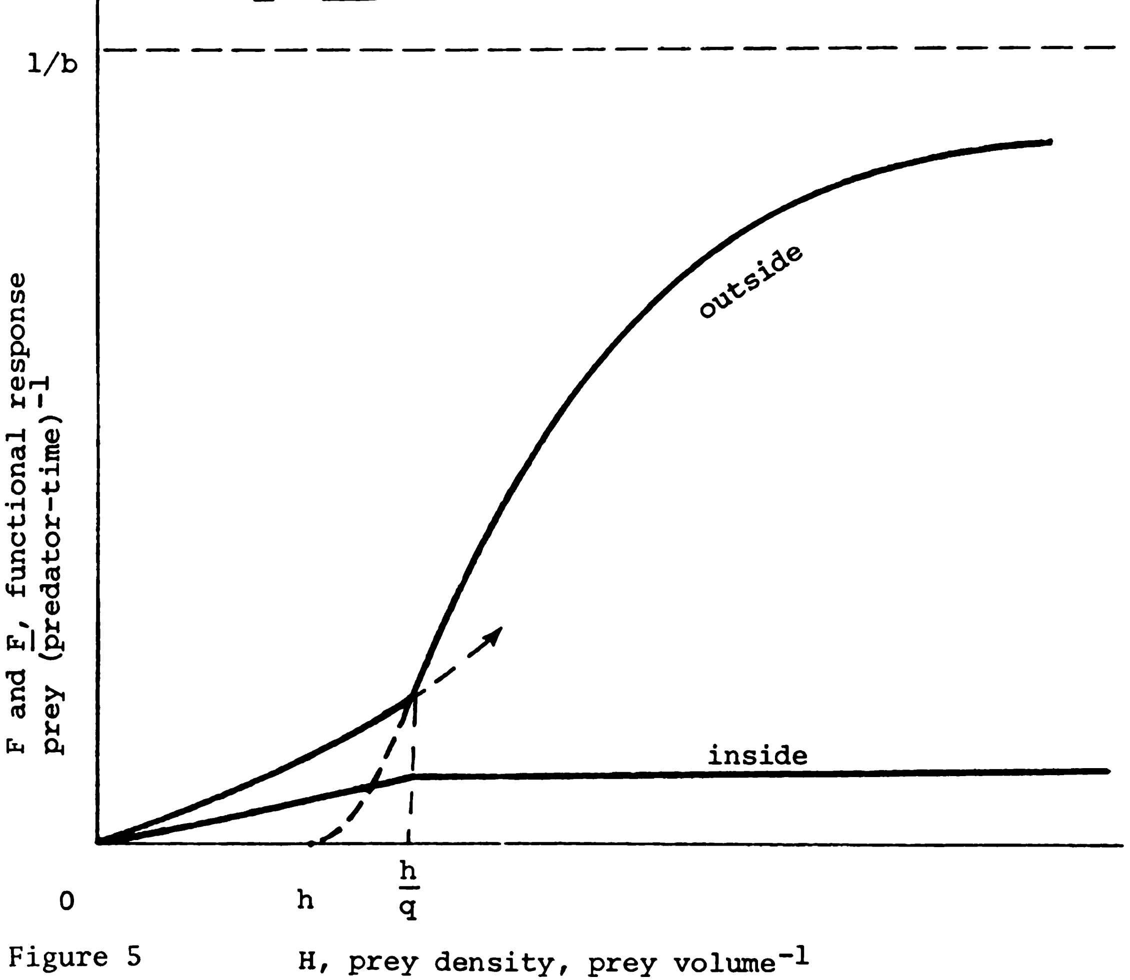


Figure 5

The outside curves of Figures 4 and 5 exemplify what Holling (1959b) has called the type 4 functional response--curves displaced along the prey density axis by a "threshold of security." Unlike the other types of functional response curves, however, these are dominated by the influence of environmental structure rather than by intrinsic biological characteristics of the predators and prey; therefore it seems preferable to view them as modified type 2 and 3 curves rather than as an additional distinct type.

Notice in Figure 4 at zero prey density that since the slope of the inside F-curve ($\underline{av}q$) exceeds the slope of the outside F-curve ($av(1-q)$), the two curves must intersect. The intersection prey density $\underline{\underline{H}}$ can be found by equating the two functional response expressions (4) for $H \geq h/q$ and solving for H:

$$\begin{aligned} \underline{\underline{H}} &= h\left(\left(\frac{\underline{av}}{av+a\underline{a}(\underline{b}-b)\underline{v}h}\right)+1\right) \\ &\approx h\left(\frac{\underline{av}}{av}+1\right) \quad \text{when } \underline{b}\approx b. \end{aligned} \tag{6}$$

Figure 4 suggests that if $\underline{av}q > av(1-q)$, predators should hunt inside the refuge space whenever $H < \underline{\underline{H}}$ and outside whenever $H > \underline{\underline{H}}$ to maximize their kill rates. This conclusion implies that the magnitudes of a, $\underline{a}$, q, and other parameters may be viewed as evolutionary "strategies" with predictable trajectories over evolutionary time in a universe of known structure. For example, it can be shown that prey facing predators with a strong tendency to aggregate in regions of high prey density should reduce their refuge occupancy quotient q when $H < \underline{\underline{H}}$ and increase q when $H > \underline{\underline{H}}$. But evolutionary arguments are peripheral to the main thrust of this paper: exploring the stability implications of spatial heterogeneity on an ecological time scale.

Appendix A presents a preliminary experimental validation of the new functional response curves in Figure 4. By modifying and rerunning the disc experiments of Holling (1959b) with and without refuge space, I obtained good agreement between data and independently-parameterized theoretical curves. The appendix also tabulates stability variables of the observed outside functional response curve that were estimated following the analysis in later sections of the text.

Much of the remainder of this analysis emphasizes the outside curves of Figures 4 and 5: hunting within the refuge space is ignored. This approach lends tractability to the algebra and approximates many actual predator-prey interactions featuring predator-exclusive refuges. Moreover, in a preliminary investigation, the non-exclusive refuge case yielded similar results unless a large proportion of the predator population hunted inside the refuge space.

Equilibrium Prey Density

If both the functional response of predators (F) and the per capita increase rate of the prey population excluding predation effects (R) are known functions of prey density (H), and if the numerical response by predators is negligible, then equilibrium prey densities (H) can be calculated by solving equation (7) for H.

$$\mathrm{R}(H)H = \mathrm{pF}(H) \tag{7}$$

where $R(H)$ is per capita increase rate of prey excluding
predation effects, time^{-1},
H is equilibrium prey density, prey volume^{-1},
and p is predator density, predators volume^{-1}.

Equation (7) states the equilibrium condition: the rate at which prey population density increases from net reproduction (RH) equals the rate at which density decreases from predation (pF).

Now consider the simple case in which both R and p are relatively independent of prey density over the density range of interest; that is, set $R = r$, a constant. From equations (4) and (7), assuming that predators are type 2 and that all are hunting outside the refuge space,

$$rH = pF = \frac{av(1-q)pH}{1+abv(1-q)H} \qquad \text{when } 0 \leq H \leq \frac{h}{q}\,, \tag{8}$$

which has at most two roots within the interval [0, h/q),

$$H = \frac{av(1-q)p - r}{abv(1-q)r} \qquad \text{and } H = 0, \tag{9}$$

where r is the <u>constant</u> per capita increase rate of prey excluding predation effects, time^{-1}.

$$rH = pF = \frac{av(H-h)p}{1+abv(H-h)} \qquad \text{when } H \geq \frac{h}{q}\,, \tag{10}$$

having two or fewer roots equal to or greater than h/q,

$$H = \frac{abvhr + avp - r \pm \sqrt{r^2(1 - abvh)^2 + avp(avp - 2r(1 + abvh))}}{2abvr} \tag{11}$$

Now for type 3 predators, by the same argument, equations (5) and (7) determine a maximum of three roots in the interval [0, h/q),

$$H = \frac{av(1-q)p-r \pm \sqrt{(r-av(1-q)p)^2-4sabv(1-q)r^2}}{2abv(1-q)r} \tag{12}$$

$$\text{and } H = 0, \qquad \text{when } 0 \le H \le \frac{h}{q} .$$

$$\text{And } (abvr)H^3 + (r-2abvrh-avp)H^2 + (sr-rh+abvrh^2 + 2avhp)H - avh^2p = 0$$

$$\text{when } H \ge \frac{h}{q} ; \tag{13}$$

this equation has at most two positive, real roots greater than or equal to h/q.

Equation (7) also implies that prey density equilibria must be the prey densities at intersection points of the functional response curve with the graph of the "prey increase function," RH/p. Figures 6 and 7 illustrate this graphical technique with R and p independent of prey density for type 2 and type 3 predators respectively.

Now consider the general case in which the prey per capita increase rate is not independent of prey density. Logistic prey population growth is the linear representative of the common class of functions for which R(H) declines monotonically with H:

$$R(H) = r(1 - \frac{H}{k}) \tag{14}$$

where r is the maximum per capita prey increase rate, time^{-1}
and k is the carrying capacity of the universe for prey,
prey volume^{-1}.

For type 2 predators hunting outside the refuge space, equations (4), (7), and (14) imply that

Figure 6. Equilibrium prey densities with type 2 predators and with prey population growth rate independent of prey density in a universe containing refuge space. $r_6/p_6 > r_5/p_5 > r_4/p_4 > r_3/p_3 > r_2/p_2 > r_1/p_1$.

"r" is the constant per capita increase rate of prey, time^{-1}. "p" is the predator density, predators volume^{-1}; "H" is the equilibrium prey density, prey volume^{-1}; "$\underset{\sim}{H}$" is now the prey density below which no predator-limited equilibrium prey density can be stable, prey volume^{-1}; and "$\tilde{H}$" is the prey density above which no predator-limited equilibrium prey density can be stable, prey volume^{-1}.

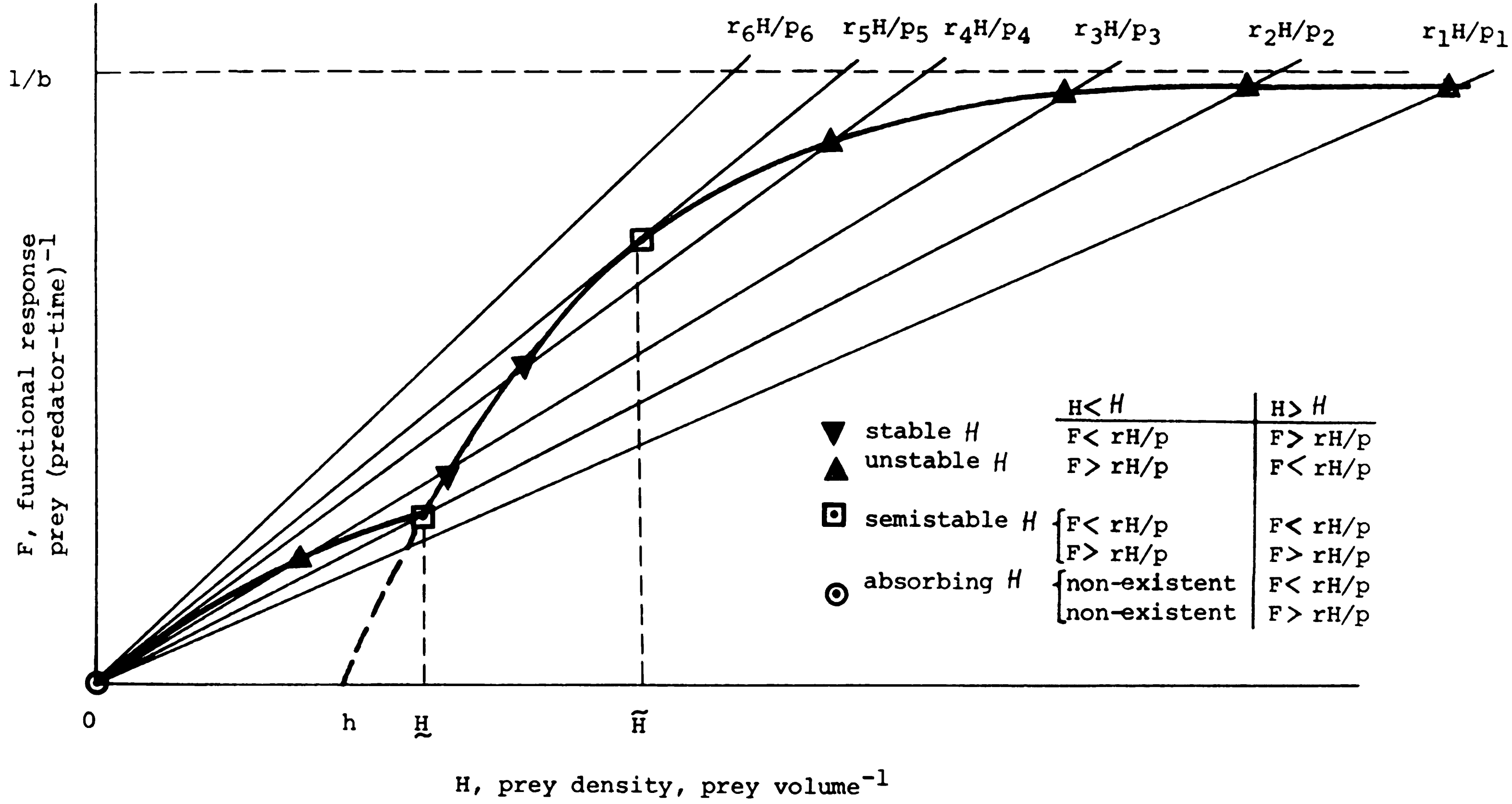

1/b
F, functional response prey (predator-time)$^{-1}$
r_6H/p_6
r_5H/p_5
r_4H/p_4
r_3H/p_3
r_2H/p_2
r_1H/p_1
0
h
$\underset{\sim}{H}$
$\tilde{H}$
H, prey density, prey volume^{-1}
▼ stable H
▲ unstable H
▣ semistable H
⊙ absorbing H
$H < H$
$H > H$
F< rH/p
F> rH/p
F> rH/p
F< rH/p
F< rH/p
F> rH/p
F< rH/p
F> rH/p
non-existent
non-existent
F< rH/p
F> rH/p

Figure 6

Figure 7. Equilibrium prey densities with type 3 predators and with prey population growth rate independent of prey density in a universe containing refuge space. $r_5/p_5 > r_4/p_4 > r_3/p_3 > r_2/p_2 > r_1/p_1$.

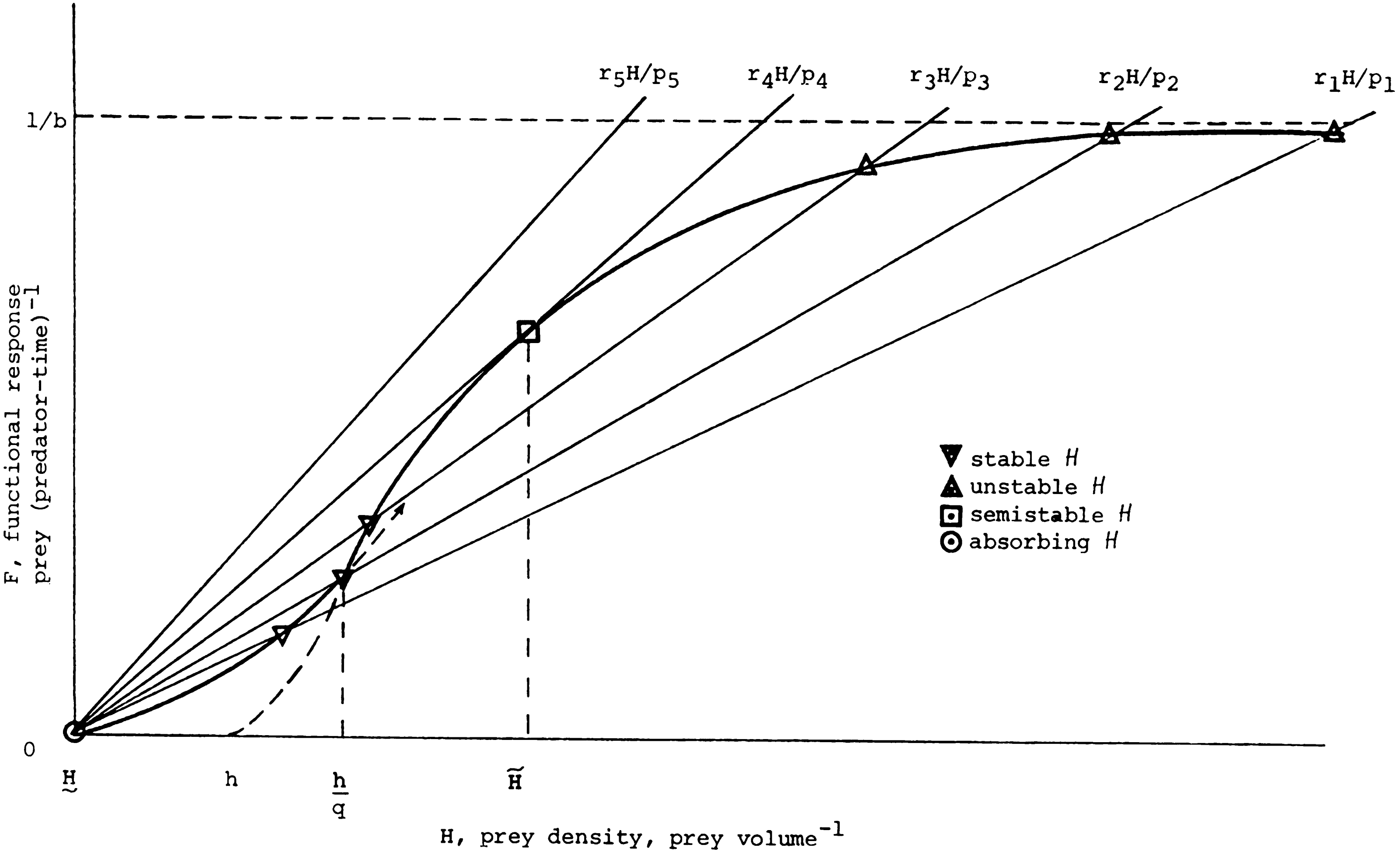

r_5H/p_5
r_4H/p_4
r_3H/p_3
r_2H/p_2
r_1H/p_1
1/b
F, functional response prey (predator-time)$^{-1}$
0
$\underset{\sim}{H}$
h
$\frac{h}{q}$
$\tilde{H}$
H, prey density, prey volume^{-1}
▼ stable H
▲ unstable H
⊡ semistable H
⊙ absorbing H

Figure 7

when $0 \leq \mathcal{H} \leq h/q$,

$$\mathcal{H} = \frac{r(abv(1-q)k-1) \pm \sqrt{r^2(abv(1-q)k+1)^2 - 4a^2bv^2(1-q)^2rkp}}{abv(1-q)r} \qquad (15)$$

and $\mathcal{H} = 0$; when $\mathcal{H} \geq h/q$,

$$(abvr)\mathcal{H}^3 + r(1-abvk-abvh)\mathcal{H}^2 + k(abvrh+avp-r)\mathcal{H} - avhkp = 0, \qquad (16)$$

an implicit solution.

From (5), (7) and (14), comparable equations could also be written for type 3 predators.

Graphical solutions in Figure 8 emphasize the similarity of these results to those for density-independent prey reproduction, except that monotonically decreasing R(H) usually generates an additional stable equilibrium slightly below the carrying capacity k. Mathematical and biological implications of this new uppermost equilibrium are mentioned in latter sections.

Notice the four different kinds of equilibria ($\mathcal{H}$) in Figures 6-8. An equilibrium prey density is <u>stable</u> if the functional response F exceeds the prey increase function RH/p at prey densities greater than $\mathcal{H}$, <u>and</u> the prey increase function exceeds the functional response below $\mathcal{H}$. Thus if H "accidentally" becomes slightly greater than $\mathcal{H}$, then the functional response exceeds the prey increase rate, and H tends to return to $\mathcal{H}$; if H becomes slightly smaller than $\mathcal{H}$, then the prey increase rate exceeds the functional response, pushing H back toward $\mathcal{H}$. At an <u>unstable</u> equilibrium, however, "accidental" shifts of prey density away from $\mathcal{H}$ tend to become accentuated; if H rises above $\mathcal{H}$, the prey can increase faster than predators can eliminate them (i.e., $RH/p > F$),

Figure 8. Equilibrium prey densities with type 2 predators and logistic population growth of prey in a universe containing refuge space. $r_2/p_2>r_1/p_1$; $k''>k'$. "k" (k', k") is the resource-limited carrying capacity of the universe, prey volume^{-1}.

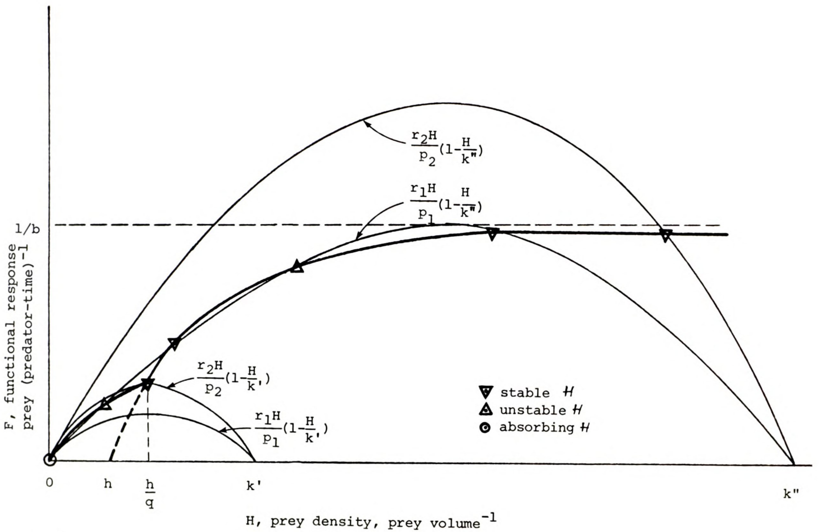

$\frac{r_2H}{p_2}(1-\frac{H}{k''})$
$\frac{r_1H}{p_1}(1-\frac{H}{k''})$
1/b
F, functional response prey (predator-time)$^{-1}$
$\frac{r_2H}{p_2}(1-\frac{H}{k'})$
$\frac{r_1H}{p_1}(1-\frac{H}{k'})$
▼ stable H
▲ unstable H
⊙ absorbing H
0
h
$\frac{h}{q}$
k'
k"
H, prey density, prey volume^{-1}

Figure 8

but if H falls below H, predators can reduce prey density faster than prey can be replaced. *Semistable* equilibria are stable for prey density shifts in one direction away from H but unstable in the other; that is, shifts along the prey density axis are accentuated in one direction but counteracted in the other. And *absorbing* equilibria may locally resemble any of the other three kinds except precisely at H: if prey density ever reaches H, it remains there permanently. In any universe closed to immigration, such as those considered here, H = 0 (prey extinction) is an absorbing equilibrium.

In addition to those with constant or logistic R, another kind of prey increase function features an "Allee Effect," in which R is negative below some critical non-zero prey density. An expression derived from the logistic to incorporate this effect is drawn with a refuge-displaced functional response curve in Figure 9, indicating patterns of equilibria similar to those in Figure 8; but note in Figure 9 that whenever $c > 0$, stable equilibria are accompanied by lower unstable equilibria (Holling, 1973).

The Escape and Extinction Thresholds

Because the magnitudes of state variables spontaneously tend to approach stable equilibria and avoid unstable equilibria, a stable equilibrium may be said to have a "domain of attraction" delimited by the adjacent unstable equilibria (Lewontin, 1969). In particular, any perturbation of prey density to a new value within its domain of attraction returns toward the stable H, but perturbations beyond the boundaries of the domain carry prey density toward a different stable H in a new domain of attraction.

Figure 9. Equilibrium prey densities with type 2 predators and with prey population growth featuring an Allee effect in a universe containing refuge space. $c_3>c_2>c_1$. "c" is the Allee coefficient, the lowest non-negative prey density at which R(H) = 0, prey volume^{-1}.

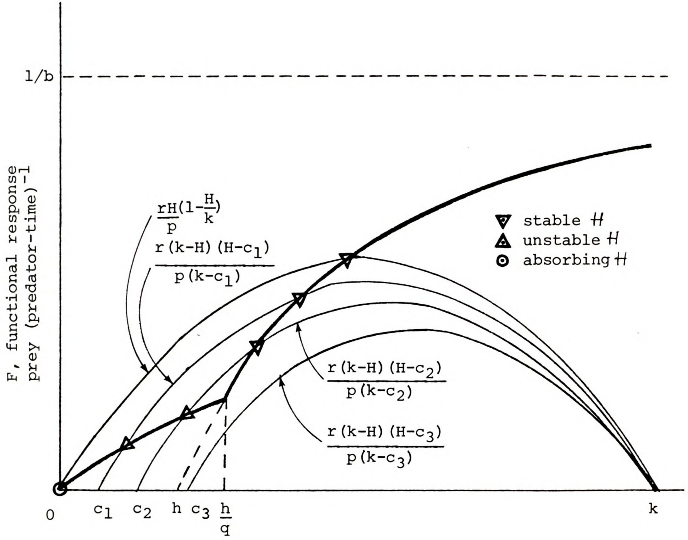

1/b
F, functional response prey (predator-time)$^{-1}$
$\frac{rH}{p}(1-\frac{H}{k})$
$\frac{r(k-H)(H-c_1)}{p(k-c_1)}$
$\frac{r(k-H)(H-c_2)}{p(k-c_2)}$
$\frac{r(k-H)(H-c_3)}{p(k-c_3)}$
▽ stable H
△ unstable H
⊙ absorbing H
0
c_1
c_2
h
c_3
$\frac{h}{q}$
k
H, prey density, prey volume^{-1}

Figure 9

A function T(H), defined as in equation (17) such that $dT/dH = -dH/dt$, can clarify the stability properties of this predator-prey interaction. In Figures 10 and 11, each r-p pair specifying a prey increase function on the functional response graph also specifies a graph of the stability topography function T(H). Imagine that the H-T plane is a vertical cross-section of a surface on which a small momentumless marble is rolling, and suppose that the marble spontaneously rolls downslope such that the horizontal component of its velocity equals the slope of T at each point. Then the marble's position along the H-axis represents the prey density varible, and the dimensions of terrain features delineate and measure the domains of attraction that constrain the marble's trajectory; for example, when $r = r_3$ and $p = p_3$ in Figures 10 and 11, the stable equilibrium at $\check{H}_3$ has as its domain of attraction the interval $(\overleftarrow{H}_3, \overrightarrow{H}_3)$. But notice that if the marble "accidentally" rolls beyond $\overleftarrow{H}_3$, then it can spontaneously roll to zero, i.e., the prey population becomes extinct; thus for those parameter values, $\overleftarrow{H}_3$ is an *extinction threshold*, the prey density below which the prey population density tends to decline to zero. On the other hand, if the marble rolls beyond $\overrightarrow{H}_3$, then it can roll toward higher prey densities, i.e., the prey population escapes regulation by predators; thus for those parameter values, $\overrightarrow{H}_3$ is an *escape threshold*, above which prey density increases toward a resource-limited maximum (cf. Holling, 1973).

When the per capita increase rate of the prey population (neglecting predation) is approximated by a constant R, this maximum prey density is not mathematically specified and presumably is at or near the resource limit k. When R(H) declines monotonically with H,

Figure 10. The prey density topography with type 2 predators and with prey population growth independent of density in a universe containing refuge space. $r_5/p_5>r_4/p_4>r_3/p_3>r_2/p_2>r_1/p_1$
"$\overleftarrow{H}$" is the extinction threshold, prey volume $^{-1}$;
"$\check{H}$" is the stable equilibrium prey density, prey volume^{-1};
"$\overrightarrow{H}$" is the escape threshold, prey volume^{-1};
"G" is a dummy variable for prey density, prey volume^{-1};
and "T" is the stability topography, prey^{2}volume^{-2} time^{-1}.

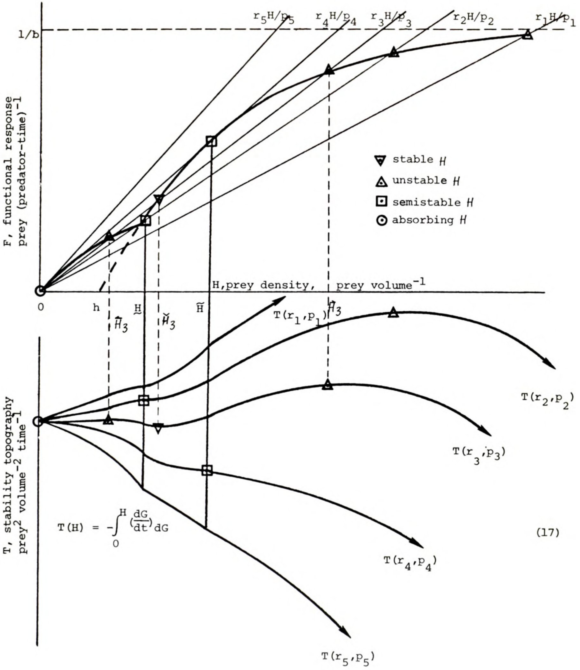

r_5H/p_5
r_4H/p_4
r_3H/p_3
r_2H/p_2
r_1H/p_1
1/b
F, functional response
prey (predator-time)-1
▼ stable H
△ unstable H
□ semistable H
⊙ absorbing H
0
h
$\underset{\sim}{H}$
$\widetilde{H}$
H,prey density, prey volume^{-1}
$\hat{H}_3$
$\check{H}_3$
$\bar{H}_3$
$T(r_1,p_1)$
$T(r_2,p_2)$
$T(r_3,p_3)$
$T(r_4,p_4)$
$T(r_5,p_5)$
T, stability topography
prey^2 volume^{-2} time^{-1}
$T(H) = -\int_0^H (\frac{dG}{dt}) dG$
(17)

Figure 10

Figure 11. The prey density topography with type 2 predators and logistic prey population growth in a universe containing refuge space. $r_4/p_4 > r_3/p_3 > r_2/p_2 > r_1/p_1$.

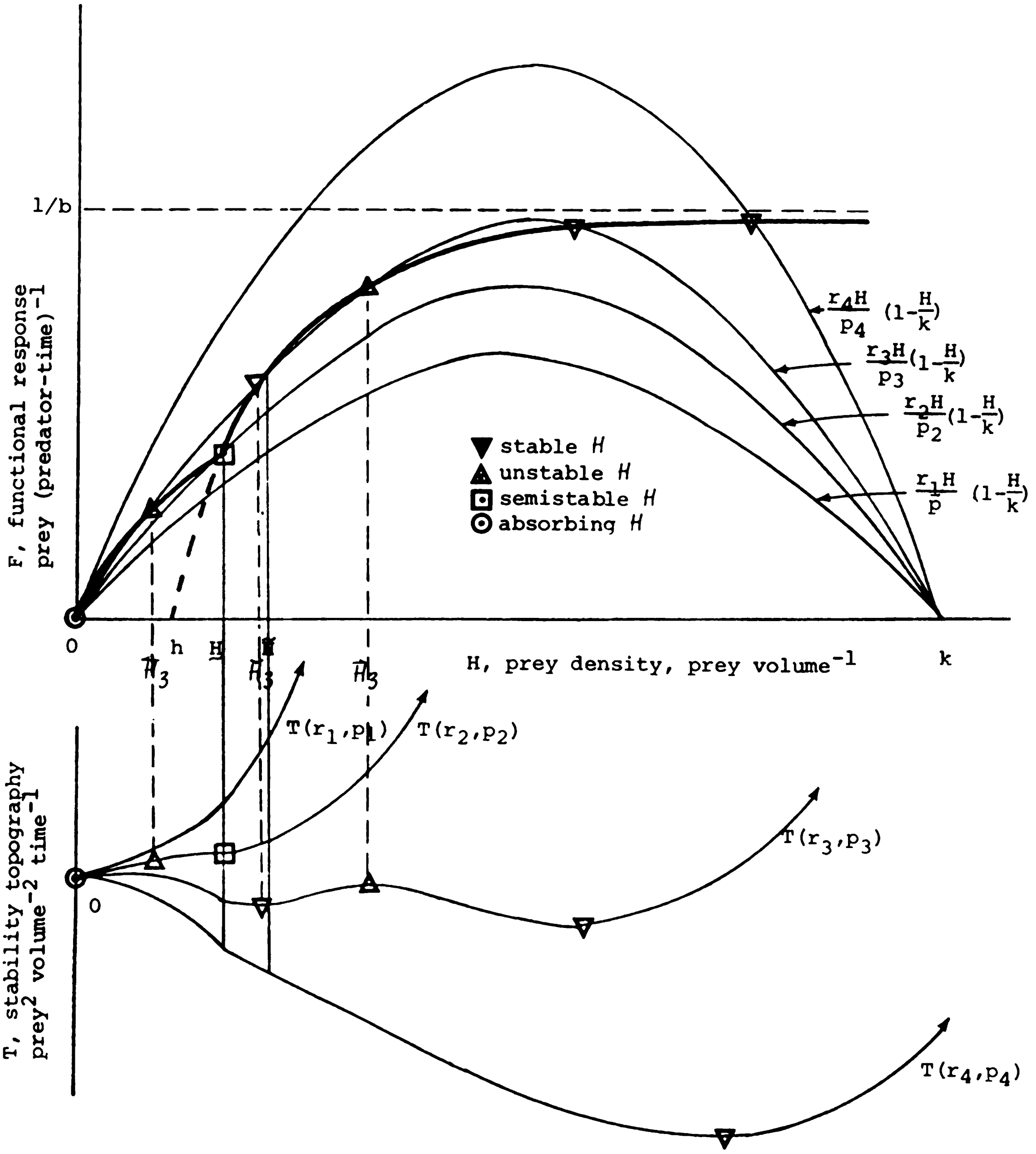

1/b
F, functional response prey (predator-time)$^{-1}$
0
h
$\underline{H}$
$\bar{H}$
$\vec{H}_3$
$\vec{H}_3$
$\vec{H}_3$
H, prey density, prey volume^{-1}
k
$\frac{r_4H}{p_4}(1-\frac{H}{k})$
$\frac{r_3H}{p_3}(1-\frac{H}{k})$
$\frac{r_2H}{p_2}(1-\frac{H}{k})$
$\frac{r_1H}{p}(1-\frac{H}{k})$
▼ stable H
▲ unstable H
▣ semistable H
⊙ absorbing H
T, stability topography prey^2 volume^{-2} time^{-1}
0
$T(r_1,p_1)$
$T(r_2,p_2)$
$T(r_3,p_3)$
$T(r_4,p_4)$

Figure 11

as in logistic population growth, then the size of the carrying capacity largely determines the density of the highest stable prey population equilibrium. Barring a precipitous drop in R(H) near k, however, Figures 8 and 11 clearly suggest that *both* predators and resources determine the level of this uppermost stable equilibrium (see May, 1973); and conversely, owing to one of the much-lamented unrealities of the logistic, prey are still partly limited by resources even at the lowermost stable equilibrium. Nevertheless, the lower and upper stable equilibria may usually be considered "predator-limited" and "resource-limited" respectively, implying that the unstable equilibrium separating their domains of attraction represents a true escape threshold.

Figure 10 indicates that the prey density interval in which a stable equilibrium can exist with constant R(H) is $(\underset{\sim}{H}, \tilde{H})$. In other words, if $r_2/p_2 < r/p < r_2/p_4$ in the figure, then there exists a stable equilibrium prey density within $(\underset{\sim}{H}, \tilde{H})$. The limits of this interval can be found as follows: For type 2 predators,

$$\underset{\sim}{H} = \frac{h}{q} , \tag{18}$$

the prey density at which the refuge space becomes full. But this calculation rests on the assumption that the refuge occupancy quotient q is really independent of prey density, even near h/q; more likely, q will decrease somewhat as H approaches h/q, smoothing out the transition between the intersecting functional response curves. In Figure 12, this effect is pronounced enough to lower $\underset{\sim}{H}$ to zero; the functional response has become positively accelerated at prey densities below h/q, resembling the type 3 functional response of Figure 2. In some instances,

Figure 12. The effect of a prey refuge occupancy quotient (q) inversely related to prey density on the functional response of type 2 predators. As the occupancy quotient increases with increasing prey density inside the refuge, the functional response rises above the biconvex curve for constant "q" and assumes a sigmoid shape.

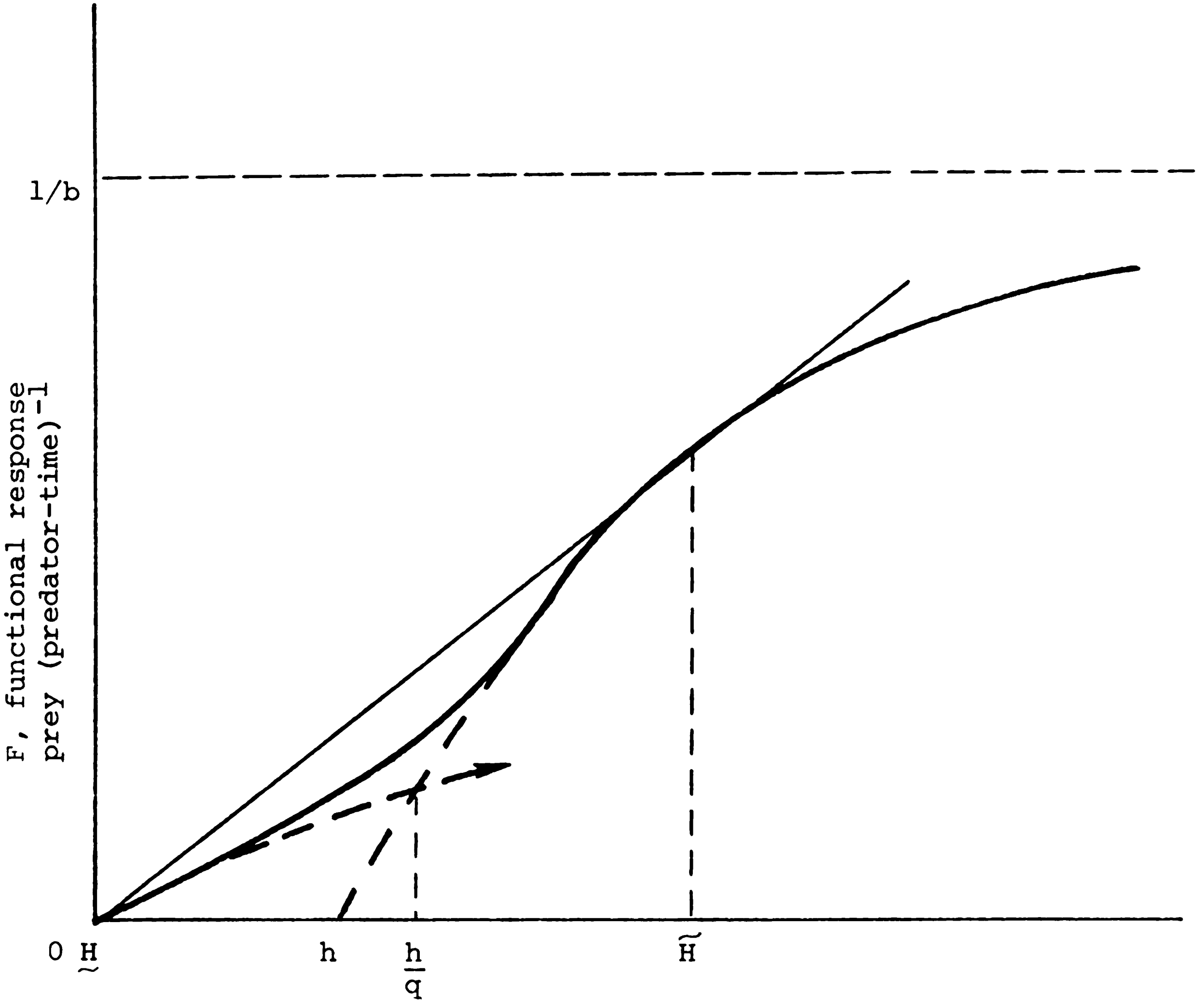

1/b
F, functional response
prey (predator-time)$^{-1}$
0
$\underset{\sim}{H}$
h
$\frac{h}{q}$
$\tilde{H}$
H, prey density, prey volume^{-1}

Figure 12

the functional response curves of Figure 10 may be more realistic than the curve in Figure 12, and equation (18) will be applicable. $\tilde{H}$, in contrast, does not depend on q, and Figure 12 suggests a means of calculating its magnitude for type 2 predators: $\tilde{H}$ is uniquely the tangent point at which F(H)/H = dF/dH. From equations (4),

$$\frac{F(\tilde{H})}{\tilde{H}} = \frac{av(\tilde{H}-h)}{(1+abv(\tilde{H}-h))\tilde{H}} \tag{19}$$

and

$$\frac{dF(\tilde{H})}{dH} = \frac{av}{(1+abv(\tilde{H}-h))^2}$$

Equating equations (19) and solving for $\tilde{H}$,

$$\tilde{H} = \sqrt{\frac{h}{abv}} + h \tag{20}$$

For type 3 predators, $\underset{\sim}{H} = 0$, since the positively accelerated functional response at low prey densities insures stable equilibria in this range; for all $r/p > 0$, prey densities very near zero tend to increase spontaneously, moving away from the absorbing equilibrium at $H = 0$. $\tilde{H}$ for type 3 predators can be found as above, using equations (5):

$$\frac{F(\tilde{H})}{\tilde{H}} = \frac{av(\tilde{H}-h)^2}{(s+\tilde{H}-h+abv(\tilde{H}-h)^2)\tilde{H}} \tag{21}$$

and

$$\frac{dF(\tilde{H})}{dH} = \frac{av(\tilde{H}-h)^2+2avs(\tilde{H}-h)}{(s+\tilde{H}-h+abv(\tilde{H}-h)^2)^2} .$$

Equating equations (21)

$$abv(\tilde{H}-h)^3 - (\tilde{H}-h)h - s(\tilde{H}+h) = 0. \qquad (22)$$

Notice from (22) that when $h = 0$, $\tilde{H} = \sqrt{s/abv}$: type 3 predators can stabilize prey density even in a homogeneous universe (Holling, 1965; and many others).

$\underset{\sim}{H}$ and $\tilde{H}$ are more difficult to express explicitly when the per capita increase rate of prey is density-dependent, even when the logistic equation provides a suitable representation of $R(H)$. In the density-dependent case, $\underset{\sim}{H}$ is usually zero, especially for type 3 predators (or for high q). $\tilde{H}$ is the same or only slightly larger than for constant $R(H)$.

Stability of a Predator-Prey Link

This analysis suggests that stability of a predator-prey link can be quantified by appropriately operationalizing elasticity and conformability. (Recall that elasticity is a measure of the tendency for perturbations of state variables to be damped; conformability is a measure of the tendency for elasticity to be maintained in the face of parameter perturbations.) Let the elasticity of a stable predator-limited equilibrium prey density, $E(\check{H})$, be an ordered pair expressing the proximities of the escape and extinction thresholds to the stable equilibrium. The simplest such expression is

$$E(\check{H}) = \langle \check{H}-\overleftarrow{H}, \overrightarrow{H}-\check{H} \rangle \qquad (23)$$

where $\overleftarrow{H}$ is a lower unstable (or absorbing) equilibrium prey density, the extinction threshold, prey(volume)$^{-1}$,

$\check{H}$ is a stable equilibrium prey density with a domain of attraction in the interval $(\overleftarrow{H},\overrightarrow{H})$ prey(volume)$^{-1}$,

and $\overrightarrow{H}$ is an upper unstable equilibrium prey density, the escape threshold, prey(volume)$^{-1}$.

E measures the size of prey density perturbations away from the stable density tolerable in each direction without forcing H beyond the domain of attraction. The domain of attraction is itself specified as the elastic region, $E(\check{H})$, the interval delimited by threshold boundaries:

$$E(\check{H}) = (\overleftarrow{H},\overrightarrow{H}) \tag{24}$$

Similarly, let the conformability of a stable predator-limited equilibrium prey density $C(\check{H})$ express the ordered pair of differences between the slope of the prey increase function and the minimum and maximum conformable slopes, respectively; that is

$$C(\check{H}) = \langle r/p - \overleftarrow{r/p},\ \overrightarrow{r/p} - r/p \rangle \tag{25}$$

where $\overleftarrow{r/p}$ is the <u>minimum</u> initial slope of the prey increase function yielding a stable or semi-stable, predator-limited equilibrium prey density, volume(predator-time)$^{-1}$,

and $\overrightarrow{r/p}$ is the <u>maximum</u> initial slope of the prey increase function yielding a stable or semi-stable, predator-limited equilibrium prey density, volume(predator-time)$^{-1}$.

Then the conformable region of a stable equilibrium prey density, $C(\check{H})$, is the range of conformable initial slopes of the prey increase function, i.e., those slopes allowing the existence of a stable, predator-limited equilibrium in the prey density interval $(\utilde{H}, \tilde{H})$:

$$C(\check{H}) = (\overleftarrow{r/p}, \overrightarrow{r/p}) \tag{26}$$

In particular, for type 2 predators and prey with constant R(H),

$$\hat{C}(\check{H}) = \langle r/p - F(\utilde{H})/\utilde{H}, F(\tilde{H})/\tilde{H} - r/p \rangle \tag{27}$$

and $$C(\check{H}) = (F(\utilde{H})/\utilde{H}, F(\tilde{H})/\tilde{H})$$

where $\tilde{H}$ is now seen to be the maximum conformable prey density,

and $\utilde{H}$ is now the minimum conformable prey density, both prey volume^{-1}.

But if q decreases with H as prey density approaches h/q, then Figure 12 suggests that the slope of the functional response curve at zero prey density may provide a more accurate estimate of minimum conformable prey density. In that case

$$C(\check{H}) = \langle r/p - dF(0)/dH, F(\tilde{H})/\tilde{H} - r/p \rangle \tag{28}$$

and $$C(\check{H}) = (dF(0)/dH, F(\tilde{H})/\tilde{H}).$$

And for type 3 predators and prey with constant R(H),

$$C(\check{H}) = \langle r/p, F(\tilde{H})/\tilde{H} - r/p \rangle \tag{29}$$

and $$C(\check{H}) = (0, F(\tilde{H})/\tilde{H}).$$

E and $\mathcal{E}$ always refer to a given state variable and a given stable equilibrium. With more than one prey population in the system, the appropriate values of $\overleftarrow{H}$, $\check{H}$, and $\overrightarrow{H}$ for some population H_1 are the corresponding H_1 coordinates of the multispecies equilibria; in other words, $E_1, E_2, \ldots E_n$ and $\mathcal{E}_1, \mathcal{E}_2, \ldots, \mathcal{E}_n$ can be calculated with n prey species following the form of equations (23)-(26) using the respective coordinates of each $H = H_1, H_2, \ldots H_n$. Similarly,

C and $\mathcal{C}$ always refer to a given stable equilibrium, a given state variable, and a given parameter or combination of parameters. The conformability analyses in this paper focus on r/p, the quotient of two crucial and biologically "noisy" parameters; calculating the upper and lower limits of r/p that allow a particular n-species stable equilibrium to exist clearly requires that $\underset{\sim}{H}$ and $\hat{H}$ be found in n-space, from which $F(\underset{\sim}{H})$ and $F(\hat{H})$ can be obtained. C and $\mathcal{C}$ are calculated for each state variable using its coordinate of the multispecies $\underset{\sim}{H}$ and $\hat{H}$. If equations (28) are used, $dF(0)/dH$ should be replaced for example by $\partial F(0)/\partial H_1$ to find C_1 and $\mathcal{C}_1$, the conformability and conformable region with respect to prey species 1.

The preceding analysis, of course, considers only a few simple mathematical expressions of elasticity and conformability; many others are possible. Lewontin (1969), for example, presents another elasticity metric, an index to characterize the topography of a domain of attraction. And the elasticity concept can be extended to other state variables--in the present analysis to dH/dt: the boundaries of its elastic region, easily found for known F(H) and R(H), specify the maximum sustained rates at which prey can be removed (fished) or introduced (stocked) without triggering extinction or escape (see Holling, 1973; Smith, 1968). So in these and other mathematical guises, elasticity and conformability may help bridge a gap between ecological theory and application (see below).

Elasticity and conformability differ not only in mathematical expression but also in biological implications. When "shock" perturbations predominate, as in coastal regions and on tropical and temperate oceanic islands, only highly elastic ecosystems can persist; when "shift" perturbations predominate, as in strongly seasonal environments such as temperate lakes and deciduous forest, only highly conformable systems can survive intact. But it may often be possible to enhance elasticity or conformability (and reduce the chances of prey extinction or escape) by tuning critical parameter values, a strategy explored briefly in the Summary of Theoretical Results and in the Discussion later in this paper.

Multiple Refuges

So far in this analysis the spatial heterogeneity of the predator-prey universe has been the contrast between inside and outside the refuge space. No distinction has yet been drawn between a universe with, say, fifty small refuges of total capacity h and a universe with a single refuge of capacity "h," nor have the implications of several distinct refuge types in the universe been considered. Both omissions will be remedied in this section.

The most ecologically significant difference between a few large refuges and many small ones is probably the relative amounts of contact between "inside" and "outside": the surface-volume ratio (or perimeter-area ratio) of the refuge space increases dramatically as this space is partitioned into many small sub-spaces. Now if the extent of contact between refuge and non-refuge space partly governs the exchange rate of prey individuals between inside and outside, as expected if prey movement has any significant random component, then the functional response and the stability properties of the interaction may depend critically on the size distribution of refuge spaces.

One simple but representative case is considered here--a system with type 2 predators, predator-exclusive refuge space, and per capita prey exchange and increase rates independent of prey density. Let "e" specify the exchange rate, the fraction of prey moving <u>out</u> across the refuge perimeter per unit time; then weighting by the occupancy quotients for inside and outside, the exchange rate of prey moving <u>in</u> is eq/(1-q). In the steady state the decrease rate of prey density inside (prey crossing to the outside) must equal the increase rate of prey density inside (prey crossing to the inside plus prey recruitment inside):

$$e\underline{H} = \frac{eq\underline{v}\bar{H}}{(1-q)v} + r\underline{H} \tag{30}$$

where $\underline{H}$ is prey density inside, prey inside (inside volume)$^{-1}$,

and $\bar{H}$ is prey density outside, prey outside (outside volume)$^{-1}$.

From (30) a new refuge occupancy quotient Q(e)--the fraction of all prey that is inside the refuge space as a function of the exchange rate--can be found by rearranging (30):

$$Q = \frac{\underline{H}/\underline{v}}{\underline{H}/\underline{v}+\bar{H}/v} = \frac{eq}{e-r(1-q)} \; . \tag{31}$$

Notice that when $e \gg r$, $Q = q$; in other words the refuge occupancy quotient is constant (as assumed in previous sections) for high exchange rates or low rates of reproduction, but it depends on both "e" and "r" when those parameters are more similar in magnitude. And note from (30) that "r" cannot exceed "e" in the steady state, i.e., $e \geq r$.

Replacing "q" by Q(e) in functional response expressions facilitates the comparison of systems featuring different distributions of refuge space as reflected in their respective prey exchange rates. Figure 13 shows that greater exchange rates (many small refuges) yield higher functional response curves at prey densities below refuge saturation than for smaller exchange rates (few large refuges); so the system containing many small refuges can have larger $\overleftarrow{H}$ and $\overleftarrow{r/p}$ and thus a greater chance of extinction than a system with few large refuges, though the chance of escape is unaffected.

There are at least two reasons to question the distinctness of this contrast: (1) Relaxing predator exclusivity and density-independent exchange should increase the effective exchange rate more for initially small "e" than for large "e". (2) "e" is often large relative to "r" anyway. Yet of the seven examples of structural SH given at the beginning of this paper, refuge size distribution could certainly be important in at least two of them: the protozoan-flask systems of Gause (1934) and the chemostat interaction of van den Ende (1973).

Taking a different slant on operationalizing spatial heterogeneity, Smith (1972) has shown that the average <u>catchability</u> of prey removed in a non-mixing, spatially heterogeneous universe exceeds the average in the initial population by the square of the coefficient of variation. This "catchability bias," though useful in quantifying exploitation, is inadequate as an index of heterogeneity: the bias disappears completely in a rapidly-mixing system even though structural SH can still be strongly stabilizing (see Figure 13).

It has recently been suggested that distributing populations and refuges in space may "spread the risk" of a destabilizing perturbation among several prey sub-populations, implying that a system with many

Figure 13. The functional response of type 2 predators hunting outside the refuge space at four differenct exchange rates of prey with constant R(H). $e_4 > e_3 > e_2 > e_1$. "e" is is prey exchange rate between inside and outside, time^{-1}.

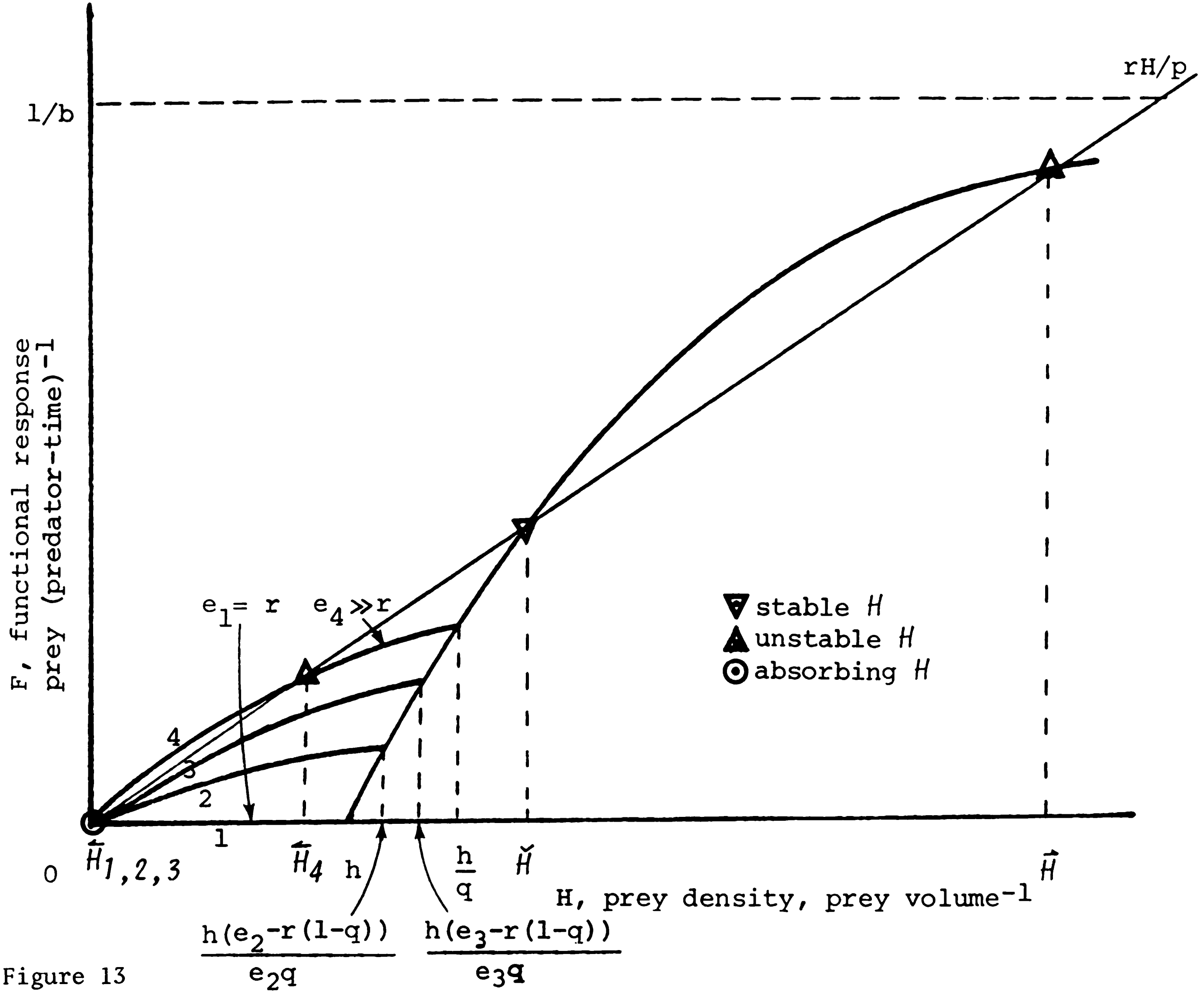

1/b
rH/p
F, functional response prey (predator-time)-1
$e_1 = r$
$e_4 \gg r$
4
3
2
1
0
$\overleftarrow{H}_{1,2,3}$
$\overleftarrow{H}_4$
h
$\frac{h}{q}$
$\check{H}$
$\vec{H}$
H, prey density, prey volume-1
$\frac{h(e_2 - r(1-q))}{e_2 q}$
$\frac{h(e_3 - r(1-q))}{e_3 q}$
▼ stable H
▲ unstable H
⊙ absorbing H

Figure 13

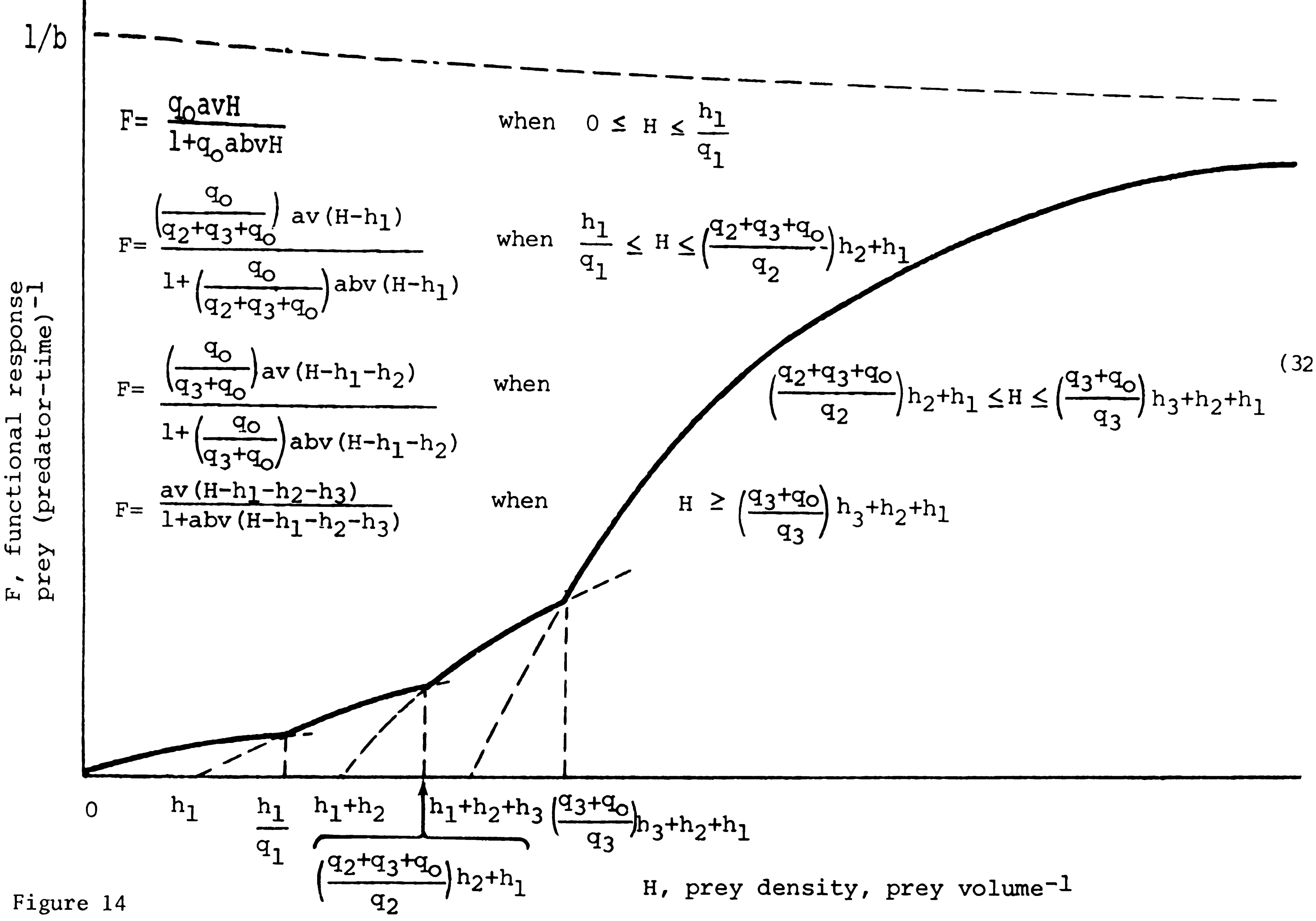
smaller refuges may be more stable than one with few large refuges. This stochastic view certainly deserves thorough theoretical elaboration--all the more so if the stability effects of stochastic and structural SH are frequently antagonistic. In its current vague form (den Boer, 1968 and 1971; Reddingus and den Boer, 1970), however, the spreading-of-risk concept has generated some confusion and valid criticism (May, 1971 and 1974b; Roff, 1974a; Levandowsky, 1974). Other recent approaches to stochastic SH (e.g., Roff, 1974b; May, 1974b), though difficult or impossible to operationalize, may eventually help clarify the relation between stochastic and structural SH.

Now consider the implications for stability of several different refuge types in the predator-prey universe. Figure 14 shows the functional response curve for type 2 predators in a 3-refuge universe, with the refuge capacities h_i and the occupancy quotients q_i independent of prey density. The functional response rises from the origin in a series of four intersecting type 2 curves: below prey density h_1/q_1, all three refuge spaces can hold additional prey with increasing H, but immediately above h_1/q_1, only spaces 2 and 3 still have room; above the next slope discontinuity, only refuge space 3 is still filling with prey, and above the highest slope break, all refuge spaces are filled with prey. Mathematically, this case simply elaborates the analysis of the outside curve of Figure 4. In fact, if all three refuge types became saturated with prey at the same prey density, then Figure 14 would have only one slope discontinuity and would be indistinguishable from the outside curve of Figure 4.

Notice that the general shape of the curve in Figure 14 is sigmoid, especially if the breaks in slope at intersection points are

Figure 14. The functional response of type 2 predators in a universe containing three kinds of refuge space. $h_3/q_3 > h_2/q_2 > h_1/q_1$.

"q_o" is the outside occupancy quotient, i.e., $q_o = 1-q_1-q_2-q_3$, dimensionless; "q_i" is the occupancy quotient of the i^{th} refuge type, where $i = 1, 2,$ or 3, dimensionless; and "h_i" is the capacity of the i^{th} refuge type, where $i = 1, 2,$ or 3, prey volume^{-1}.



$$
\begin{aligned}
F&=\frac{q_oavH}{1+q_oabvH} && \text{when} \quad 0 \le H \le \frac{h_1}{q_1}\\
F&=\frac{\left(\frac{q_o}{q_2+q_3+q_o}\right) av(H-h_1)}{1+\left(\frac{q_o}{q_2+q_3+q_o}\right)abv(H-h_1)} && \text{when} \quad \frac{h_1}{q_1} \le H \le \left(\frac{q_2+q_3+q_o}{q_2}\right)h_2+h_1\\
F&=\frac{\left(\frac{q_o}{q_3+q_o}\right)av(H-h_1-h_2)}{1+\left(\frac{q_o}{q_3+q_o}\right)abv(H-h_1-h_2)} && \text{when} \quad \left(\frac{q_2+q_3+q_o}{q_2}\right)h_2+h_1 \le H \le \left(\frac{q_3+q_o}{q_3}\right)h_3+h_2+h_1\\
F&=\frac{av(H-h_1-h_2-h_3)}{1+abv(H-h_1-h_2-h_3)} && \text{when} \quad H \ge \left(\frac{q_3+q_o}{q_3}\right)h_3+h_2+h_1
\end{aligned}
\tag{32}
$$

Figure 14

smoothed out by a tendency of each occupancy quotient to decrease slightly near saturation of its refuge space (see Figure 12). In the limit, in a spatially complex universe partitioned into an infinite array of refuge types with different capacities and occupancy quotients--a spatial continuum from "totally protected" to "totally unprotected"--the functional responses of either type 2 or type 3 predators must resemble the sigmoid curve in Figure 2 (Smith, 1972, cf. Comins and Blatt, 1974).

Interference Among Predators

Although its importance in nature remains a source of controversy (e.g., see Griffiths and Holling, 1969; Hassell and May, 1973), interference among individual predators has been shown to have a potentially tabilizing effect in some predator-prey models (e.g., Hassell and ogers, 1973). Thus it seems appropriate to briefly consider the nfluence of interference on the functional response and on stability in spatially heterogeneous universe.

The most commonly-cited models of interference effects on the ctional response are the purely descriptive equations of Watt (1959) of Hassell and Varley (1969), which ignore the underlying behavioral hanisms. Recognizing this inadequacy, Rogers and Hassell (1974) mpted to account for the reduction in available search time resulting encounters between pairs of randomly searching parasitoids by the owing argument: If it can be assumed that each encounter costs two ites some constant amount of search time (see Ullyett, 1949, but see Hassell, 1971b), then the fraction of parasites effectively nted from searching at any given time will reach a steady state

depending upon the rate of encounter, the parasite density, and the time lost per parasite per encounter. Unfortunately, however, the rate of encounter in Rogers and Hassell's model depends on host density, confounding their searching efficiency parameter.

Consider an alternative approach: In his derivation of the disc equation, Holling writes an equation analogous to

$$F = aH(1-bF), \tag{33}$$

which can be rearranged to yield equation (1); in the above form, however, the type 2 functional response can be extended to include several prey populations hunted by a single predator population. If predators hunt prey of n prey populations via simultaneous and independent searching but with separate handling of individual prey, then the functional response of predators to the ith of n prey populations may be written

$$F_i = a_i v_i H_i (1 - \sum_{j=1}^{n} b_j F_j) \cdot \tag{34}$$

(The v_i terms correct prey densities to allow for refuge space.) Solving all n equations (34) simultaneously for F_m,

$$F_m = \frac{a_m v_m H_m}{1 + \sum_{j=1}^{n} a_j b_j v_j H_j} \tag{35}$$

(cf. Marten, 1973; Timin, 1973; Murdoch, 1973; Lawton et al., 1974; Harris, 1974). Now if Rogers and Hassell's assumption of a constant search time cost per encounter between two searching parasites or predators is valid, then such encounters are closely analogous to capturing prey of another species, imposing another kind of "handling

time" on the searchers. For interference, then, equations (34) can be replaced by

$$F = avH(1-bF-b^*F^*) \tag{36}$$

and

$$F^* = a^*v\bar{p}(1-bF-b^*F^*)$$

where a^* is the rate of "encountering" predators, volume per predator time

b^* is interference time, predator time per predator encountered,

$\bar{p}$ is the effective predator density to which each individual predator is exposed, i.e., the density of predators-minus-one, predators volume^{-1},

and F^* is the number of predators interfered with per predator time, time^{-1}.

Now solving equations (36) simultaneously for the functional response,

$$F = \frac{avH}{1+abvH+a^*b^*v\bar{p}} \tag{37}$$

(cf. Timin, 1973 and see Salt, 1974).

For type 2 predators in a universe with a perfect refuge, prey densities of equations (37) must be reduced by "h" density units to allow for prey inside the refuge space, yielding equation (38) in Figure 15. The figure illustrates two related but separable effects on the stability of the system: (1) varying predator density for a given intensity of interference and (2) varying the intensity of interference with a given predator density.

First, suppose that p_1 is one predator per universe volume; that is, $\bar{p} = 0$, and there can be no interference. Now increasing p not only reduces the slope of the prey increase line rH/p, but, in effect, it

igure 15. The prey density topography with interference among type 2 predators in a universe containing refuge space. $p_4 > p_3 > p_2 > p_1$. "a*" is the rate of "encountering" predators, volume (predator-time)$^{-1}$, "b*" is the interference time, predator-time predator^{-1}; and "$\bar{p}$" is the effective predator density to which each predator is exposed, i.e., predators-minus-one density, predators volume^{-1}.

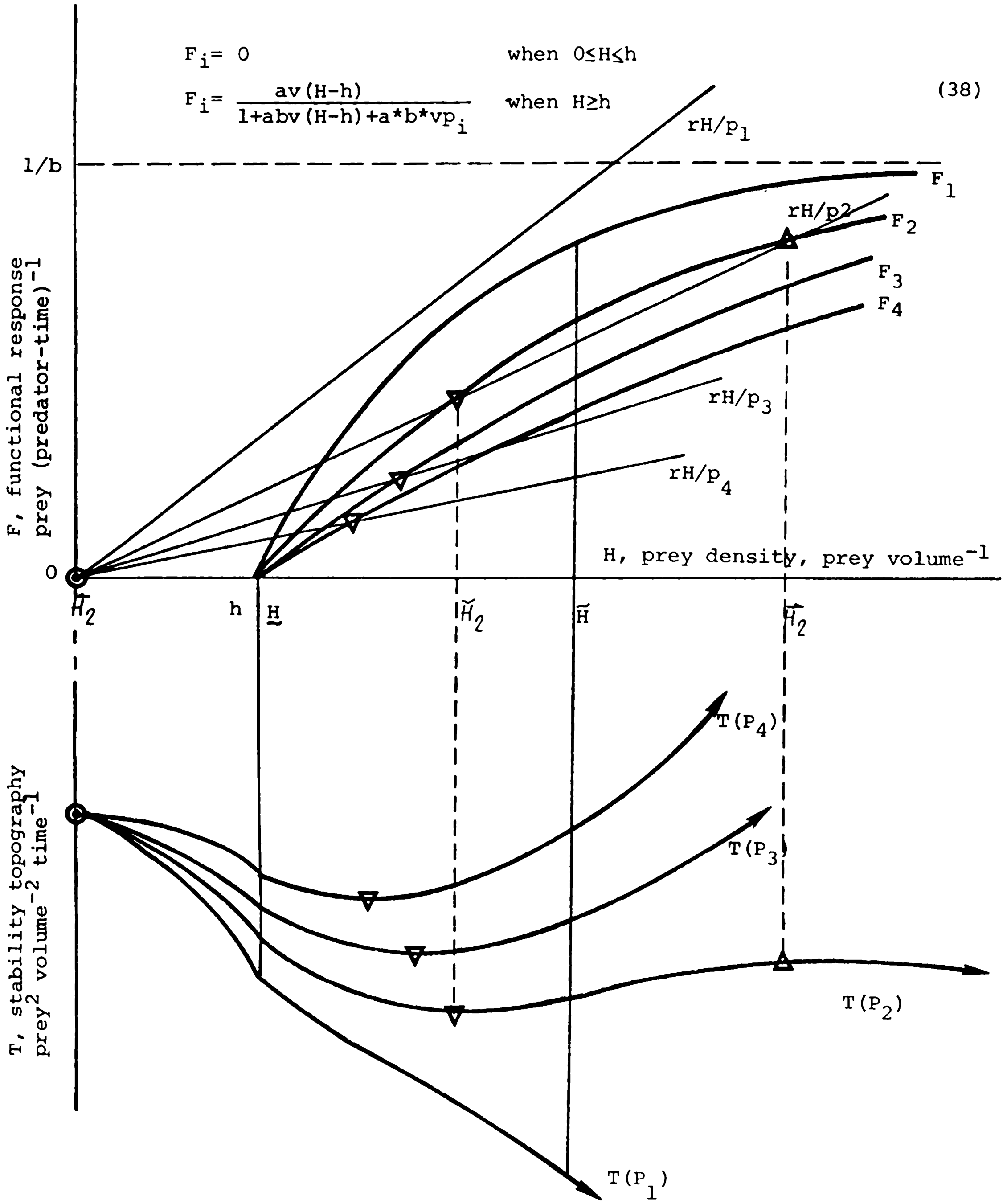

$F_i = 0$ when $0 \leq H \leq h$
$F_i = \frac{av(H-h)}{1+abv(H-h)+a^*b^*vp_i}$ when $H \geq h$
(38)
1/b
0
rH/p_1
$rH/p2$
rH/p_3
rH/p_4
F_1
F_2
F_3
F_4
F, functional response prey (predator-time)$^{-1}$
H, prey density, prey volume^{-1}
$\overleftarrow{H}_2$
h
$\underset{\sim}{H}$
$\breve{H}_2$
$\breve{H}$
$\overrightarrow{H}_2$
T, stability topography prey^2 volume^{-2} time^{-1}
$T(P_4)$
$T(P_3)$
$T(P_2)$
$T(P_1)$

Figure 15

also lowers the rate of successful attack, depressing the functional response at all prey densities in the interval (h, ∞). Figure 15 shows that stable equilibrium prey density still decreases, the chance of extinction increases, and the chance of escape decreases with increasing predator density just as in the absence of interference, though the relative magnitudes of those effects are reduced by interference.

Second, suppose that predator density remains constant at p_3, fixing the prey increase function, but the term a*b* of equation (38) increases from zero (curve F_1) to larger values (F_2, F_3, and F_4 respectively); increasing a*b* amounts to intensifying interference at a constant density of predators. This shift clearly increases $\check{H}$, decreases the chance of extinction, and increases the chance of escape. Therefore, contrary to the results of Williamson (*in* Hassell, 1971b), Hassell and May (1973), and Rosenzweig (1971, 1972), interference apparently increases stability only in the sense of avoiding extinction; escape actually becomes more likely as interference among predators is intensified.

This analysis can also be extended to include effects of *inter*specific interference among predators by simply adding a term of the form a*b*vp to the denominator of equations (37) or (38) for each additional interfering predator population; note that the appropriate predator density in such terms would be *total* density, not predator-minus-one density.

Summary of Theoretical Results

The operational definitions of elasticity and conformability in previous sections can be used to predict the effects of parameter changes on the stability of a predator-prey link. Since changes of parameter values tend to shift the boundaries of the elastic region and of the conformable region all in the same direction, qualitative effects of such changes on elasticity and conformability also depend on the magnitudes of the other parameters. But the qualitative effects of parameter shifts on the chances of prey extinction or escape are unequivocal and can be inferred from the altered proximities of $\check{H}$ and r/p to the elastic and conformable boundaries, respectively. Table 1 summarizes the *qualitative* effects of increasing each of thirteen parameters on the stable equilibrium, the boundaries of the elastic and conformable regions, and the chances of extinction and escape. (Decreasing each parameter invariably reverses its effect.) The *quantitative* implications of any actual or potential set of parameter magnitudes can be found by substitution into the elasticity and conformability equations (23)-(29). In the discussion and the appendix of this paper, both qualitative and quantitative parameter analyses are used to examine experimental results and suggest applications in ecosystem management.

The principal theoretical results of this analysis, with references to pertinent figures and tables in the text, are enumerated below:

1. Heterogeneity of spatial structure can stabilize a predator-prey interaction, and its stability effects can be quantified (Figures 6 and 10).
2. The functional responses of predators to prey density in a universe containing refuge space are basically sigmoid (Figures 6, 7, 12, and 14).

Table 1.--Qualitative effects of increases in each of thirteen parameters on the stable equilibrium density $\check{H}$, the extinction and escape thresholds (elastic boundaries) $\overleftarrow{H}$ and $\overrightarrow{H}$, the conformable boundaries $\overleftarrow{r/p}$ and $\overrightarrow{r/p}$, and the overall chances of extinction and escape. "+" denotes an increase in the magnitude of a variable, "-" a decrease, and "0" no change. Where the outcome is ambiguous and depends on the other parameters, all possible outcomes are given. Note particularly that the stable equilibrium density and the chance of escape respond identically to all parameters, and that the chances of extinction and escape usually respond reciprocally.

parameter increased	$\check{H}$	$\overleftarrow{H}$	$\overrightarrow{H}$	$\overleftarrow{r/p}$	$\overrightarrow{r/p}$	chance of extinction	chance of escape
a, successful attack rate	-	+,0	+	+,0	+	+	-
a*, predator encounter rate	+	-,0	-	-,0	-	-	+
b, handling time	+	-,0	-	-,0	-	-	+
b*, interference time	+	-,0	-	-,0	-	-	+
c, Allee coefficient	-	+	+	+,0	+	+	-
e, exchange rate	0	+,0	0	+,0	0	+	0
h, refuge capacity	+	0	-	-,0	-	-	+
k, carrying capacity	+	-,0	-	-,0	-	-	+
p, predator density	-	+,0	+	0	0	+	-
q, occupancy quotient	0	-,0	0	-,0	0	-	0
r, prey increase rate	+	-,0	-	0	0	-	+
s, sigmoid coefficient	+	0	-	0	-	-	+
v, volume ratio	-	+,0	+	+,0	+	+	-

3. Shifts of parameter values usually cause mutually reciprocal shifts in the chances of prey extinction and escape; stable equilibrium prey density responds like the chance of escape (Table 1).
4. Increasing the amount of refuge space in a system decreases the chance of extinction and increases the chance of escape; <u>reducing</u> the amount of refuge space has the opposite effects (Table 1).
5. A system containing many small refuges can have a higher chance of prey extinction than one with few large refuges (Figure 13, Table 1).
6. Intraspecific interference enhances the chance of prey escape and reduces the chance of their extinction; but increasing predator density <u>decreases</u> the chance of escape and <u>increases</u> the chance of extinction, even with particularly intense interference (Figure 15, Table 1).

DISCUSSION

Three Predator-Prey Interactions Revisited

In this section three predator-prey studies are reconsidered from the viewpoint emphasized in this paper. Two of them provide specific but qualitative examples of how this analysis can help interpret the effects of spatial structure in predation, and the third attempts a more quantitative (though somewhat speculative) application to data from an experimental field study.

Tribolium vs. Oryzaephilus

Crombie (1946) observed the interaction between populations of the flour beetles *Tribolium confusum* and *Oryzaephilis surinamensis* in renewed wheat and flour media. In wheat, the populations coexisted, but in flour *T. confusum* consistently eliminated *O. surinamensis* via "voracious" predation on its pupae. However, when the flour medium contained glass tubing of 1 mm. internal diameter--large enough to allow orzyaephilus to enter and pupate but small enough to exclude tribolium adults and large larvae--both populations survived just as in wheat.

Apparently the glass tubing in flour and the bran in wheat can provide refuges for the vulnerable oryzaephilus pupae, allowing coexistence of the two beetle populations. The functional response of tribolium to the density of oryzaephilus pupae is displaced to the right by the capacity of all tubes or bran within the critical size

range. Since self-limitation of predators by cannabalism allows relatively high predator densities (low r/p), and since the prey exchange rate is low and the occupancy quotient is high, then the stable equilibrium prey density $\check{H}$ must approximately equal the refuge capacity h. In other words, almost all surviving oryzaephilus pupae must be inside tubes or bran, and pupal density should be quite stable, as Crombie observed. This interaction exemplified curve 1 of Figure 13 (but with smaller r/p).

Typhhlodromus vs. *Tarsonemus*

Huffaker and Kennett (1956) studied the interaction between the predatory mite *Typhlodromus sp*. and the cyclamen mite *Tarsonemus pallidus* in an attempt to develop a program for control of *T. pallidus* in strawberry fields. The strawberry plant provides an unusually favorable microenvironment for tarsonemus within the many folds and crevices in the crown of the plant, furnishing food, humidity, and protection from predators.

> Physical barriers, representing a security threshold that results from the great heterogeneity in the microenvironment, seem to preclude actual extermination of the prey on any unit as large as an entire plant, or at least a group of adjacent plants. Hence, equilibrium is reached and a rough, although disturbed, balance at very low densities is characteristic (Huffaker and Kennett, 1965, p. 194).

Structural spatial heterogeneity has clearly stabilized this interaction much as for tribolium and oryzaephilus.

But there is another important facet of this mite predator-prey link, recognized by Huffaker and Kennett: even though the predators' reproductive rate at high prey densities is comparable to the prey's, this reproductive numerical response is "almost meaningless" for

controlling the prey population without a high searching capacity and the ability to survive at low prey densities. In other words, the functional response plays a much more vital role in determining the stability properties of this interaction than does the reproductive numerical response, despite similar increase rates of the two populations (see also Huffaker and Kennett, 1966; and Stabilizing Responses of Predators below).

Ishnura vs. *Simocephalus*

Johnson (1973) studied the effects of predation by damselfly naiads (*Ishnura verticalis*) on a littoral cladoceran population (*Simocephalus serrulatus*) in plastic wading pools. Each of the eight pools contained 40 artificial "weeds" composed of thin strips of plastic window screen hanging down from above the surface to near the bottom. Three weeds in each pool were sampled every fourth day to estimate prey and predator densities; by comparing observed prey densities with predictions of a mathematical model from the densities and egg counts four days before, Johnson could calculate mortalities due to predation over the interval.

The time-course of simocephalus density in the eight pools, modified from Johnson's Figure 4, is presented in Figure 16. In my view, these curves suggest the existence of an escape threshold at a density of about 180 prey liter^{-1}; below that level densities tend to remain relatively constant, but once above 180 prey liter^{-1} densities increase in a sharp, irregular pattern, decreasing again only at the end of the experimental period with falling ambient temperature. Note particularly the wide variation in the number of days from predator

Figure 16. Densities of simocephalus in eight wading pools observed at 4-day intervals. The left triangle indicates the date of ishnura introduction; the right triangle marks the date at which a given simocephalus population exceeded the postulated threshold density, near 180 animals liter^{-1} (data from Johnson, 1973).

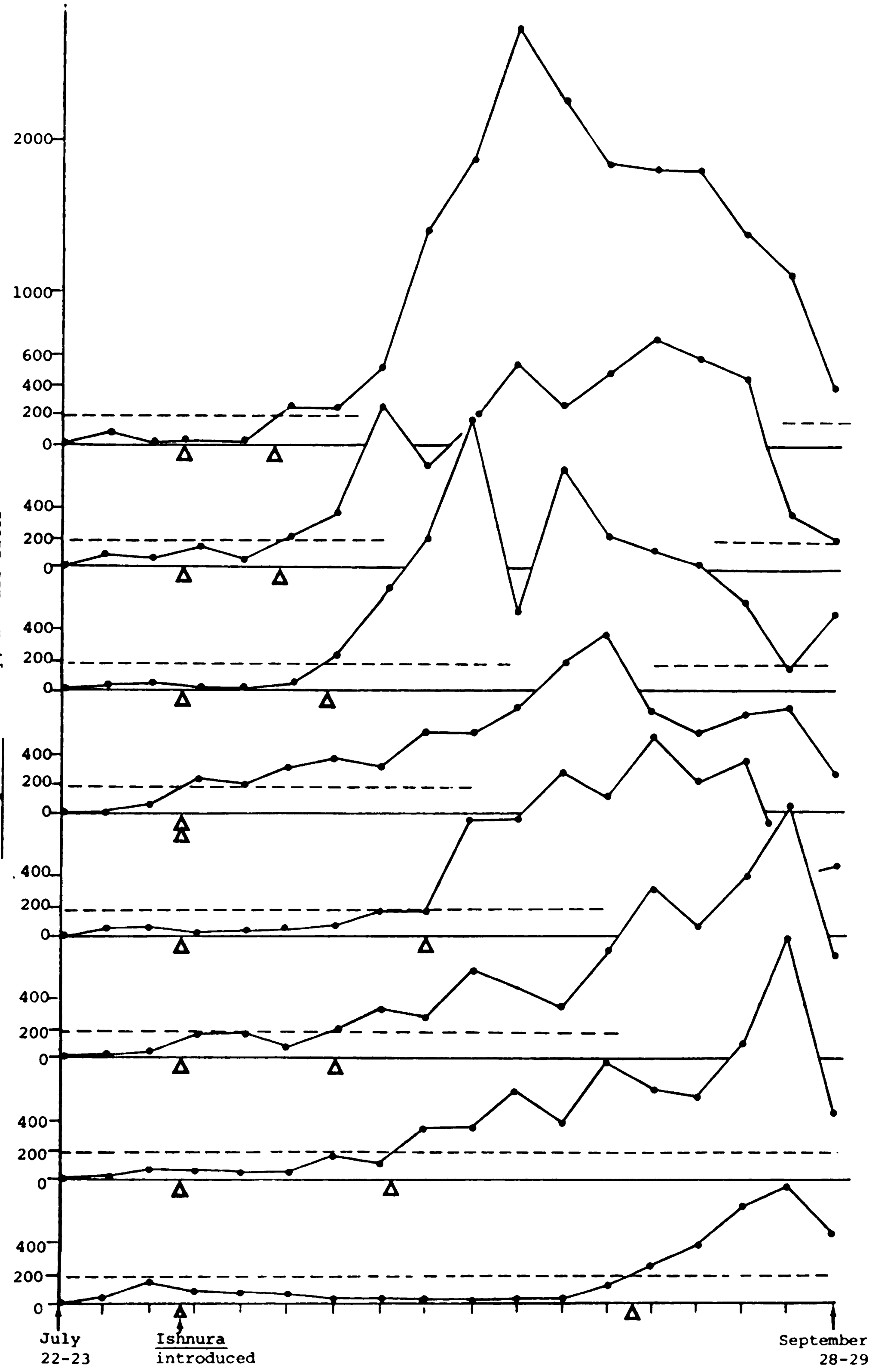

2000
1000
600
400
200
0
400
200
0
400
200
0
400
200
0
400
200
0
400
200
0
400
200
0
400
200
0
Simocephalus density, animals liter^{-1}
July
22-23
Ishnura
introduced
September
28-29
sampling dates, 4-day intervals

Figure 16

introduction until the hypothetical threshold is crossed: 8,9,13,0,22,14, 18, and 38 days respectively. It is tempting to suppose that during the interval following predator introduction, each simocephalus population was regulated by ishnura until prey density "accidentally" exceeded the escape threshold, freeing the prey from limitation by predators. But since ishnura is not a type 3 predator (at least not without significant densities of alternate prey--see Lawton et al., 1974) and exhibits negligible numerical or developmental response to simocephalus density (Johnson, 1973), spatial heterogeneity should be investigated as a possible critical stabilizing factor in this interaction.

Johnson's experimental universe contained two kinds of refuge space:

1. The sides of the pools, representing about 30% of the vertical surface area (weeds accounted for the other 70%), were essentially inaccessible to hunting damselflies; about 30% of the simocephalus were associated with the sides at all prey densities.

2. The weed surfaces themselves provided a partial refuge for simocephalus. Because ishnura hunts mainly by ambush, grasping passing prey that contact its antennae with a quick extention of its labium, simocephalus attached to weeds (via cervical glands located dorsally on the carapace) must have been much less vulnerable to damselflies than those actively swimming within a weed. The pool-side population, not counted in Johnson's density estimates, increased the effective per capita increase rate of the prey exposed to predators by a factor of 1.43 (100% ÷ 70%), assuming fairly rapid exchange of prey between the sides and the weeds, but could not displace the type 2 functional response curve to stabilize the interaction. The weed surfaces, however,

probably could have such a stabilizing effect. As the density of simocephalus attached to a surface increases, they become much more active, and the percent of attached animals decreases; if this occurred at relatively low densities within the artificial weeds, the functional response of the damselflies could assume a potentially stabilizing, sigmoid shape (cf. Haynes and Sisojevic, 1966).

Now examine Figure 17. The data points were calculated from the positive predation mortality estimates of Johnson (1973). The dashed line is his unpublished fit to the circled points, for which estimated and observed prey density differed significantly. Though this curve was obtained using standard techniques--linear transformation and least squares analysis (Holling, 1959b)--it clearly fails to fit or describe the data satisfactorily, especially near the origin. By displacing this same type 2 functional response curve 30 animals liter^{-1} to the right, however, a much more plausible fit for low prey densities is found. (Such a displacement is equivalent to postulating the existence of about 200 highly-sought, essentially invulnerable hiding places for simocephalus per weed, an interpretation which could only be adequately evaluated by directly observing simocephalus activity in the weeds as a function of density.) A high refuge occupancy quotient that decreased with increasing prey density would imply the very low extinction threshold and the initial positively-accelerated functional response illustrated in Figure 17 (cf. Figure 12).

Using the observed mean predator density "p", and estimates of per capita prey increase rate "r" mathematically predicted by Johnson's growth model for each interval, the prey increase function rH/p has been calculated. The lower straight line in Figure 17 incorporates the

Figure 17. The functional response of ishnura to simocephalus density in eight wading pools. Data points are calculated from the positive predation mortality estimates in Johnson, 1973; circled points differ significantly from zero at the 5% level. The dotted curve is Johnson's unpublished fit of equation (1) to the significant data points; from his fitted curve displaced 30 prey density units to the right, the sigmoid plot is drawn. The two straight lines are prey increase functions--the lower an average for intervals during which prey were presumably regulated by predators, and the upper an average for intervals during which escape occurred.

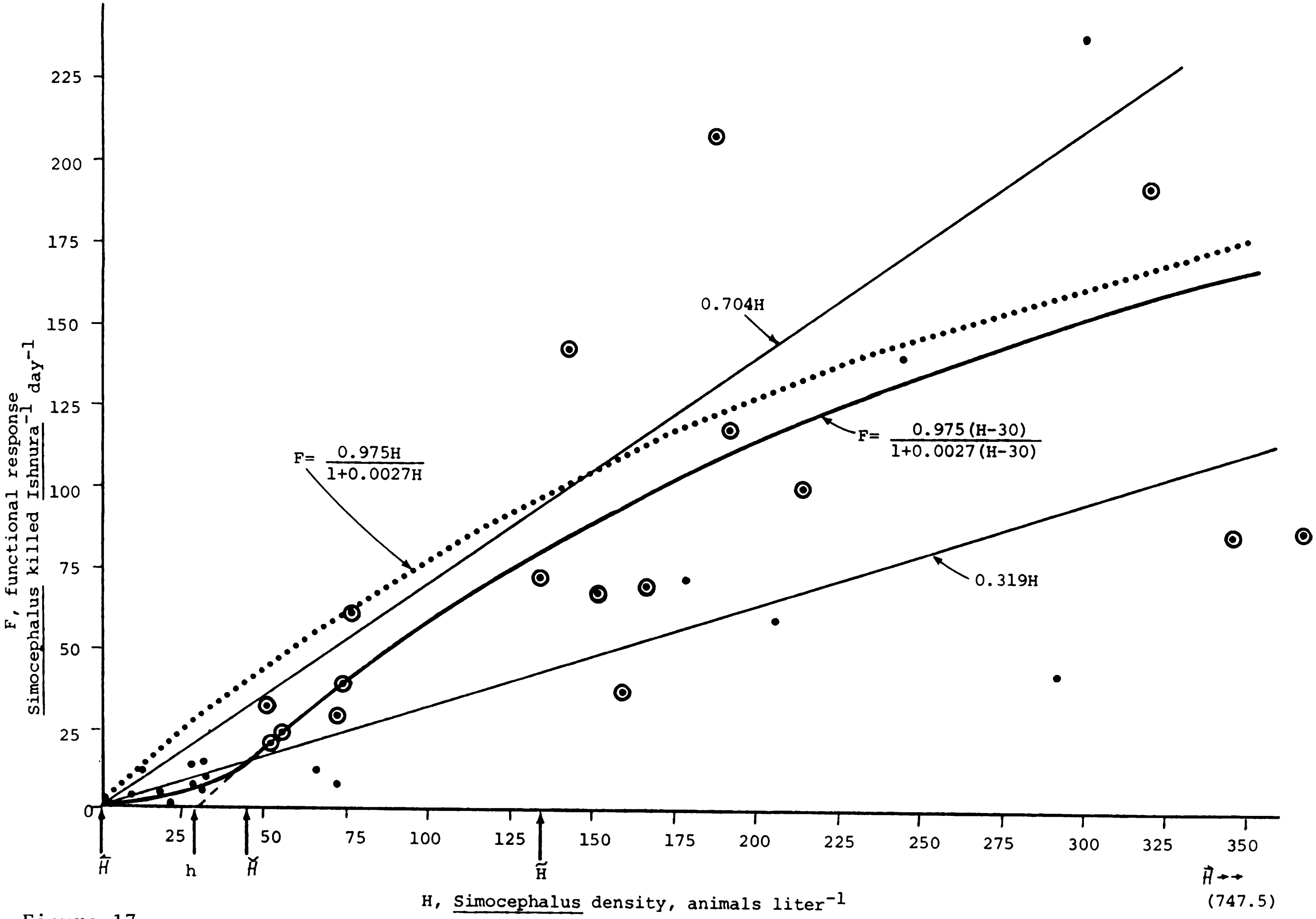

F, functional response
Simocephalus killed Ishnura^{-1} day^{-1}
225
200
175
150
125
100
75
50
25
0
25
50
75
100
125
150
175
200
225
250
275
300
325
350
$\hat{H}$
h
$\check{H}$
$\tilde{H}$
$\vec{H}$ →→
(747.5)
H, Simocephalus density, animals liter^{-1}
0.704H
$F = \frac{0.975H}{1+0.0027H}$
$F = \frac{0.975(H-30)}{1+0.0027(H-30)}$
0.319H

Figure 17

mean "r" for the predator-regulated sampling intervals (0.217 day^{-1}); from equation 11, the stable equilibrium at the intersection of this function with the functional response curve (45.5 prey liter^{-1}) is reasonably close to mean prey density during predator-regulated intervals (66.7 prey liter^{-1}). The *upper* straight line in the figure uses the mean "r" for sampling intervals in which the prey presumably escaped regulation by predators (0.480 day^{-1}); since this prey increase function exceeds the functional response at all positive prey densities, such "r" values do appear consistent with prey escape during the corresponding sampling intervals.

Johnson (1973) emphasizes another source of fluctuating predator influence on prey. He argues that predation rates of individual damselflies probably change considerably during each instar such that any significant degree of molting synchrony could produce important shifts in effective predator density during the experimental period (also see Johnson et al., 1975). Thus *both* parameters of the prey increase function, "r" and "p", seem relatively "noisy"; with the prey increase function bobbing up and down erratically, the effective escape threshold must be near or somewhat above $\tilde{H}$, the maximum conformable prey density. And in fact, the apparent threshold in Figure 16, about 180 prey liter^{-1}, does only slightly exceed the $\tilde{H}$ found from equation 17, 135.4 simocephalus liter^{-1}.

Fortunately, neither the magnitude of $\tilde{H}$ nor the possibility of regulation and escape of the simocephalus population depends very strongly on the exact shape of the functional response curve through the scattered data points at high prey densities. Other parameter values may alter the $\hat{H}$ estimate slightly, but for many cases with refuge capacities near 30 prey liter^{-1}, the observed prey density sequences seem to agree with the postulated stability properties of the system.

Stabilizing Responses of Predators

Errington (1946, 1956) believed that most predators, especially mammals, merely skim off the "excess" from the prey population and exert no real stabilizing effect; he labelled such predation "compensatory." If he had attempted to define "excess" objectively by relating prey density to environmental structure, Errington might have recognized the stabilizing potential of "compensatory" predators (Huffaker and Watson *in* Huffaker, 1971; Maynard Smith, 1974).

In fact, Errington's view implies that predators in a universe with limited refuge space should tend to have sigmoid functional responses to prey density, since capture rates increase sharply as prey density exceeds his "threshold of security" (cf. Figure 12). Holling (1959b), Solomon (1964), and Murdoch (1973) recognized this effect but did not emphasize its significance for stability in spatially complex environments; they and many others have concentrated on behaviorally-generated sigmoid curves that can be analyzed in simple laboratory systems, largely ignoring the ubiquitous but conceptually elusive spatial effects (Tullock, 1970). But the stability implications of the sigmoid functional response itself (whatever its cause) now seem to be widely appreciated: wherever the curve increases with prey density faster than linearly, a stable, predator-limited equilibrium prey density could occur (e.g., Holling, 1959b; Huffaker et al., 1968; May, 1973).

Of course, this criterion for a stabilizing functional response does not strictly require a smooth sigmoid curve, as Figures 6-11 clearly demonstrate (cf. Hassell, 1966; Steele, 1974); nor does it necessitate learning by the predator, or search-image hunting, or the presence of alternate prey. The following three general conditions, implicitly quantified in the foregoing derivation, are sufficient to generate such a curve for ordinary type 2 predators:

1. limited (saturable) refuge space,
2. some tendency for prey to occupy this space, and
3. some tendency for predators to avoid it or be excluded.

Refuge space for pey, at least "relative" refuge space, must be present in virtually all natural ecosystems. Furthermore, in systems with an evolutionary history, natural selection must enforce a strong preference by prey for safe hiding places, as noted previously. And though adapting to safer surroundings may be a comparatively minor behavioral or evolutionary feat, evolving the ability to hunt effectively in new terrane must usually imply such relatively drastic modification that relative ineffectiveness of predators inside the refuge space is expected (see Slobodkin, 1974). But Smith's marble game suggests that "prey populations with predation present will tend to be found in the more hidden places of their environment, <u>even if they do not select such places</u>" whenever exploitation can reduce catchability (Smith, 1972).

The least generally recognized of the three conditions above is perhaps the most restrictive: that the average vulnerability of prey must increase with density over some range below the carrying capacity--i.e., that the refuge space can become <u>saturated</u> with prey (Smith, 1972).

For type 2 predators with a negligible numerical response, protecting a <u>constant number</u> of their prey yields the stabilizing positive displacement of the functional response curve along the prey density axis (see Figures 2 and 12): per capita protection of prey decreases as the refuge space fills up. In contrast, protecting a <u>constant fraction</u> of prey at all densities is equivalent to proportionally shrinking the rate of successful attack "a" in equation (1) (see Griffith's 1969 analysis of "spatial coincidence"); since the shape of a type 2 functional response remains convex upward after any such shift of "a", any positive, predator-limited equilibrium must remain unstable.

The stability effects of these two kinds of protection can be compared for several published models: In Rosenzweig and MacArthur's classic graphical model (1963) both kinds of protection are stabilizing, whereas Maynard Smith (1974), using modified Lotka-Volterra equations, shows that only the "constant number" case lends stability to the interaction. And for Nicholson and Bailey's (1935) model, Varley (1947) claims that protecting a constant fraction of prey is stabilizing, but Bailey et al. (1962) reply that neither kind of protection can be a common source of stability. Yet because in each of these models the functional response is over-simplified and masked by the numerical response, their lack of predictive agreement is not surprising.

In nature, if not always in mathematical models, the relative impacts of the functional and the numerical responses on stability reflect the reproductive rates and lags of predators and prey:

1. If the time scale of the predator's numerical response (inverse per capita increase rate plus lag time) T_N is small relative to the

time scale of prey increase (inverse per capita increase rate of prey) R, then the numerical response determines stability, yielding a tightly damped oscillatory response to density perturbations (e.g., the host-helminth parasite interactions of Anderson, 1974).

2. If $N \sim R$, then a stabilizing functional response is necessary but insufficient for system stability, and population densities oscillate with large amplitude in response to perturbations (e.g., the Typholodromus-Tarsonemus interaction of Huffaker and Kennett, 1956; see Solomon, 1964; Huffaker and Kennett, 1969).

3. If $N \gg R$, then a stabilizing functional response is necessary and sufficient for system stability, and population densities respond asymptotically to perturbations (e.g., the marine copepod-phytoplankton interactions of Steele, 1974; see Takahashi, 1964).

Since a numerical response in nature can be expressed only after a time lag, the elasticity of an ecosystem must be independent of the numerical response. Conformability, however, can be increased considerably by the capability for relatively rapid changes in predator density. For example, a seasonal increase in "r" may increase reproduction by predators, counteracting the rise in initial slope of the prey increase function with higher "r". But as implied by the three categories above, this enhanced conformability depends critically on the magnitude of time lags in the numerical response: any negative feedback expressed only after a lag that is long relative to the natural time scale of the system will be destabilizing (May, 1973).

Application to Biological Control and Game Management

The purpose of biological control is to confine a pest population below an "economic threshold" density, whereas in game management a relatively high, constant density of the game population is usually desirable. Yet both can require stabilizing a predator-prey interaction in the face of environmental perturbations, often in structurally heterogeneous environments. The theroetical analysis in this paper shows that with some knowledge of the frequency distribution of environmental perturbations as a function of type (i.e., shocks or shifts) and amplitude, system parameters can be adjusted to reduce the risk of extinction or escape or alter stable equilibrium density (see Summary of Theoretical Results).

Suppose, for example, that a game bird population is under such heavy predation pressure from hunters and other mammalian populations that a hard winter could cause local extinction. A program calling for enrichment (supplementary food to increase "r" and "k"), barrier construction (fences to reduce "e" and exclude predators from refuges), and additional refuge space (increasing "h") could be designed to greatly reduce the chance of extinction. Similarly, for an insect pest with a tendency for seasonal outbreaks, direct predator stocking (increasing "p"), control of alternate prey, and limiting refuge space (a special crop variety to decrease "h") may prevent outbreaks or at least reduce their frequency. Note, however, that overcompensation could also be disastrous; for the pest example, extinction or near extinction of the pest may drastically reduce or eliminate any highly specific predator, facilitating escape by the pest after a rebound or reintroduction. Thus the stability effects of projected parameter adjustments must be <u>quantified</u>, perhaps using techniques like those outlined here, if ecosystem management is to progress much beyond ecological trial-and-error.

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APPENDIX A

DISC EXPERIMENTS

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When Holling (1959) derived equation (1), he attempted to validate it experimentally with his blindfolded secretary "preying" on sandpaper discs thumbtacked to the tope of a small table. Using estimates of handling time and successful search rate obtained from earlier results, he drew a theoretical curve like Figure 1 which the data from his disc experiments fit very well.

Rogers (1972) performed similar experiments with polyethylene discs that were either removed by the predator (to simulate predation) or marked and replaced (to stimulate parasitism). He showed theoretically that when exploitation is taken into account--as it must be if prey are removed by the predator faster than they are replaced during the experiment--the randomly searching predator must actually have a higher successful search rate than Holling had supposed to fit data from this type of experiment. Since his predator apparently removed discs without replacing them, Holling's estimate of the successful search rate must have been automatically biased downward by this exploitation effect.

In order to obtain experimental support for the equations and curves of Figure 4, I have repeated and modified the disc experiments of Holling (1959). But to avoid the exploitation effects considered by Rogers (1972) and to obtain a truly instantaneous response, I replaced the discs as the predator removed them. The predator, a blindfolded lab technician, searched a circular bulletin board one meter in diameter by probing with a fingertip.

Three separate sets of experiments were performed:

1. Holling's (1959) experiments were repeated, using discs of coarse emergy paper 5 cm in diameter thumbtacked to the board. The number of discs picked up in three minutes was observed at six densities presented to the predator in random order: 10, 20, 40, 70, 110, and 160 discs per 7854 cm^2. Three replicates were run at each density.

2. Additional experiments were run with 5 cm discs as prey, but in a universe containing a single refuge having a capacity of 20 prey. The refuge space, a 90° wedge containing a fourth of the total area, was bounded by a thin aluminum strip taped to the board, and the predator was restricted to hunting outside the refuge only. The refuge occupancy quotient "q" was arbitrarily set at 0.667; dice were thrown to determine the actual distribution of prey inside and outside the refuge. Six replicates were run at each of the six densities.

3. In the third set of experiments, the universe again contained the refuge of capacity 20, but the predator was told to hunt only inside the refuge. Prey were 2.5 cm discs, for which the rate of successful attack was about one third that for 5 cm discs. As in experiment 2, a "q" of 0.667 was simulated using dice, and six replicates were performed at each of the six densities.

At various times between experimental runs, handling times for both large and small discs, tap rate, and effective fingertip radius were measured independently of the experimental procedure. Disc handling, clocked to the nearest 0.1 sec with a stopwatch, averaged 2.37 ± 0.05 sec for the 5 cm discs and 2.49 ± 0.06 sec for the 2.5 cm discs; the difference between these means is not statistically significant (t-test, 58 d.f., $0.1 < P < 0.2$). Tap rate, counted for one minute on three separate occasions, averaged 62 ± 2.0 taps per minute. And effective tap radius, obtained by inking the predator's finger before she tapped around the perimter of a disc, measured 0.5 ± about 0.05 cm.

From these independent measurements of handling times, tap rate, and fingertip radius, the parameters of equations (4) were evaluated (see Table 2) and the curves of Figures 18 and 19 were drawn. Data points ± 2 S.E. from experiment 1 are plotted in Figure 18; data points ± 2 S.E. from experiments 2 and 3 are plotted in Figure 19. Note that the error intervals include the theoretical curves in all cases except two data points from experiment 2. Only one of these points (density 160) has a 95% confidence interval which does not contain the curve. Careful observation of the predator in action suggests that handling time may actually have decreased slightly at this highest density, at which most taps touched a disc--see also density 160 in Figure 18.

These results provide an initial validation of equations (4) in a simple, generalized predator-prey system. Since derivation of equations (4), parameterization of these equations, and gathering of experimental data were all accomplished independently of each other,

Table 2.--Parameters from the disc experiments.

parameter	magnitude	units	calculation
a, rate of successful attack outside	0.670	7854 cm^2 $(3min)^{-1}$	(effective area of tap)(taps per 3 min) = $(\pi\ (d+f)^2)(3g)$ where d is large disc radius, cm, f is effective finger-tip radius, cm, and g is tap rate, taps min^{-1}
$\underline{a}$, rate of successful attack inside	0.228	7854 cm^2 $(3min)^{-1}$	(effective area of tap)(taps per 3 min) = $(\pi(d'+f)^2)(3g)$ where d' is small disc radius, cm
b, handling time for 5 cm discs	0.0132	3 min $disc^{-1}$	direct measurement [1/b = 75.8 discs $(3\ min)^{-1}$]
$\underline{b}$, handling time for 2.5 cm discs	0.0138	3 min $disc^{-1}$	direct measurement [1/$\underline{b}$ = 72.5 discs $(3\ min)^{-1}$]
h, refuge carrying capacity	20	discs $(7854\ cm^2)^{-1}$	arbitrarily predetermined
q, refuge occupancy quotient	0.667	dimensionless	die rolled for each disc: 1,2,3, or 4 inside--5 or 6 outside, with a maximum of 20 discs inside
u, area of experimental universe	7854	cm^2	arbitrarily predetermined
v, area ratio outside	1.333	dimensionless	total area of experimental universe ÷ area outside refuge
$\underline{v}$, area ratio inside	4	dimensionless	total area of experimental universe ÷ area inside refuge

Figure 18. The functional response of a lab technician to the density of sandpaper discs thumbtacked to a bulletin board (no refuge space). Data points are means of three replicates bracketed ± 2 standard errors; parameters of the curve drawn through these points were evaluated independently of experimental data.

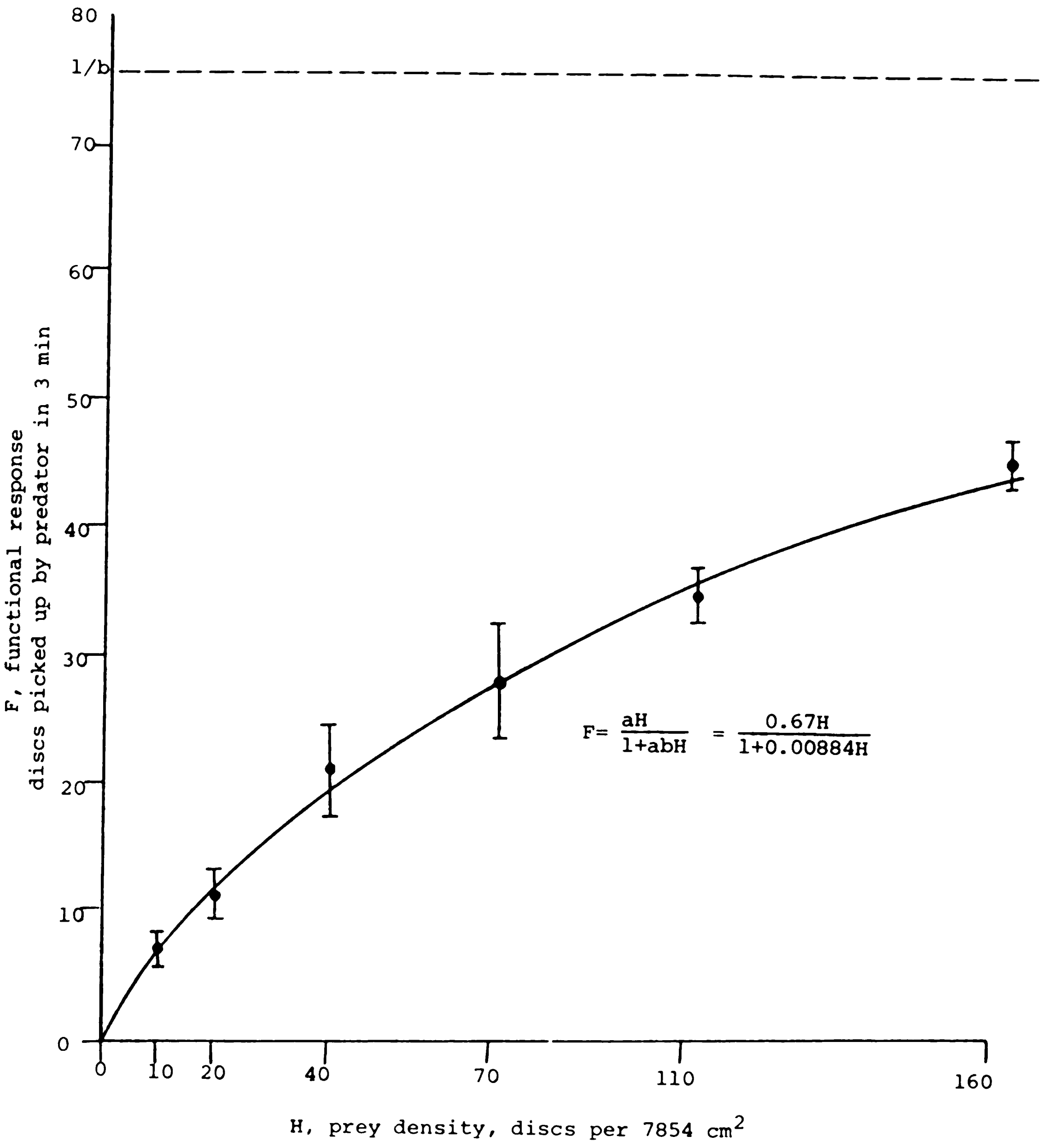
80
1/b
70
60
50
40
30
20
10
0
F, functional response
discs picked up by predator in 3 min
0
10
20
40
70
110
160
H, prey density, discs per 7854 cm^2
$F = \frac{aH}{1+abH} = \frac{0.67H}{1+0.00884H}$

Figure 18

Figure 19. The functional response of a lab technician to the density of sandpaper discs thumbtacked to a bulletin board (with refuge space). The open-circle points are means of six replicates in which the predator hunted only inside a wedge-shaped refuge; the solid points are means of six other replicates in which the predator hunted only outside. Error intervals bracket ± 2 standard errors. Parameters of the curves drawn through the points were evaluated independently of experimental data.

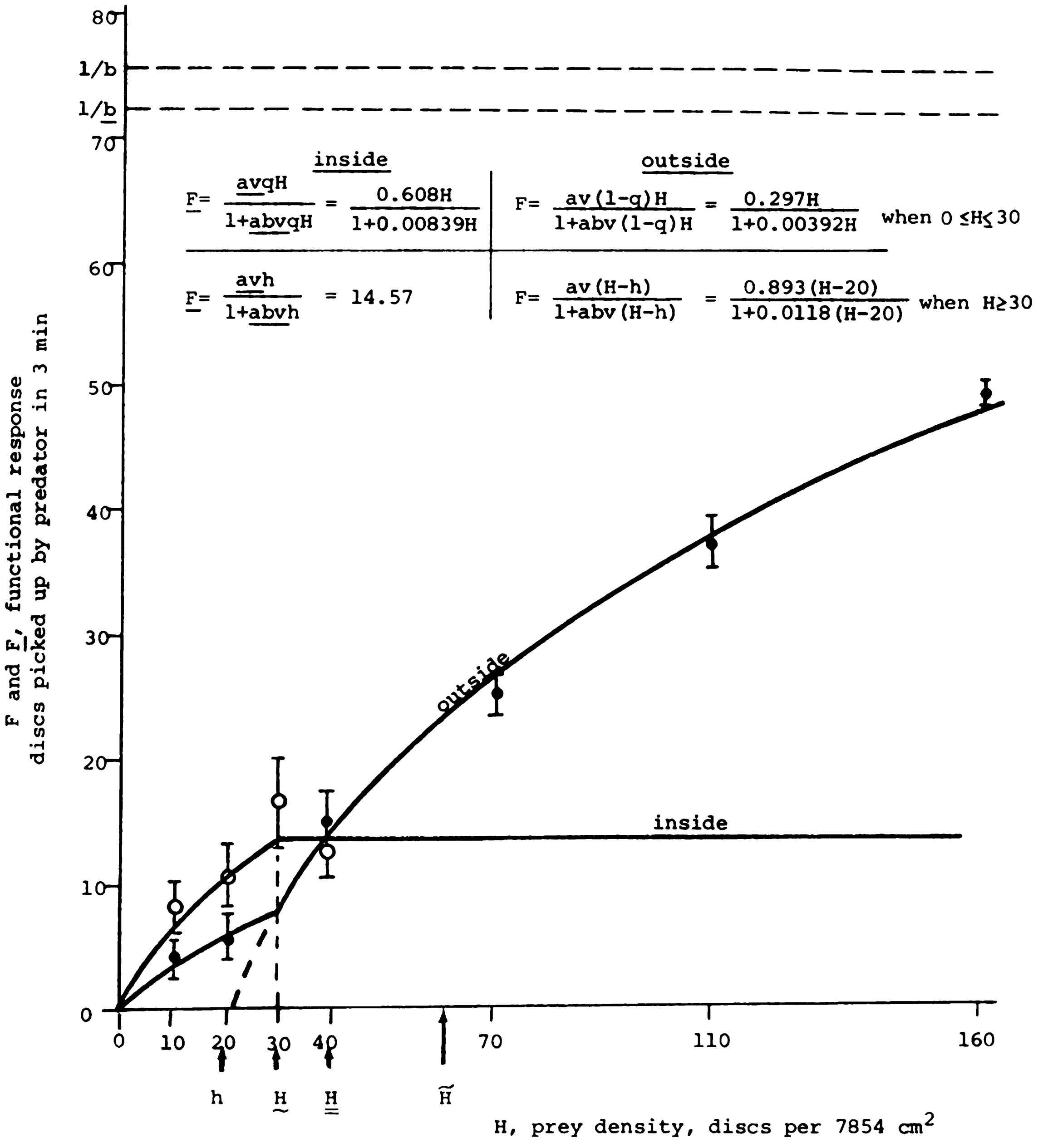
80
1/b
1/b
70
60
50
40
30
20
10
0
inside
outside
F= avqH / 1+abvqH = 0.608H / 1+0.00839H
F= av(1-q)H / 1+abv(1-q)H = 0.297H / 1+0.00392H when 0 ≤H≤ 30
F= avh / 1+abvh = 14.57
F= av(H-h) / 1+abv(H-h) = 0.893(H-20) / 1+0.0118(H-20) when H≥30
F and F, functional response
discs picked up by predator in 3 min
outside
inside
0
10
20
30
40
70
110
160
h
H
H
H
H, prey density, discs per 7854 cm²

Figure 19

there is no cause to suspect accident or artifact in the reasonable fits of curves and data in Figures 18 and 19.

The predator was not allowed to choose whether to hunt inside, outside, or both during an experimental run. Such "free choice" experiments, though they may more realistically reflect options open to predators in nature, would in this case yield results confounded by such extraneous factors as the duration of experimental runs and the motives of the human predator. An alternative approach to the question of spatial allocation of hunting effort--the approach assumed in these experiments and in the theoretical development--is to measure the functional response inside and outside separately; an overall functional response can then be obtained as an average weighted by the proportions of predators in each area or by the proportion of the exposure time spent per area by each predator.

If the disc population were increasing at a per capita rate related to prey density by a known function, then some of the stability properties of this predator-prey system could be calculated from equations (24)-(27) or equations (24), (25), and (29). Even without knowing the function $R(H)$, however, $\underline{\underline{H}}$, $\underset{\sim}{H}$, $\tilde{H}$, and C can be found for separate cases in which the predator hunts only outside or the predator hunts wherever the functional response is highest. See Table 3.

Table 3.--Stability variables from the disc experiments.

variable	magnitude	units	calculation
$\underset{\sim}{H}$, lower boundary of the conformable interval for a predator restricted to the outside; also h/q, the slope discontinuity	30	discs $(7854\ cm^2)^{-1}$	equation (18)
$\underline{\underline{H}}$, the intersection density	40.3	discs $(7854\ cm^2)^{-1}$	equation (6)
$\tilde{H}$, upper boundary of the conformable interval	61.1	discs $(7854\ cm^2)^{-1}$	equation (20)
C, conformable interval for a predator restricted to the outside	(0.226, 0.405)	$7854\ cm^2$ (predator-3min)$^{-1}$	equation (26)
C, conformable interval for a predator hunting prey with q that decreases significantly with density	(0,297 0.405)	$7854\ cm^2$ (predator-3min)$^{-1}$	equation (28)