

EFFECTS OF INITIAL NUMBERS AND INTRINSIC
RATES OF INCREASE ON THE OUTCOME OF
INTERSPECIFIC COMPETITION AS
PREDICTED BY THE LOTKA-
VOLTERRA COMPETITION
EQUATIONS

By

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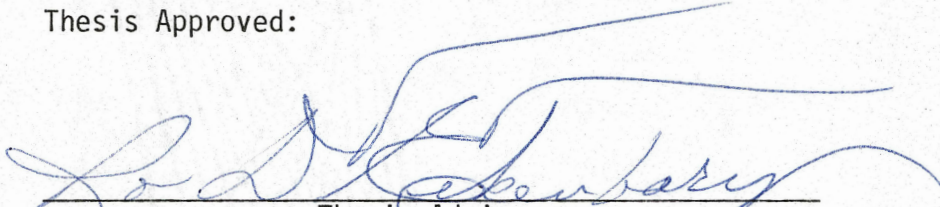
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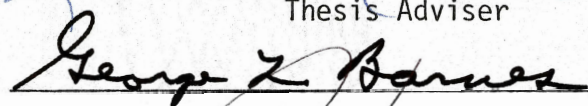


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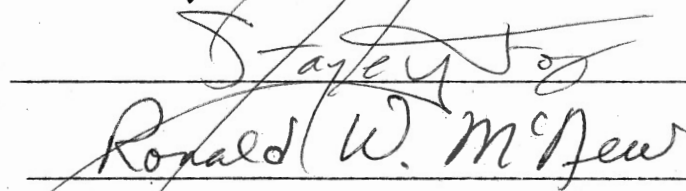
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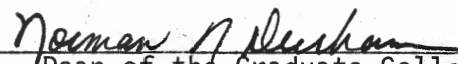
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CHAPTER I

INTRODUCTION

The well known competition equations of Lotka-Volterra can be written as a set of differential equations, namely,

$$\begin{aligned} 1) \quad \frac{dN_1}{dt} &= r_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right) \\ 2) \quad \frac{dN_2}{dt} &= r_2 N_2 \left(\frac{K_2 - N_2 - \alpha_{21} N_1}{K_2} \right) \end{aligned}$$

where N_1 and N_2 are the population sizes of the two competing species with K_1 and K_2 their respective carrying capacities and r_1 and r_2 their instantaneous per capita rates of growth (biotic potentials). The two alphas are competition coefficients: α_{12} is the per capita inhibitory influence of species 2 on species 1 and α_{21} is the reciprocal effect of species 1 on species 2. When these equations are coupled, they describe the simultaneous growth of two competing species in a homogenous environment over ecological time.

Ecologists have utilized these competition equations, and continue to do so, despite recognized drawbacks. These include linear approximations of the competition coefficients (Gilpin and Justice 1973, Smith-

Gill and Gill 1978, Abrams 1980), the assumption that all individuals are competitive equivalents, and that biotic potentials and carrying capacities are constant (Pianka 1978). Lacking from these equations are such considerations as stochastic fluctuations (Rao 1979) and time lags (Wangersky and Cunningham 1957, Hassel and Comins 1976). Nonlinear alternatives are discussed in Vandermeer (1973), Rosenzweig and MacArthur (1963) and Gilpin (1973). Due to these deficiencies, the equations are generally considered to be poor representatives of reality (Wilbur 1972), but they still model competition adequately for some species in nature (Istock 1977). Even Gause (1934) concluded that in all probability no population ever grows exactly according to the Lotka-Volterra predictions but that the true equations are likely to yield solutions very similar to those of Lotka-Volterra.

Simple algebraic manipulations of the equations can define the conditions where the growth of either population is zero in the presence of its competitor for any given values of K_1 , K_2 , α_{12} , and α_{21} . Four possible outcomes are realized depending upon the geometric configurations formed when the resulting isoclines are plotted (Gause and Witt 1934, Vandermeer 1970, Pianka 1978).

The outcomes, or cases, may be described by a set of inequalities formed by the competition coefficients and carrying capacities (Reiners, et al. 1973, Pianka 1978). These are:

$$\begin{array}{ll}
 1) \quad \alpha_{12} < \frac{K_1}{K_2} \quad \text{and} \quad \alpha_{21} > \frac{K_2}{K_1} & 2) \quad \alpha_{12} > \frac{K_1}{K_2} \quad \text{and} \quad \alpha_{21} < \frac{K_2}{K_1} \\
 3) \quad \alpha_{12} > \frac{K_1}{K_2} \quad \text{and} \quad \alpha_{21} > \frac{K_2}{K_1} & 4) \quad \alpha_{12} < \frac{K_1}{K_2} \quad \text{and} \quad \alpha_{21} < \frac{K_2}{K_1}
 \end{array}$$

Species 1 is the sole survivor, or winner, in case 1 whereas species 2 wins in case 2. A stable two species equilibrium is realized in case 4; but of greatest interest is case 3, because its outcome is not determined by these inequalities alone.

The superimposed isoclines of species 1 and species 2 have the same general appearance in all competitions of case 3 (Fig. 1). For each species, population size will decrease for points above its isocline and increase for points below its isocline. The point of isocline intersection is regarded as an unstable equilibrium condition; arrows pointing toward it indicate the areas where both species will grow or decrease, arrows pointing away from the intersection denote regions in which only one species is able to grow. An arrow at either carrying capacity, K_1 or K_2 , indicates a stable condition where the competitor has become extinct.

Under case 3, each species inhibits the other's growth more than its own and the outcome of competition has been generally thought to depend solely upon the initial densities of species 1 and species 2 (Vandermeer 1970, Pianka 1978).

Park (1962) was able to correlate environmental conditions with success or failure in interspecific competition including a zone of indeterminate outcome where slight changes in initial numbers could alter the usual competitive outcome. In other experiments, Park (1957) found starting densities to make little difference. However, in each of these papers it is unclear as to which case the competitions represent. Using initial numbers, Coste et al. (1978) delineated the stability domains of each species under case 3 and showed that r values can influence the outcome of competition. Strobeck (1973) has determined r values to be

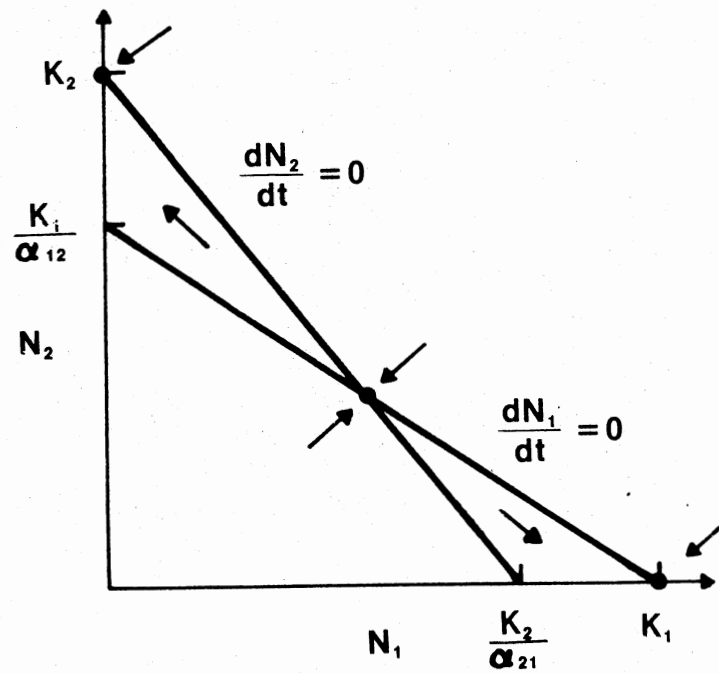


Figure 1. Generalized Graphical Appearance of Case 3 of the Lotka-Volterra competition equations.

important in the coexistence of $n > 2$ species only, but MacArthur (1969) did not consider them important even in this. Gill (1972) suggested that competitive ability is unrelated to either r or K , but later (Gill 1974) showed graphically that r values can alter the outcome of case 3 competition.

The objective of this study was to determine the effects of initial population sizes and biotic potentials on the outcome of case 3 of the Lotka-Volterra equations. For more detailed information on these and other related equations, the reader is advised to turn to Wangersky (1978) and May (1976).

CHAPTER II

MATERIALS AND METHODS

The objectives of this study were met through the utilization of "compet-1", a computer program modeling the Lotka-Volterra competition equations (Reiners et al, 1973). "Compet-1" was altered to allow the winning population to reach its exact K while the numbers of its competitor fell to zero and to output values for dN/Ndt and dN/dt . Further trivial changes facilitated input.

The values for K_1 , K_2 , α_{12} , and α_{21} were chosen in such a manner as to satisfy the inequalities appropriate for case 3. Species isoclines were plotted and initial population sizes were chosen which represented appropriate areas of the plot. The effects of different r values for populations at given starting densities were determined by holding the r of one species constant and altering the other. The data collected over 445 trials included the survivor (or winner) of the struggle, the amount of time required for the survivor to reach K (dubbed saturation time), and the exact numerical path in $N_1 - N_2$ space taken by the populations as the winner reached its K over time.

CHAPTER III

RESULTS

A difference in the r values of two competing species affects events leading to the outcome of competition often without changing the outcome itself. A difference in r values elicits some general effects, no matter what the initial densities. The greater the disparity between r_L and r_W (either $r_L < r_W$ or $r_L > r_W$; $r = r_L$ of loser, $r_W = r$ of winner) the longer the saturation time (Figs. 2 & 3). More growth is obtained by the losing species before its eventual demise if r_L is increased relative to r_W (r_L/r_W increases) for either $r_L < r_W$ (Fig. 4) or $r_L > r_W$ (Fig. 5) providing competition is initiated below both isoclines. The disparity between r_L and r_W also affects the precision with which the two species follow the isocline of the winner in N_1-N_2 space. The precision increases as r_W/r_L increases for either $r_L < r_W$ (Fig. 4) or $r_L > r_W$ (Fig. 5).

Initial population size also affects saturation time when r values are held constant. The greater the initial size of the eventual winner, the faster it reaches K (Fig. 2). Conversely, the greater the initial numbers of the eventual loser, the more slowly the winner reaches K (Fig. 3).

The intersection of the two species' isoclines in case 3 competition is generally regarded as an unstable equilibrium; the point that falls directly on this intersection will remain stable at that value of N_1 and N_2 (coexistence), but points that fall away from this intersection should

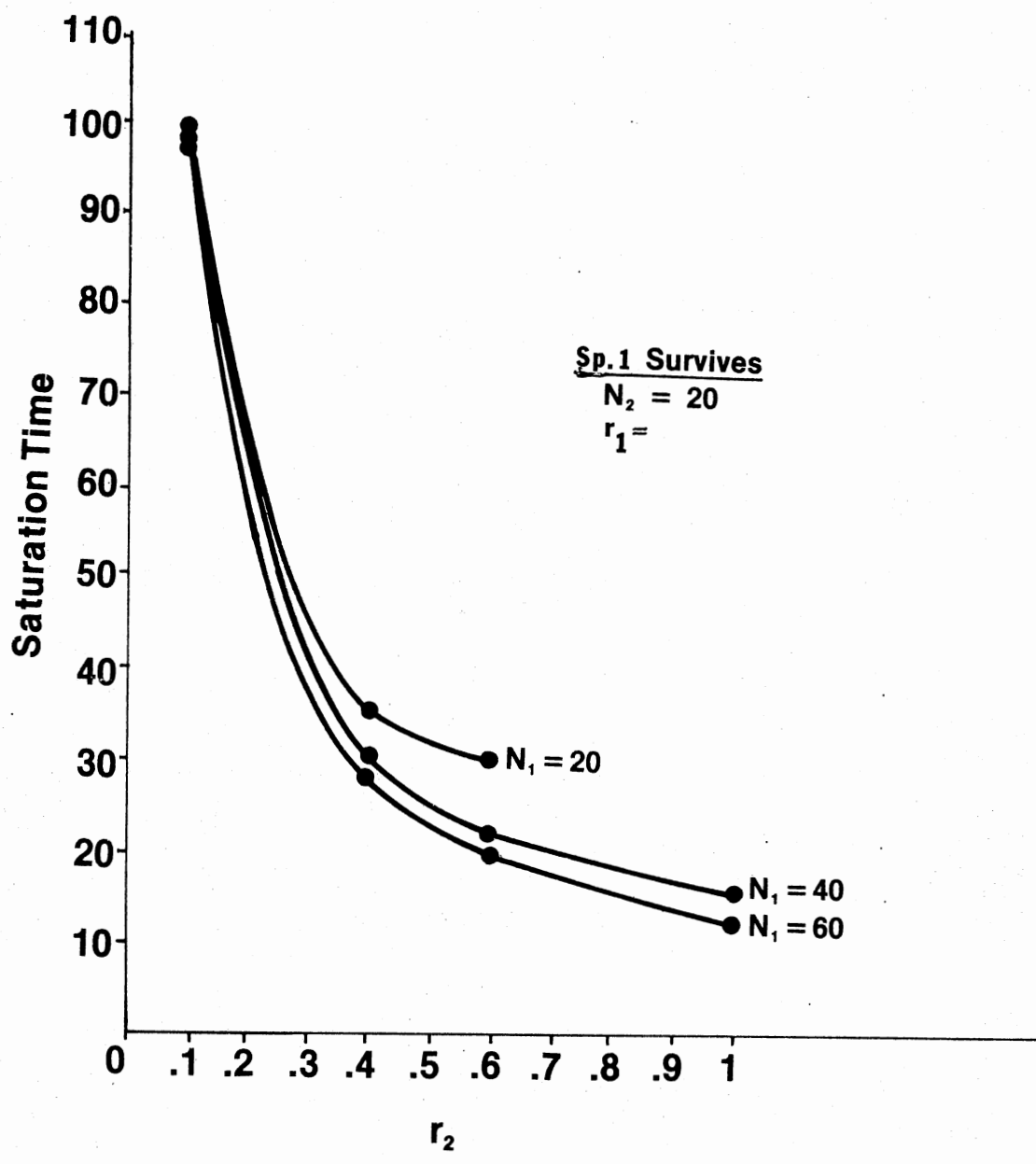


Figure 2. Saturation Time VS r_2 for Different Initial Numbers
When $r_L < r_W$.

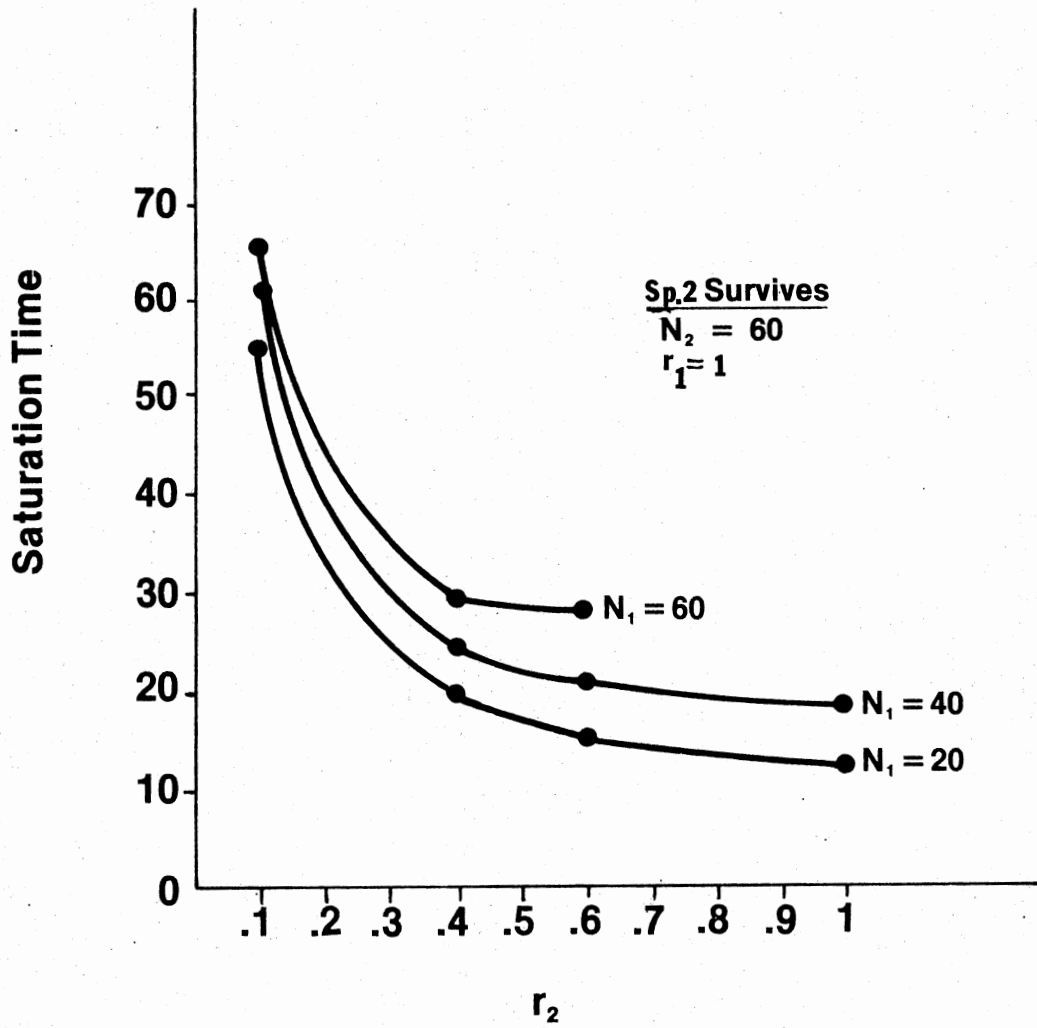


Figure 3. Saturation Time VS r_2 for Different Initial Numbers when $r_L > r_W$.

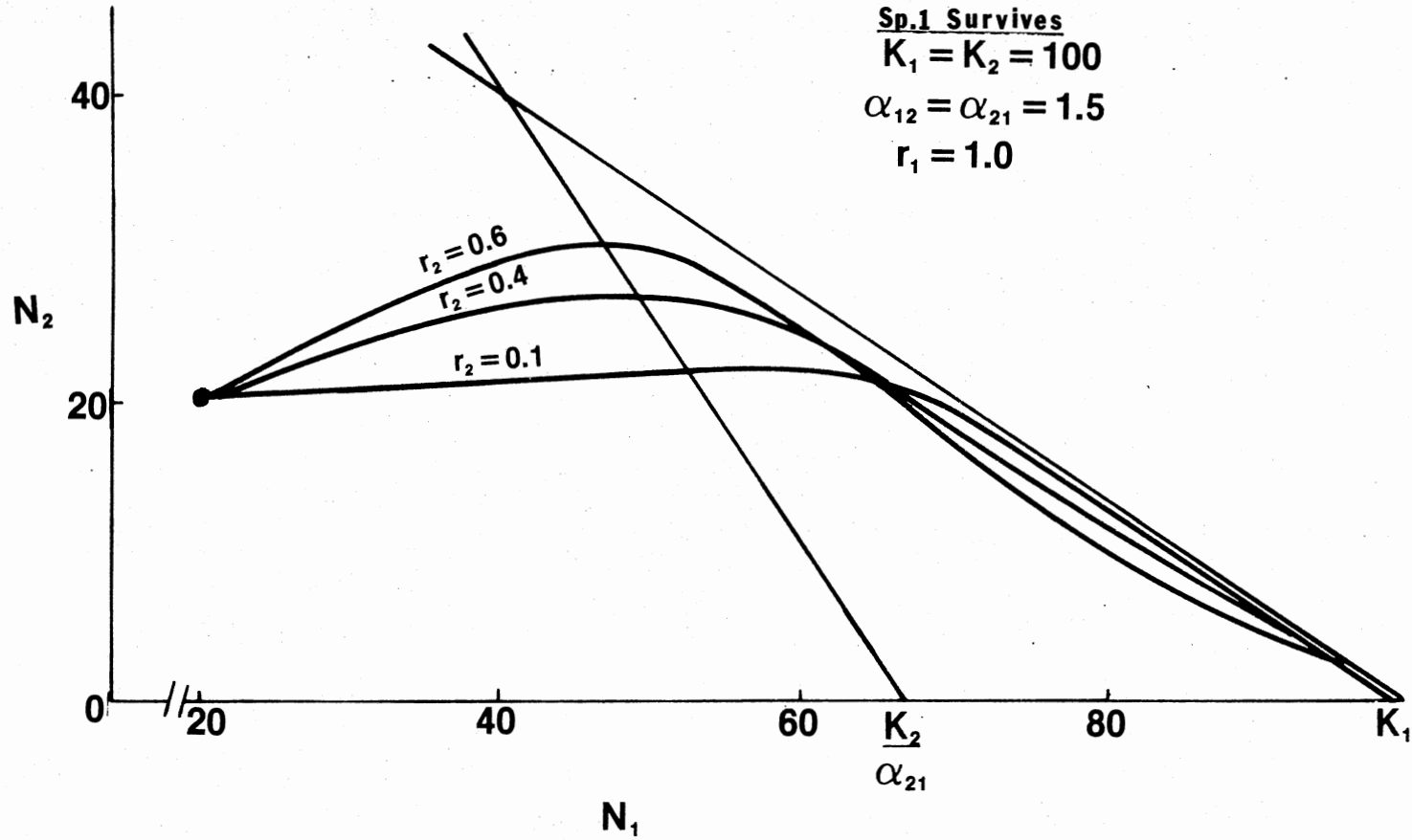


Figure 4. Paths in $N_1 - N_2$ Space for Two Competing Species With Three Values of r_2 Where $r_L < 2r_W$.

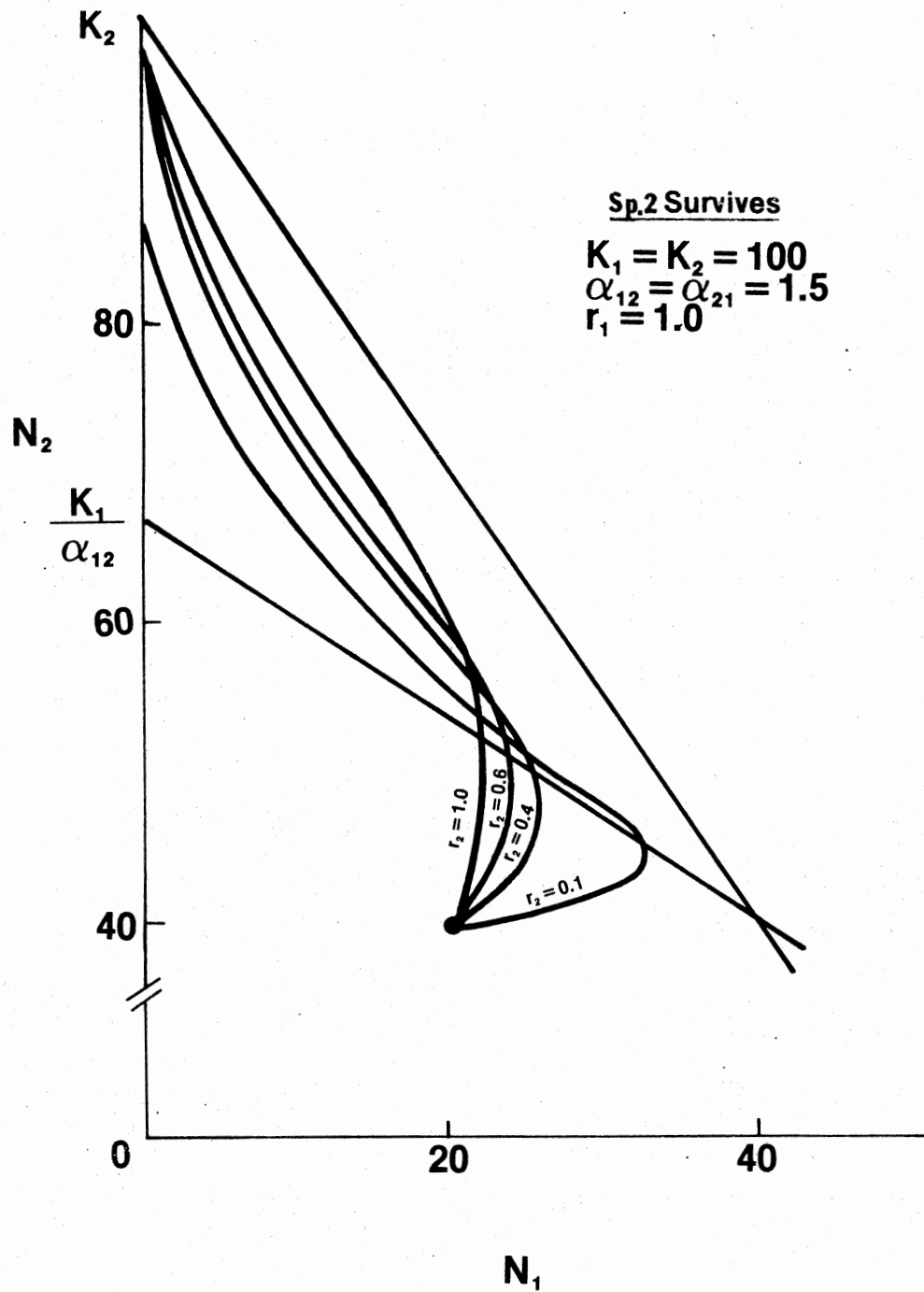


Figure 5. Paths in $N_1 - N_2$ Space for Two Competing Species With Four Values of r_2 Where $r_L \geq r_W$.

move toward the K of either species as the other goes extinct. There is, however, a specialized condition wherein points off the intersection are attracted to the intersection and, thus, coexistence. If initial densities fall directly on an extended line connecting the origin and the isocline intersection (coexistence line), and r_1 equals r_2 , the two species approach the intersection from either above or below (Fig. 6). Coexistence of the two species is realized. In various computer runs within this specialized condition, one or the other species often won, but only after considerable "generations" (Tables I, II, Appendix B). Lack of coexistence in some cases is thought to be an artefact of the approximation technique of the computer model and the mathematical impossibility of obtaining an exact slope of the line from division of two endless decimals. In these cases, the initial densities could not be placed directly onto the coexistence lines, so true coexistence was not obtained.

For initial densities near but not on the coexistence line, saturation time increases as the distance from the line decreases (Table III, Appendix B, Fig. 7). This increase is most pronounced when initial numbers fall very close to the coexistence line and reaches infinity (coexistence) as the line is reached.

Given r_1 equal to r_2 , the outcome of competition for all initial densities is deterministic. Initial densities that fall below the coexistence line grow to K_1 , leaving species two extinct; initial densities that fall above the line grow to K_2 , leaving species one extinct (Figs. 8-11).

When r values are unequal, the outcome of competition is still deterministic, but is no longer dependent on initial densities relative to the extended straight line connecting the origin and the isocline

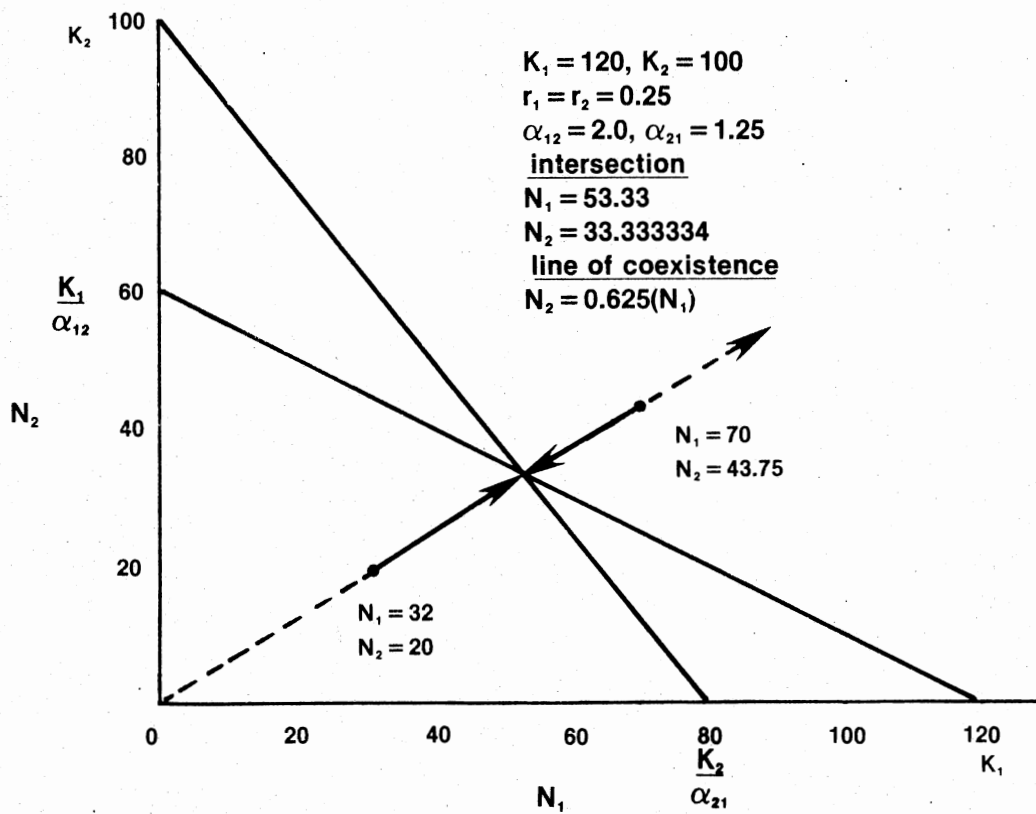


Figure 6. Convergence on the Isocline Intersection When Initial Numbers fall on the Coexistence Line and $r_1 = r_2$.

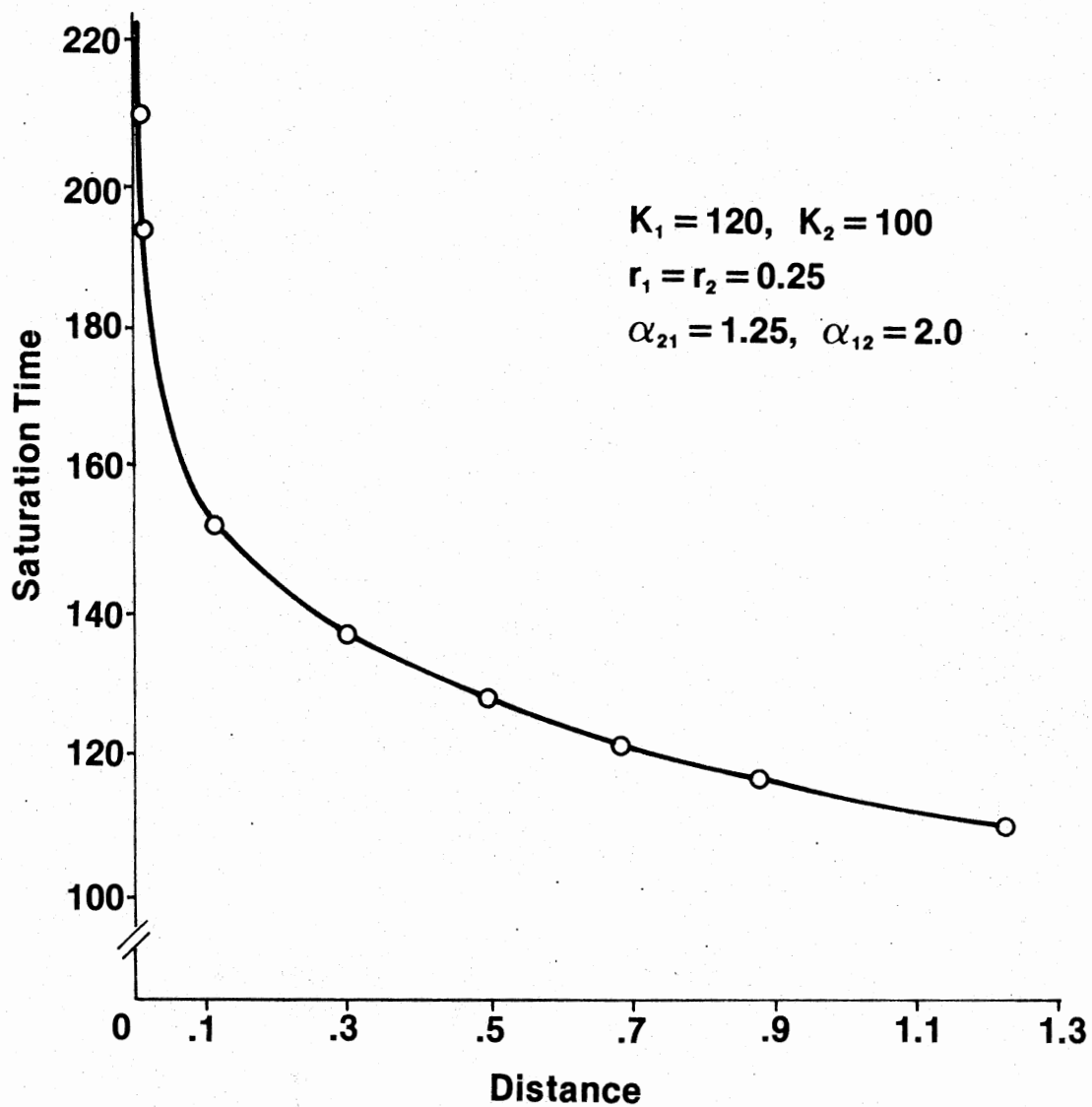


Figure 7. The Effect of Distance From the Coexistence Line on the Saturation Time of a Competitive Interaction when $r_1 = r_2$.

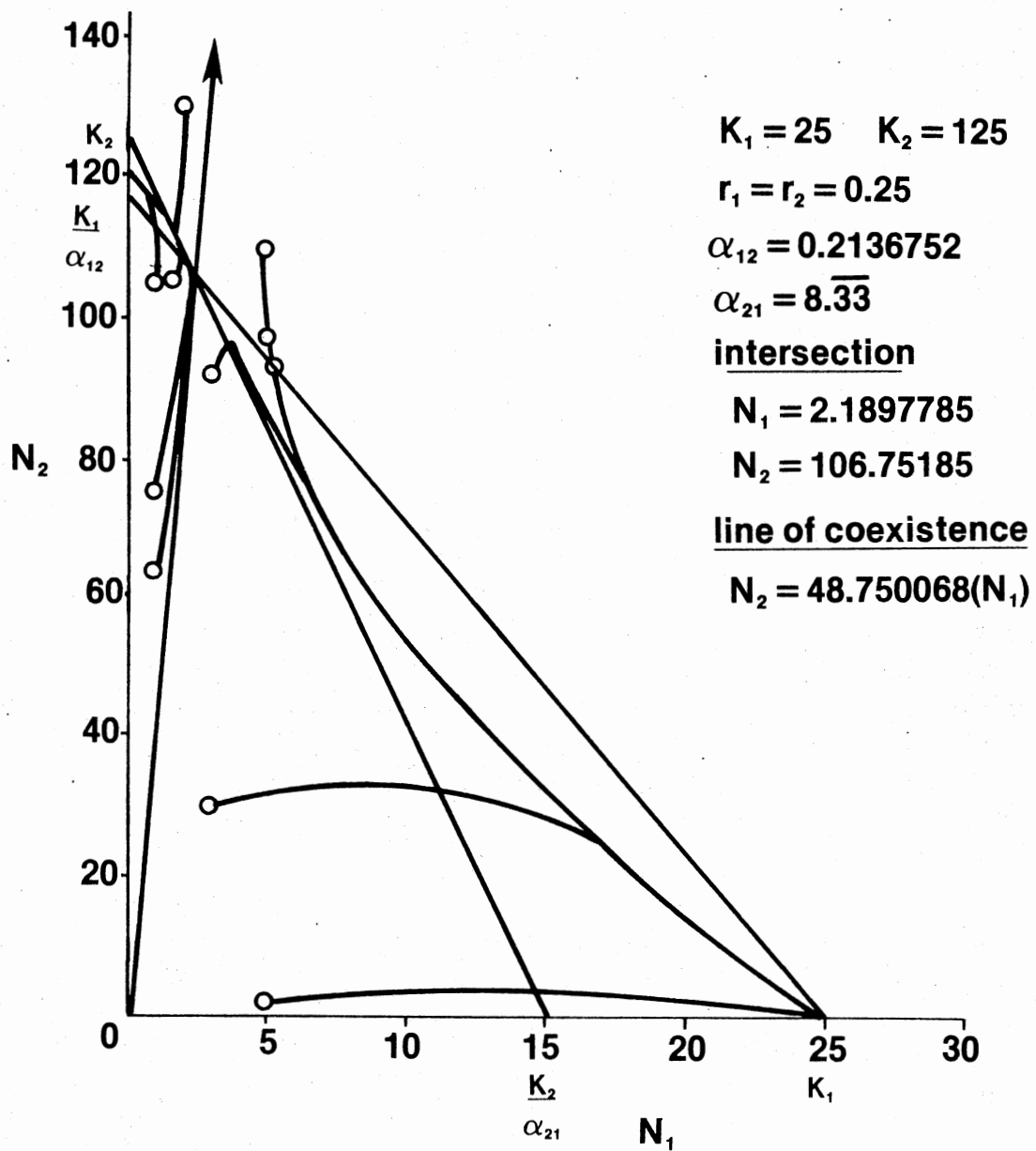


Figure 8. The Effect of Various Starting Densities on the Outcome of Interspecific Competition when $r_1 = r_2$.

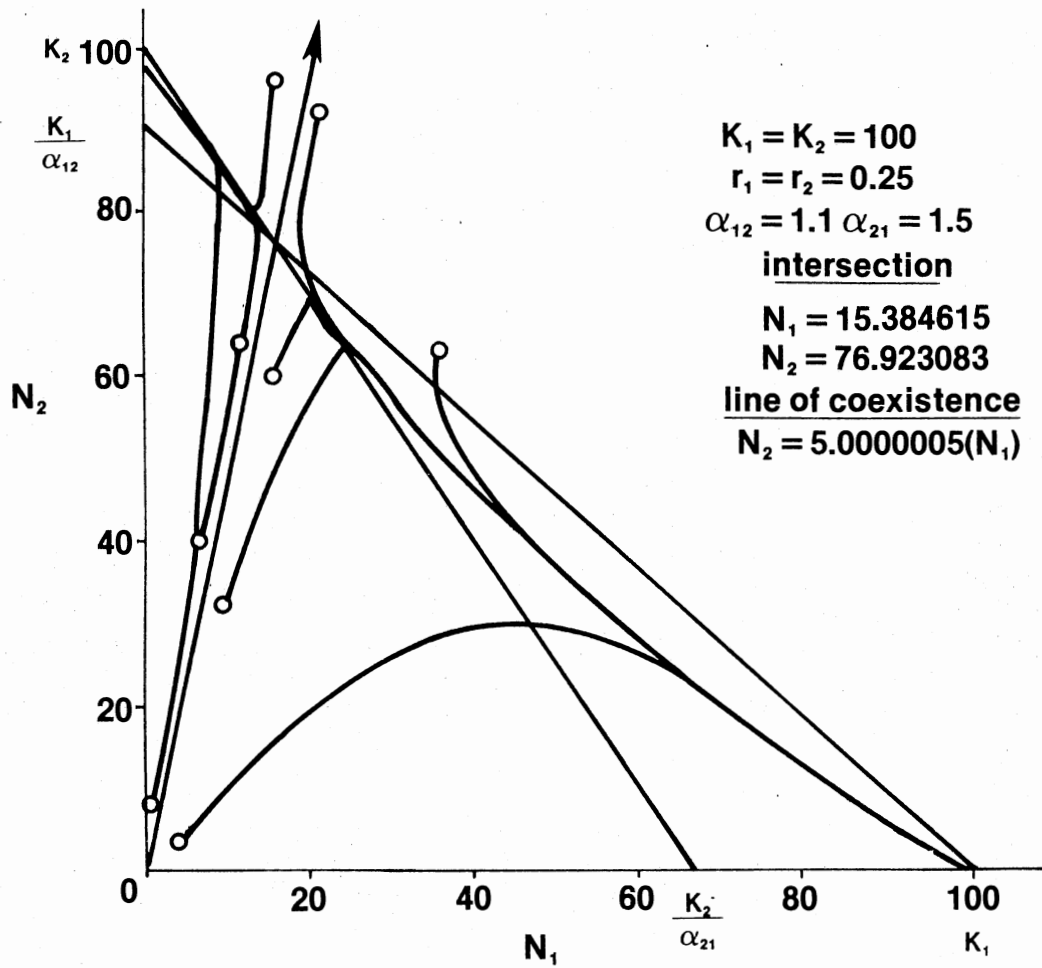


Figure 9. The Effect of Various Starting Densities on the Outcome of Interspecific Competition When $r_1 = r_2$.

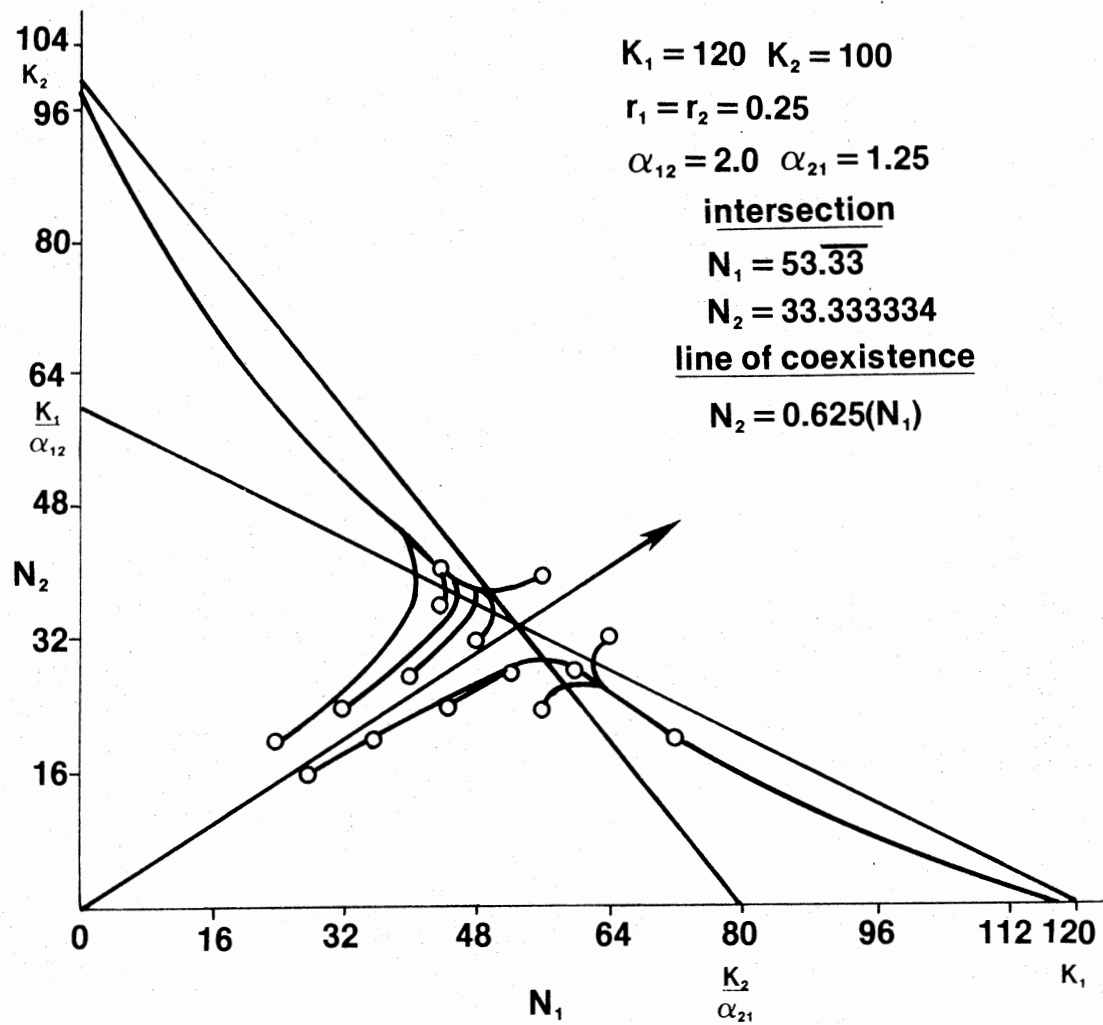


Figure 10. The Effect of Various Starting Densities on the Outcome of Interspecific Competition When $r_1 = r_2$.

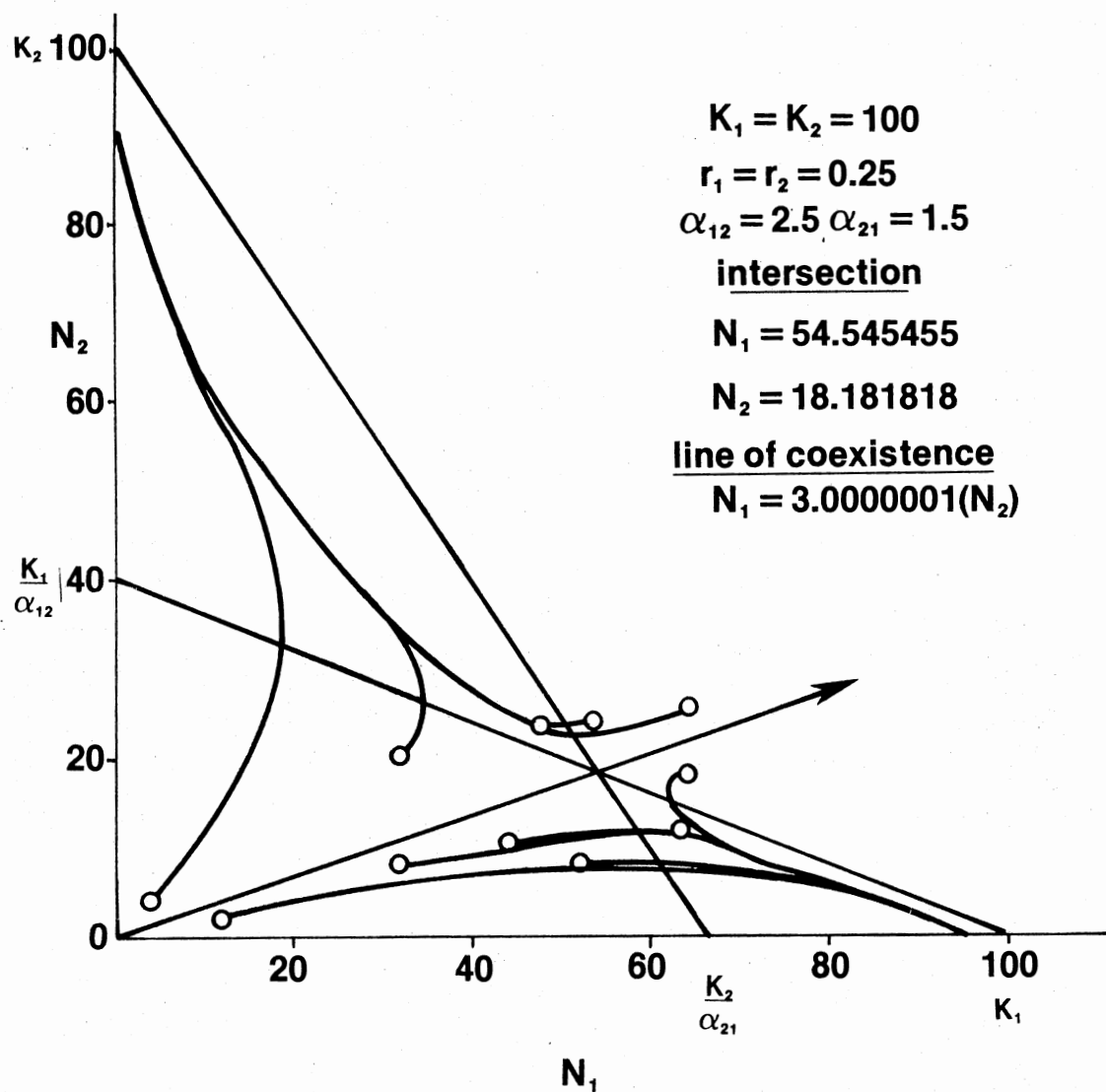


Figure 11. The Effect of Various Starting Densities on the Outcome of Interspecific Competition When $r_1 = r_2$.

intersection (coexistence line). Instead, the boundary that predicts the outcome is an extended curve from the origin, through the isocline intersection and beyond in N_1-N_2 space. The curve is concave for $r_2 > r_1$, convex for $r_1 > r_2$, and steeper for more disparate r values (Fig. 12). Initial densities that fall above this curved coexistence line grow until species 2 wins (Fig. 13, points A, B); initial densities that fall below this curved line grow until species 1 wins (Fig. 13, points C, D). This is true regardless where the initial points fall with respect to the original straight coexistence line (Fig. 13, Points B, C). In other words, at any perpendicular to the original straight coexistence line, the further away initial numbers are from the line, the more different r values must become in order to distort the curved coexistence line enough such that these points then lay to the opposite sides of this curve and thus reverse the outcome of competition predicted from equal r values (Fig. 14).

When r values are different, their effect on the competitive outcome is dependent upon where competition is initiated in relation to the isocline intersection. To reverse the outcome of competition predicted from equal r values, initial points below the intersection require a sufficient inequality as $r_1 > r_2$ (Fig. 15). Initial densities above the intersection require a sufficient inequality as $r_2 > r_1$ (Fig. 16).

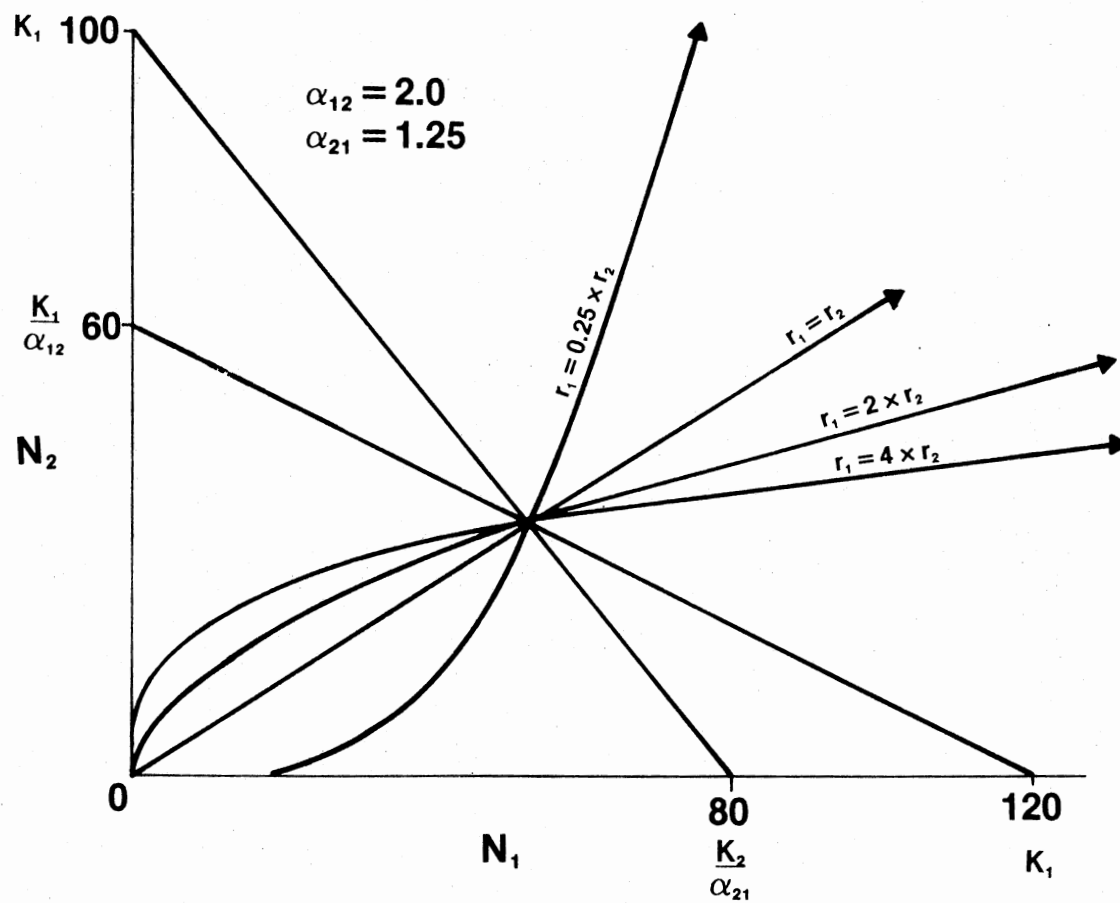


Figure 12. Effect of Diverging r Values on the Coexistence Line in $N_1 - N_2$ Space.

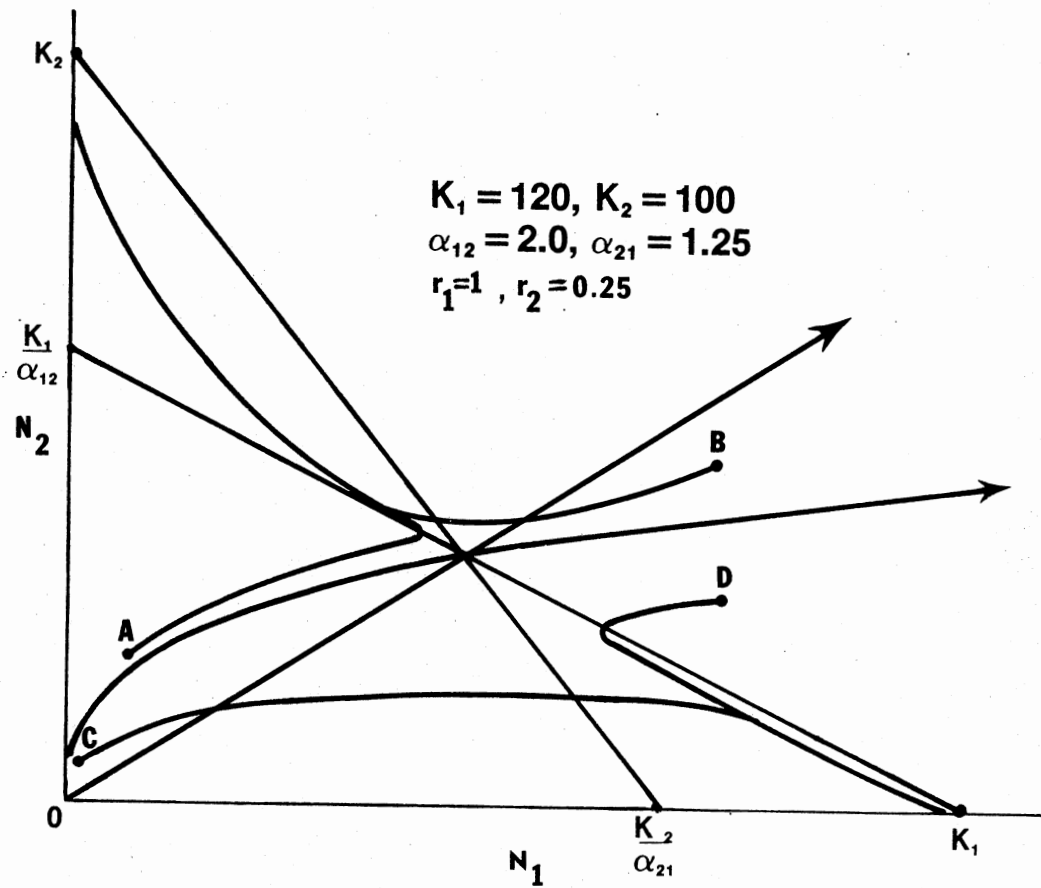


Figure 13. Paths in $N_1 - N_2$ Space for Four Different Initial Densities With Various Orientations to the Straight and Curved Coexistence Lines When $r_1 \neq r_2$.

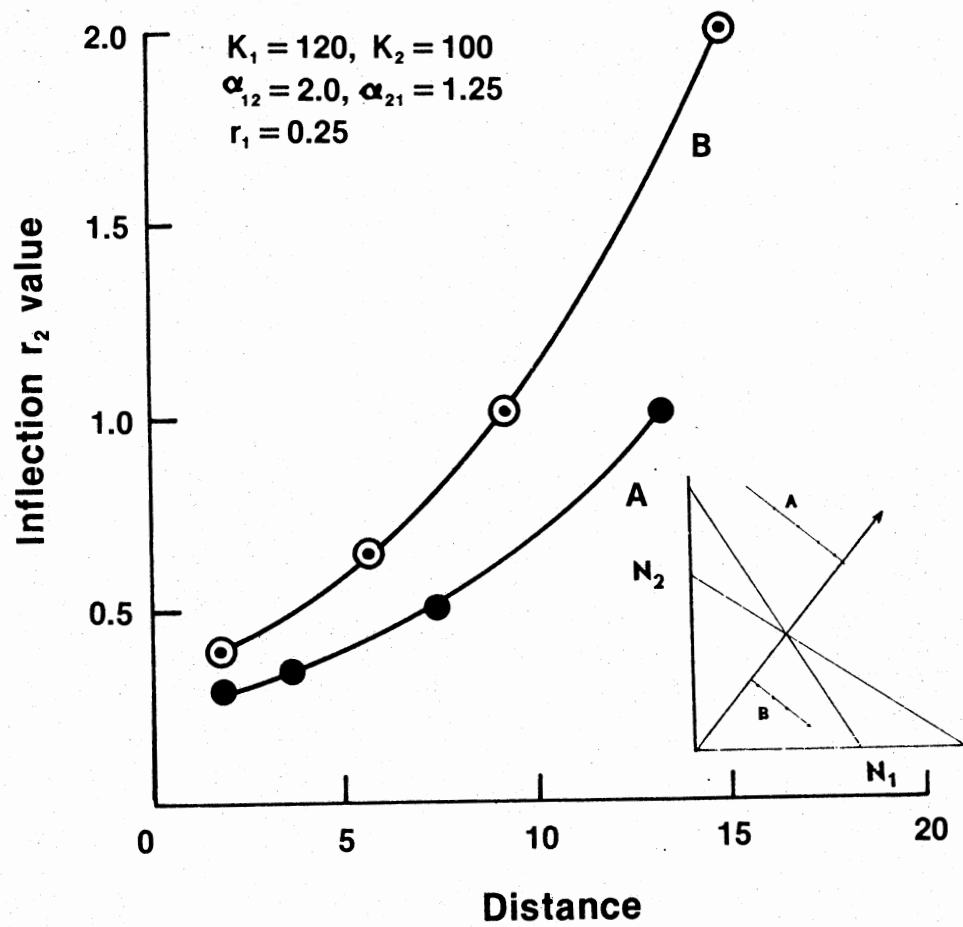


Figure 14. Relationship Between Distance From the Coexistence Line and the Infection r Value. Infection r Value is that Value Which Results in Population Numbers Crossing the Straight Coexistence Line. Curve A Represents Initial Densities Above the Intersection and Coexistence Line; Curve B Contains Initial Numbers Below the Intersection and Coexistence Line.

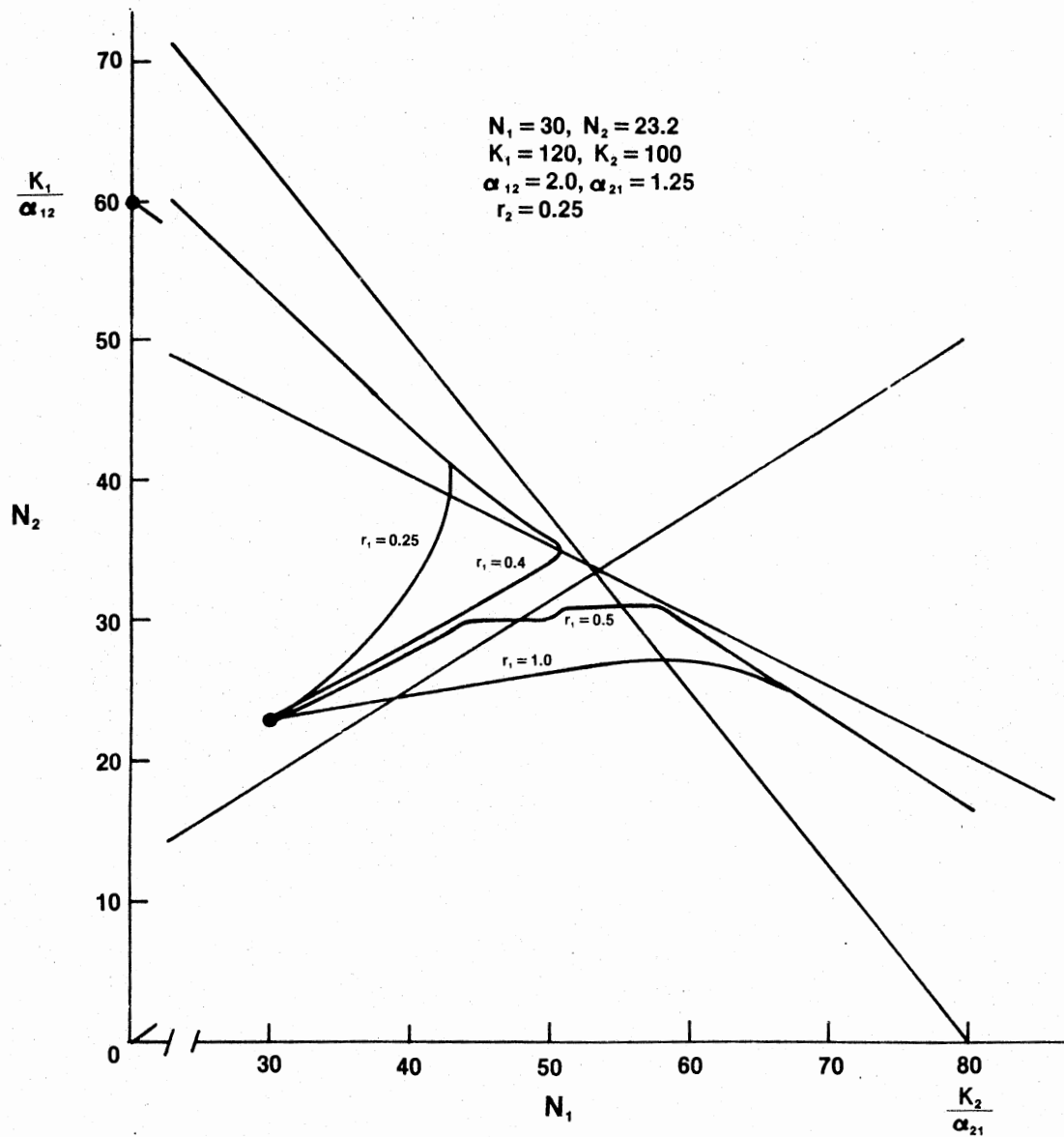


Figure 15. Paths in $N_1 - N_2$ space for Four Values of r_1 Showing a Reversed Competitive Outcome as r_1 Becomes Sufficiently Larger Than r_2 .

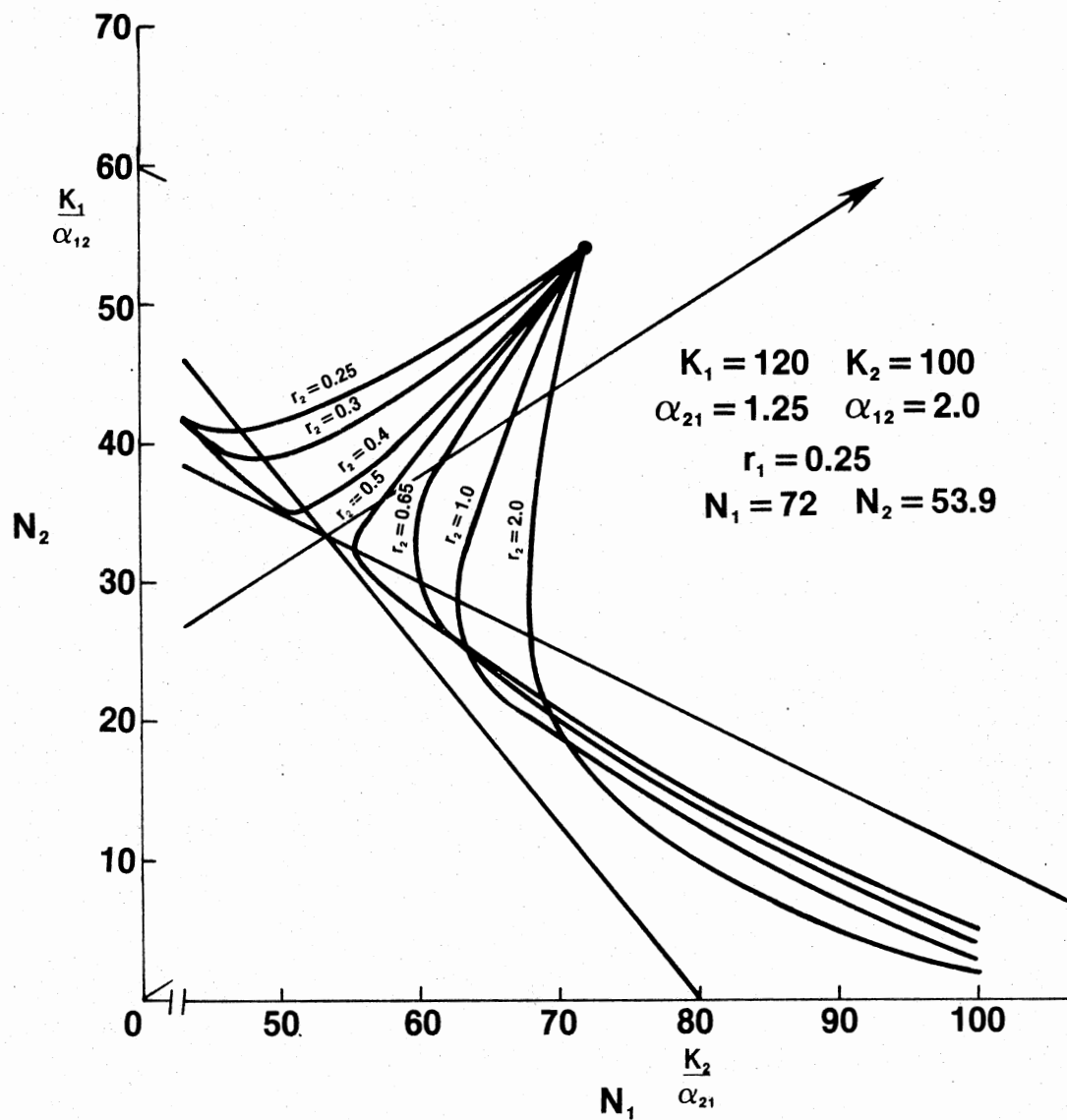


Figure 16. Paths in $N_1 - N_2$ Space for Seven Values of r_2 Showing a Reversed Competitive Outcome as r_2 Becomes Sufficiently Larger Than r_1 .

CHAPTER IV

DISCUSSION

Some effects due to unequal r values of two competitors are intuitive. One would expect, if there is room for both species to increase initially, that the eventual loser would grow at a faster rate with increasing r values until its isocline is reached. One would expect that the winning species would reach its K faster as its initial numbers are increased and that the greater the initial numbers of the loser, the more time it would take for the winner to reach its K . It is also reasonable that the eventual winner of a competition would require more time to reach its K with progressively lower r values. It seems counter intuitive, however, to expect a longer competitive interaction as observed when r_W became progressively larger than r_L .

Perhaps the most interesting effects of unequal r values were those dealing with the coexistence line. Coste et al. (1978) correctly delineated the stability domains of a 2-species case 3 competitive interaction but failed to elucidate the effects of unequal r values in shaping these areas. They correctly stated that it is possible for the competitive process to select a particular species (say species one) whose growth rate, r_1 , is smaller than that of its competitor. This is possible, however, only when a certain inequality is met, namely:

$$r_1 > \frac{r_2}{\alpha_{12}}$$

But this inequality does not include initial numbers and therefore cannot account for their effect in determining competitive outcomes. There are initial densities which always favor the species with the lower biotic potential regardless of the magnitude of the competitor's r .

Another effect of unequal r values may be observed by invoking the concept of r -selection. When individuals are not in competition (density independence by definition) natural selection is thought to favor the genotype with the highest Malthusian parameter, resulting in a larger r for the population as a whole. This is the process of r -selection which can be graphically depicted by the addition of a third axis, the per capita logarithmic growth rate (dN/Ndt), to the already familiar plot of competitive isoclines in N_1 - N_2 space. At the point of density independence the per capita logarithmic growth rates are maximal and equal to r_1 and r_2 . As populations grow each dN/Ndt decreases and reaches zero at each respective carrying capacity. Growth rates then become negative for densities beyond these points.

Using this concept, the coexistence line is seen as the two dimensional projection of the line where $dN_1/N_1dt = dN_2/N_2dt$ when $r_1 = r_2$ (Fig. 17). However, r -selection warps this straight line into a curve which is convex for $r_1 > r_2$ and concave for $r_2 > r_1$.

Gill (1974) showed determinancy of outcome in a case 3 interaction dependent on disparity of r values but failed to appreciate some of the complexities of the relationship. In the case of $r_1 > r_2$, Gill maintained that species two must attain at least $N_2 > K_1/\alpha_{12}$ because at any density lower than this the vector field favors species 1. This statement is clearly fallacious as species 2 may initiate competition at densities far less than this and still emerge victorious (Fig. 18). Conversely,

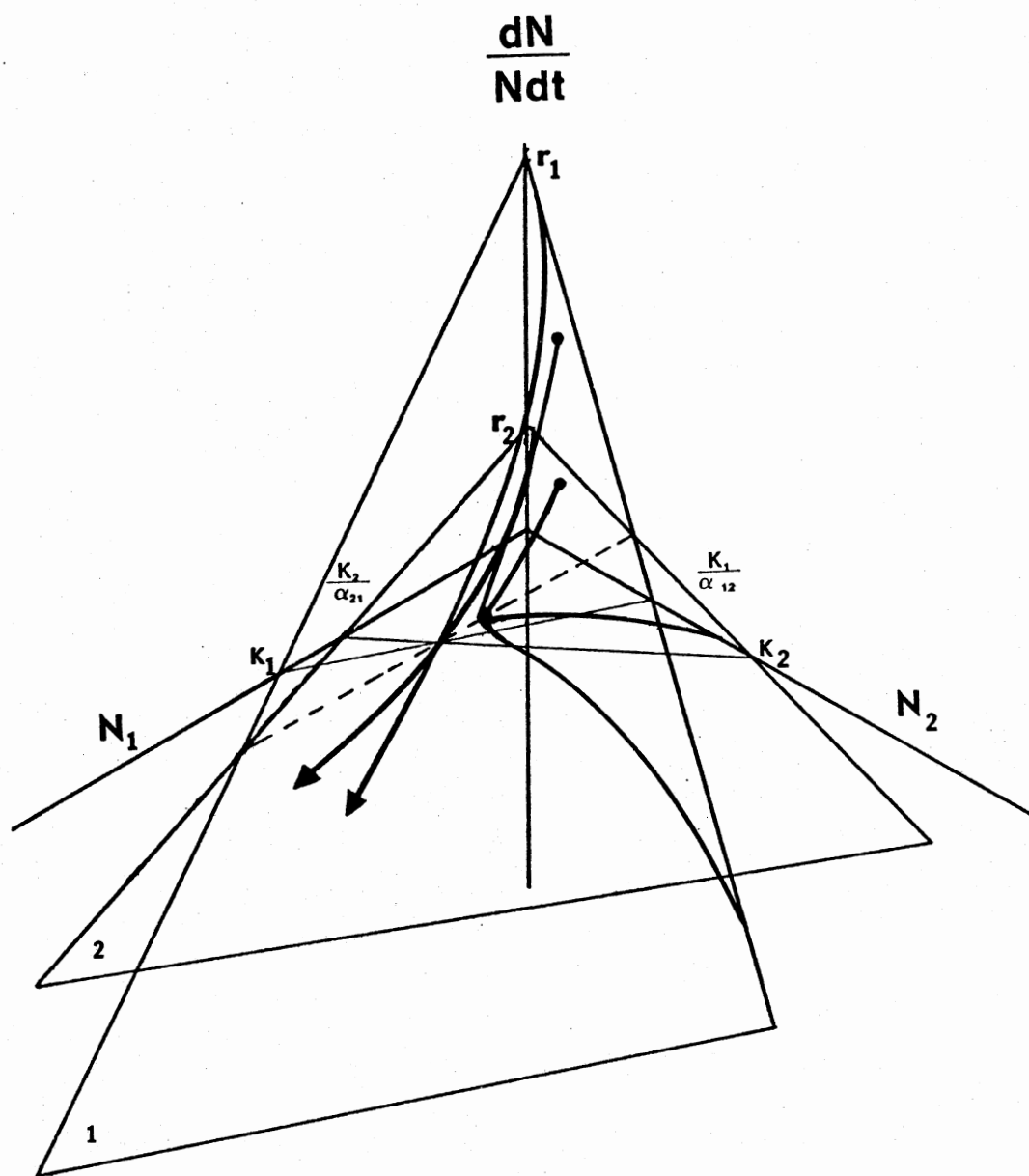


Figure 18. Vector Fields When Unequal Growth Rates ($r_1 > r_2$) Are Plotted as a Function of N_1 and N_2 . Dotted Line Represents all Points Where $\frac{dN_1}{N_1dt} = \frac{dN_2}{N_2dt}$ and Curved Lines with Arrows Represent the Curved Coexistence Line. A Competitive Interaction is Depicted in Which Species 2 Survives Despite Initial Numbers $< K_1/\alpha_{12}$.

species 1 is not doomed to extinction if introduced at densities greater than those separated by the line where $dN_1/N_1 dt = dN_2/N_2 dt$ (Fig. 19). A species may reach such high densities during periods of mass movement instigated by migration or ecological disaster, as in a fire.

One applied area where this work is of potential use is in biological control. It is generally agreed upon that the larger the number of beneficial species in a complex, the greater the chances that the complex will regulate a host population. For this reason, researchers in biological control may strive for the establishment of exotic beneficials but at the same time do not want their potential competitors (the indigenous beneficials) to become extinct. If the inequalities formed by the exotic and indigenous species match those of case 3, competitive exclusion of one of the species may not necessarily be the end result. These findings suggest that there are initial population numbers that may result in coexistence or very long saturation times which would make extinction in a short time very unlikely. Workers should introduce the appropriate number of exotics that will result in a point on or near the line of coexistence, or the isocline intersection.

Another benefit may be visualized utilizing the process of competitive exclusion. Certain desirable species may be useful as competitors of an undesirable species. Numbers should be introduced resulting in a point that lies to the proper side of the curved coexistence line. For example, if there exists a pest of a desirable species which is detrimental due to a certain physiological factor (ie. a toxin) an ecological equivalent may be found that does not exhibit this trait. The harmless competitor could then be introduced in the appropriate numbers and the extinction of the harmful species would be the predicated outcome of the struggle.

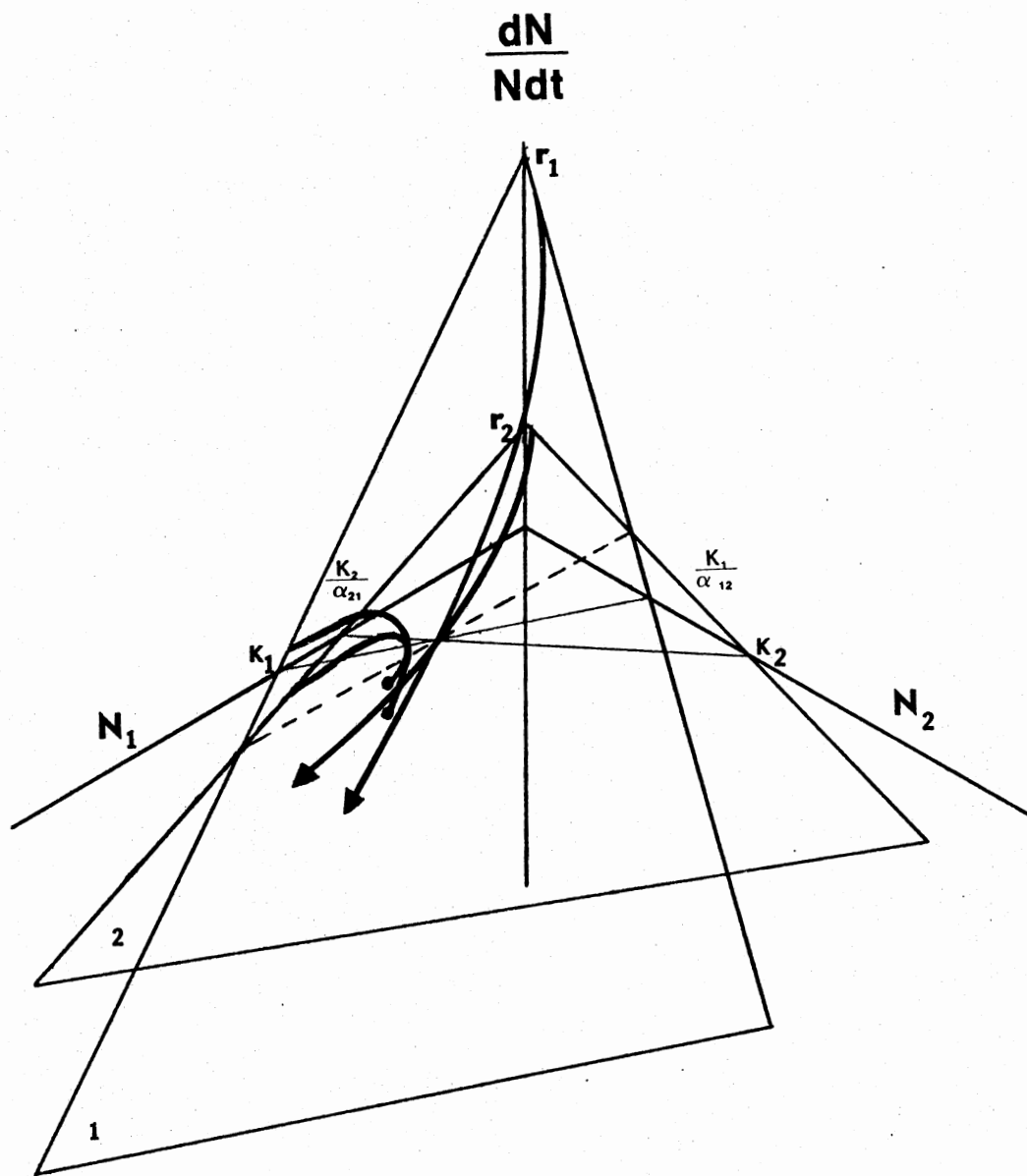


Figure 19. Vector Fields When Unequal Growth Rates ($r_1 > r_2$) are Plotted as a Function of N_1 and N_2 . A Competitive Interaction is Shown in Which Species 1 Survives Despite Initial Numbers Greater Than Those Separated by $\frac{dN_1}{N_1 dt} = \frac{dN_2}{N_2 dt}$.

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APPENDIX A

EDITED VERSION OF COMPET-1

10 REM FOR FURTHER INFORMATION ABOUT THIS PROGRAM CONTACT
20 REM CONDUIT P. O. BOX 388, IOWA CITY, IOWA 52240 (319) 353-3170
30 REM REGISTRY NUMBER: B10083
40 REM LAST REVISION 7/26/77 BY NEIL S. FERGUSON FOR CONDUIT
50 REM THIS PROGRAM IS DISTRIBUTED WITH THE SUPPORT OF THE NATIONAL
60 REM SCIENCE FOUNDATION GRANT NO. SED75-06596. ANY OPINION, FINDINGS,
70 REM CONCLUSIONS, OR RECOMMENDATIONS EXPRESSED OR IMPLIED ARE THOSE
80 REM OF THE AUTHORS AND DO NOT NECESSARILY REFLECT THE VIEWS OF THE
90 REM NATIONAL SCIENCE FOUNDATION.
100 REM "COMPET-1" -- (BASIC PROGRAM BEGINS AT LINE 360)
110 REM
120 REM VERSION 1: WRITTEN BY WILLIAM E. GLANZ '70, AND WILLIAM A.
130 REM REINERS. DEPT. OF BIOLOGY. DARTMOUTH COLLEGE. WRITTEN IN
140 REM BASIC ON THE DARTMOUTH TIME-SHARING SYSTEM.
150 REM
160 REM COPYRIGHT 1974 BY THE TRUSTEES OF DARTMOUTH COLLEGE
170 REM
180 REM DESCRIPTION:
190 REM
200 REM THIS PROGRAM IS AN INTERSPECIFIC COMPETITION MODEL BASED
210 REM ON THE CLASSICAL LOTKA-VOLTERRA EQUATION. IT CALCULATES THE
220 REM POPULATION SIZE OF TWO COMPETING SPECIES IN SUCCESSIVE TIME
230 REM STEPS USING DATA FROM WITHIN THE PROGRAM. THE CALCULATIONS
240 REM ARE DONE USING INCREMENTAL ADDITION.
250 REM
260 REM
270 REM

```
280 REM THIS PROGRAM IS TAKEN FROM THE TEXT ECOLOGICAL MODELING BY
290 REM WILLIAM E. GLANZ AND WILLIAM A. REINERS.
300 REM
310 REM
320 REM
330 REM * * * * *
340 REM READ DATA FOR POPULATION ONE! INITIAL POPULATION SIZE, GROWTH
350 REM RATE, ENVIRONMENTAL CAPACITY, AND FRACTION OVERLAP BY POP. #2.
360 DIM Z$(3)
370 PRINT "          VALUES FOR POPULATION ONE"
380 PRINT
390 PRINT "ENTER INITIAL POPULATION SIZE"
400 INPUT N1
410 PRINT "ENTER GROWTH RATE"
420 INPUT R1
430 PRINT "ENTER ENVIRONMENTAL CAPACITY"
440 INPUT K1
450 PRINT "ENTER FRACTION OF OVERLAP BY POPULATION #2"
460 INPUT J1
470 PRINT
480 PRINT "
490 PRINT
500 PRINT "ENTER INITIAL POPULATION SIZE"
510 INPUT N2
520 PRINT "ENTER GROWTH RATE"
530 INPUT R2
540 PRINT "ENTER ENVIRONMENTAL CAPACITY"
```

```
550 INPUT K2
560 PRINT "ENTER FRACTION OF OVERLAP BY POPULATION #1"
570 INPUT J2
580 REM READ NUMBER OF TIME PERIODS TO SIMULATE AND CALCULATION
590 PRINT          INVERAL
620 PRINT "INTERVAL OF COMPUTATION IS 0.1"
630 LET I=0.1
640 PRINT
650 PRINT "TIME", "POP, #1", "POP, # 2"
660 PRINT
661 LET E=1
670 FOR T=1 TO 2000
672 LET P1=0
674 LET P2=0
676 LET D1=0
678 LET D2=0
680 REM I IS COMPUTATION INTERVAL, SO 1/I IS NUMBER OF INTERVALS
690 FOR A=1 TO INT (1/I+.5)
700 LET G1=I*R1*N1*(K1-N1-J1*N2)/K1
710 LET G2=I*R2*N2*(K2-N2-J2*N1)/K2
712 LET P1=G1/N1+P1
714 LET P2=G2/N2+P2
720 LET N1=N1+G1
730 LET N2=N2+G2
732 LET D1=D1+G1
734 LET D2=D2+G2
740 NEXT A
```

```
750  REM INTEGER VALUES FOR POPULATION SIZES
760  LET Q1=INT (N1+.5)
770  LET Q2=INT (N2+.5)
780  PRINT T, Q1, Q2, P1, P2, D1, D2
781  IF Q1=0, OR, Q1=K1  GOTO 783
782  GOTO 784
783  IF Q2=0, OR, Q2=K2  GOTO 791
784  LET E=E+1
785  NEXT T
786  PRINT
791  PRINT "EXTINCTION TIME WAS", E
792  PRINT
793  PRINT
800  PRINT "DO YOU WISH TO RERUN THIS PROGRAM" (YES/NO)"
810  INPUT Z$
820  IF Z$="YES" THEN 370
830  IF Z$="NO" THEN 860
840  PRINT "PLEASE ENTER A YES OR A NO"
850  GOTO 800
860  END
```

APPENDIX B

TABLES

TABLE I

THE EFFECT OF VARIOUS r VALUES ON THE OUTCOME
OF INTERSPECIFIC COMPETITION WHEN INITIAL
SPECIES NUMBERS FALL ON THE COEXISTENCE
LINE ABOVE, BELOW, AND AT THE POINT
OF ISOCLINE INTERSECTION

For: $K_1 = K_2 = 100$ $\alpha_{12} = \alpha_{21} = 1.5$							
		(below) $N_1 = 20$ $N_2 = 20$		(intersection) $N_1 = 40$ $N_2 = 40$		(above) $N_1 = 60$ $N_2 = 60$	
r_1	r_2	sat. time	winner	sat. time	winner	sat. time	winner
1	0.01	966	N_1	> 2,000	tie	517	N_2
1	0.1	106	N_1	> 2,000	tie	65	N_2
1	0.2	60	N_1	> 2,000	tie	40	N_2
1	0.4	32	N_1	> 2,000	tie	29	N_2
1	0.5	30	N_1	> 2,000	tie	28	N_2
1	0.6	30	N_1	> 2,000	tie	28	N_2
1	0.9	31	N_1	> 2,000	tie	32	N_2
1	0.99	41	N_1	> 2,000	tie	42	N_2
1	0.999	64	N_1	> 2,000	tie	66	N_2
1	1	> 2,000	tie	> 2,000	tie	> 2,000	tie
0.01	1	966	N_2	> 2,000	tie	517	N_1
0.1	1	106	N_2	> 2,000	tie	65	N_1
0.6	1	30	N_2	> 2,000	tie	28	N_1
0.99	1	41	N_2	> 2,000	tie	42	N_1

TABLE I (Continued)

FOR $K_1 = 120$, $K_2 = 100$, $\alpha_{12} = 2.0$, $\alpha_{21} = 1.25$							
		$N_1 = 32$		$N_1 = 53.\overline{33}$		$N_1 = 76$	
		$N_2 = 20$		$N_2 = 33.333334$		$N_2 = 47.5$	
r_1	r_2	sat. time	winner	sat. time	winner	sat. time	winner
2	0.25	48	N_1	> 2,000	tie	30	N_2
0.25	2	37	N_2	> 2,000	tie	27	N_1
0.25	0.25	253	N_1	> 2,000	tie	257	N_1
FOR $K_1 = K_2 = 100$, $\alpha_{12} = 1.1$, $\alpha_{21} = 1.5$							
		$N_1 = 8$		$N_1 = 15.384615$		$N_1 = 20$	
		$N_2 = 40.000004$		$N_2 = 76.923083$		$N_2 = 100.00001$	
r_1	r_2						
0.25	0.25	615	N_1	> 2,000	tie	> 2,000	tie
1	0.25	61	N_1	> 2,000	tie	63	N_2
0.25	1	179	N_2	> 2,000	tie	97	N_1
FOR $K_1 = 25$, $K_2 = 125$, $\alpha_{12} = 0.2136752$, $\alpha_{21} = 8.\overline{33}$							
		$N_1 = 1$		$N_1 = 2.1897785$		$N_1 = 3$	
		$N_2 = 48.750068$		$N_2 = 106.75185$		$N_2 = 146.2502$	
r_1	r_2						
0.25	0.25	850	N_2	> 2,000	tie	201	N_1
1	0.25	50	N_1	> 2,000	tie	41	N_2
0.25	1	230	N_2	> 2,000	tie	30	N_1

TABLE I (Continued)

FOR: $K_1 = K_2 = 100$, $\alpha_{12} = 2.5$, $\alpha_{21} = 1.5$

$N_1 = 36.000001$	$N_1 = 54.545455$	$N_1 = 72.000002$
$N_2 = 12$	$N_2 = 18.181818$	$N_2 = 24$

<u>r_1</u>	<u>r_2</u>						
0.25	0.25	202	N_1	>2,000	tie	201	N_1
1	0.25	51	N_1	>2,000	tie	41	N_2
0.25	1	26	N_2	>2,000	tie	30	N_1

TABLE II
 THE EFFECT OF VARIOUS STARTING DENSITIES ON
 THE OUTCOME OF INTERSPECIFIC COMPETITION

$K_1 = K_2 = 100, \alpha_{12} = 1.1, \alpha_{21} = 1.5, r_1 = r_2 = 0.25$

N_1	N_2	Winner	Saturation Time
16	60	N_1	139
12	64	N_2	311
12	81	N_2	226
16	96	N_2	253
22	92	N_1	161
36	64	N_1	80
10	32	N_1	121
7	40	N_2	274
4	20.000002	N_1	600
15.384615	76.923083	tie	> 2,000
20	100.00001	tie	> 2,000

$K_1 = K_2 = 100, \alpha_{21} = 1.5, \alpha_{12} = 2.5, r_1 = r_2 = 0.25$

52	8	N_1	50
12	2	N_1	60
4	4	N_2	44
48	24	N_2	49
54	24	N_2	53
64	26	N_2	58

TABLE II (Continued)

64	18	N_1	56
64	12	N_1	56
36.000001	12	N_1	207
54.545455	18.181818	tie	>2,000
70.000002	24	N_1	201

$K_1 = 25, K_2 = 125, \alpha_{12} = 0.2136752, \alpha_{21} = 8.\overline{33}, r_1 = r_2 = 0.25$

2	105	N_2	399
5	94	N_1	81
1	115	N_2	210
4	97.5	N_1	98
5	110	N_1	90
5	2	N_1	25
3	30	N_1	62
1	64	N_2	307
1	75	N_2	271
3	92	N_1	121
1	48.750068	N_2	850
2.1897785	106.75185	tie	> 2,000
3	146.2502	N_2	850

TABLE II (Continued)

$K_1 = K_2 = 100, \alpha_{12} = \alpha_{21} = 1.5, r_1 = r_2 = 1.0$

40	20	N_1	16
60	20	N_1	13
20	40	N_2	16
60	40	N_1	18
20	60	N_2	13
40	60	N_2	18
20	20	tie	> 2,000
40	40	tie	> 2,000
60	60	tie	> 2,000

$K_1 = 120, K_2 = 100, \alpha_{12} = 2.0, \alpha_{21} = 1.25, r_1 = r_2 = 0.25$

44	40	N_2	65
56	40	N_2	83
44	36	N_2	71
48	32	N_2	96
40	28	N_2	87
32	24	N_2	79
24	20	N_2	72
64	32	N_1	81
60	28	N_1	76
72	20	N_1	57
52	28	N_1	89

TABLE II (Continued)

44	24	N_1	91
36	20	N_1	95
28	16	N_1	101
$53.\overline{33}$	33.333334	tie	> 2,000
32	20	N_1	253
76	47.5	N_1	257
36	48	N_2	52

TABLE III
 INFLUENCE OF DISTANCE FROM THE COEXISTENCE
 LINE ON THE SATURATION TIME OF A
 COMPETITIVE INTERACTION

$K_1 = 120, K_2 = 100, \alpha_{12} = 2.0, \alpha_{21} = 1.25, r_1 = r_2 = 0.25$				
N_1	N_2	Winner	Sat. Time	Distance
76	47.5	N_1	257	0.000
77	45.9	N_1	108	1.887
79	42.7	N_1	88	5.660
81	39.5	N_1	78	9.434
85	33.1	N_1	66	16.98
93	20.3	N_1	52	32.076
75	49.1	N_2	101	1.887
74	50.7	N_2	88	3.774
72	53.9	N_2	76	7.547
69	58.7	N_2	66	13.208
61	71.5	N_2	53	28.302
32	20	N_1	253	0.000
33	18.4	N_1	96	1.887
35	15.2	N_1	75	5.66
37	12	N_1	64	9.434
40	7.2	N_1	52	15.094
31	21.6	N_2	89	1.887
30	23.2	N_2	77	3.774
27	28	N_2	61	9.434
21	37.6	N_2	50	20.755

TABLE III (Continued)

N_1	N_2	Winner	Sat. Time	Distance
53.333	33.333334	tie	2,000	0.000
53.3335	33.33307	N_1	220	0.0003124
53.335	33.33067	N_1	216	0.0031426
53.336	33.3291	N_1	209	0.005004
53.338	33.3259	N_1	200	0.0087775
53.34	33.32267	N_1	193	0.0125766
53.4	33.22667	N_1	152	0.1257843
53.5	33.06667	N_1	136	0.314464
53.6	32.90667	N_1	127	0.5031436
53.7	32.74667	N_1	121	0.6918232
53.8	32.58667	N_1	117	0.8805028
54	32.26667	N_1	110	1.2578621
54.5	31.46667	N_1	100	2.2012618
55	30.66667	N_1	94	3.1446583
57	27.46667	N_1	79	6.9182507
61	21.06667	N_1	64	14.465436
68	9.86667	N_1	47	27.673
53	33.86667	N_2	115	0.6289342
51	37.06667	N_2	81	4.4025
49	40.26667	N_2	70	8.1761
44	48.26667	N_2	57	17.6101
37	59.46667	N_2	47	30.8177
76.01	47.484	N_1	191	0.018868

TABLE III (Continued)

N_1	N_2	Winner	Sat. Time	Distance
76.05	47.42	N_1	162	0.0943398
76.09	47.356	N_1	152	0.1698
76.14	47.276	N_1	144	0.2642
76.2	47.18	N_1	137	0.3774
76.27	47.068	N_1	132	0.5094
76.32	46.988	N_1	129	0.6038
76.45	46.78	N_1	123	0.8491
76.55	46.62	N_1	119	1.0377
76.65	46.46	N_1	116	1.2264

TABLE IV
 THE EFFECT OF VARIOUS r VALUES AND
 INITIAL DENSITIES ON THE OUTCOME
 OF INTERSPECIFIC COMPETITION

$K_1 = K_2 = 100 \quad \alpha_{12} = \alpha_{21} = 1.5$					
r_1	r_2	N_1	N_2	Winner	Sat. Time
1	0.1	40	20	N_1	99
1	0.4	40	20	N_1	30
1	0.6	40	20	N_1	22
1	0.1	60	20	N_1	99
1	0.4	60	20	N_1	28
1	0.6	60	20	N_1	20
1	0.1	20	40	N_2	97
1	0.4	20	40	N_2	27
1	0.1	60	40	N_1	167
1	0.4	60	40	N_1	41
1	0.6	60	40	N_1	28
1	0.1	20	60	N_2	57
1	0.4	20	60	N_2	20
1	0.6	20	60	N_2	16
1	0.1	40	60	N_2	62
1	0.4	40	60	N_2	24
1	0.6	40	60	N_2	21
0.1	1	40	20	N_1	96
0.4	1	40	20	N_1	27

TABLE IV (Continued)

r_1	r_2	N_1	N_2	Winner	Sat. Time
0.1	1	20	60	N_2	99
0.4	1	20	60	N_2	28
0.1	1	40	60	N_2	167
0.6	1	40	60	N_2	18
0.1	1	21	20	N_2	109
1	0.1	21	20	N_1	106
<hr/>					
$K_1 = 120, K_2 = 100, \alpha_{12} = 2.0, \alpha_{21} = 1.25$					
<hr/>					
1	0.1	24	24	N_1	135
0.1	1	24	24	N_2	78
1	0.1	40	8	N_1	80
0.1	1	40	8	N_2	123
<hr/>					
$K_1 = 25, K_2 = 125, \alpha_{12} = 0.2136752, \alpha_{21} = 8.\overline{33}$					
<hr/>					
1	0.1	3	30	N_1	74
0.1	1	3	30	N_1	176
1	0.1	1	80	N_1	130
0.1	1	1	80	N_2	510

TABLE IV (Continued)

$K_1 = K_2 = 100, \alpha_{12} = 2.5, \alpha_{21} = 1.5$

1	0.1	44	12	N_1	111
0.1	1	44	12	N_2	59
1	0.1	44	20	N_2	99
0.1	1	44	20	N_2	53

$K_1 = K_2 = 100, \alpha_{21} = 1.5, \alpha_{12} = 1.1$

1	0.1	10	32	N_1	109
0.1	1	10	32	N_2	482
1	0.1	12	64	N_1	164
0.1	1	12	64	N_2	526

TABLE V
 THE EFFECT OF UNEQUAL r VALUES ON
 THE COEXISTENCE LINE IN N_1-N_2
 SPACE

For: $K_1 = 120$, $K_2 = 100$, $\alpha_{12} = 2$, $\alpha_{21} = 1.25$, $r_1 = 1.0$, $r_2 = 0.25$

N_1	N_2	Winner	N_1	N_2	Winner
1	5	N_1	68	38	N_2
1	12	N_2	78	36	N_1
3	12	N_1	78	40	N_2
6	12	N_2	86	36	N_1
4	16	N_2	86	38	N_1
6	16	N_1	86	39	N_2
5	20	N_2	92	38	N_1
8	20	N_2	92	40	N_2
9	20	N_2	98	40	N_1
10	20	N_1	98	42	N_2
12	23	N_2	106	40	N_1
14	23	N_1	106	42	N_2
16	23	N_1	114	42	N_1
18	25	N_2	114	44	N_2
20	25	N_2	120	42	N_1
22	25	N_1	120	44	N_2
24	26	N_1	46	34	N_2
36	28	N_1	54	31	N_1
36	32	N_2	54	36	N_2
46	31	N_1	68	35	N_1

TABLE V (Continued)

N_1	N_2	Winner	N_1	N_2	Winner
$r_1 = 0.5, r_2 = 0.25$					
2	4	N_1	32	26	N_2
2	6	N_2	44	28	N_1
4	8	N_1	44	30	N_2
8	10	N_1	62	36	N_1
8	12	N_2	70	38	N_1
12	14	N_1	70	40	N_2
12	16	N_2	86	42	N_1
16	16	N_1	86	44	N_2
16	18	N_2	140	56	N_1
22	20	N_1	140	58	N_2
22	22	N_2	140	62	N_2
32	24	N_1			
$r_1 = 0.25, r_2 = 1.0$					
16	1	N_2	48	22	N_1
20	1	N_2	48	24	N_2
24	1	N_1	56	38	N_1
18	.5	N_1	56	40	N_2
24	3	N_2	59	44	N_1
28	4	N_1	59	46	N_2

TABLE V (Continued)

N_1	N_2	Winner	N_1	N_2	Winner
28	6	N_2	62	50	N_1
36	8	N_1	62	54	N_2
36	10	N_2	66	64	N_1
42	14	N_1	66	66	N_2
42	15	N_2			
70	76	N_1			
70	78	N_2			
73	86	N_1			
73	88	N_2			
76	98	N_1			
76	100	N_2			

TABLE VI

THE EFFECTS OF BIOTIC POTENTIAL AND DISTANCE
FROM THE COEXISTENCE LINE ON THE OUTCOME
OF INTERSPECIFIC COMPETITION

For: $K_1 = 120$, $K_2 = 100$, $\alpha_{21} = 1.25$, $\alpha_{12} = 2.0$

N_1	N_2	r_1	r_2	Winner	Sat. Time	Distance
77	45.9	0.25	0.25	N_1	108	1.887
77	45.9	0.3	0.25	N_2	136	1.887
77	45.9	0.4	0.25	N_2	72	1.887
77	45.9	0.5	0.25	N_2	58	1.887
77	45.9	0.65	0.25	N_2	48	1.887
77	45.9	1.0	0.25	N_2	39	1.887
77	45.9	2.0	0.25	N_2	31	1.887
79	42.7	0.25	0.25	N_1	88	5.66
79	42.7	0.3	0.25	N_1	90	5.66
79	42.7	0.4	0.25	N_1	104	5.66
79	42.7	0.5	0.25	N_2	79	5.66
79	42.7	0.65	0.25	N_2	58	5.66
79	42.7	1.0	0.25	N_2	44	5.66
79	42.7	2.0	0.25	N_2	34	5.66
81	39.5	0.25	0.25	N_1	78	9.434
81	39.5	0.4	0.25	N_1	79	9.434
81	39.5	0.5	0.25	N_1	82	9.434
81	39.5	0.65	0.25	N_1	92	9.434
81	39.5	1.0	0.25	N_2	57	9.434
81	39.5	2.0	0.25	N_2	40	9.434

TABLE VI (Continued)

N_1	N_2	r_1	r_2	Winner	Sat. Time	Distance
85	33.1	0.25	0.25	N_1	66	16.98
85	33.1	0.3	0.25	N_1	65	16.98
85	33.1	0.4	0.25	N_1	63	16.98
85	33.1	0.5	0.25	N_1	63	16.98
85	33.1	0.65	0.25	N_1	62	16.98
85	33.1	1.0	0.25	N_1	62	16.98
85	33.1	2.0	0.25	N_1	64	16.98
75	49.1	0.25	0.25	N_2	101	1.887
75	49.1	0.25	0.3	N_1	128	1.887
75	49.1	0.25	0.4	N_1	72	1.887
75	49.1	0.25	0.5	N_1	57	1.887
75	49.1	0.25	0.65	N_1	46	1.887
75	49.1	0.25	1.0	N_1	36	1.887
75	49.1	0.25	2.0	N_1	28	1.887
74	50.7	0.25	0.25	N_2	88	3.774
74	50.7	0.25	0.3	N_2	97	3.774
74	50.7	0.25	0.4	N_1	81	3.774
74	50.7	0.25	0.5	N_1	61	3.774
74	50.7	0.25	0.65	N_1	48	3.774
74	50.7	0.25	1.0	N_1	37	3.774
74	50.7	0.25	2.0	N_1	28	3.774

TABLE VI (Continued)

N_1	N_2	r_1	r_2	Winner	Sat.Time	Distance
72	53.9	0.25	0.25	N_2	76	7.547
72	53.9	0.25	0.3	N_2	77	7.547
72	53.9	0.25	0.4	N_2	88	7.547
72	53.9	0.25	0.5	N_1	77	7.547
72	53.9	0.25	0.65	N_1	55	7.547
72	53.9	0.25	1.0	N_1	40	7.547
72	53.9	0.25	2.0	N_1	30	7.547
69	58.7	0.25	0.25	N_2	66	13.208
69	58.7	0.25	0.3	N_2	66	13.208
69	58.7	0.25	0.4	N_2	66	13.208
69	58.7	0.25	0.5	N_2	70	13.208
69	58.7	0.25	0.65	N_2	96	13.208
69	58.7	0.25	1.0	N_1	46	13.208
69	58.7	0.25	2.0	N_1	32	13.208
61	71.5	0.25	0.25	N_2	53	28.302
61	71.5	0.25	0.3	N_2	52	28.302
61	71.5	0.25	0.4	N_2	51	28.302
61	71.5	0.25	0.5	N_2	51	28.302
61	71.5	0.25	0.65	N_2	51	28.302
61	71.5	0.25	1.0	N_2	53	28.302
61	71.5	0.25	2.0	N_2	99	28.302

TABLE VI (Continued)

N_1	N_2	r_1	r_2	Winner	Sat.Time	Distance
33	18.4	0.25	0.25	N_1	96	1.887
33	18.4	0.25	0.3	N_1	106	1.887
33	18.4	0.25	0.4	N_2	77	1.887
33	18.4	0.25	0.65	N_2	53	1.887
33	18.4	0.25	1.0	N_2	45	1.887
33	18.4	0.25	2.0	N_2	38	1.887
35	15.2	0.25	0.25	N_1	75	5.66
35	15.2	0.25	0.3	N_1	71	5.66
35	15.2	0.25	0.4	N_1	70	5.66
35	15.2	0.25	0.5	N_1	84	5.66
35	15.2	0.25	0.65	N_2	67	5.66
35	15.2	0.25	1.0	N_2	50	5.66
35	15.2	0.25	2.0	N_2	41	5.66
37	12	0.25	0.25	N_1	64	9.434
37	12	0.25	0.3	N_1	59	9.434
37	12	0.25	0.4	N_1	54	9.434
37	12	0.25	0.5	N_1	53	9.434
37	12	0.25	0.65	N_1	55	9.434
37	12	0.25	1.0	N_2	63	9.434
37	12	0.25	2.0	N_2	44	9.434
40	7.2	0.25	0.25	N_1	52	15.094
40	7.2	0.25	0.3	N_1	48	15.094
40	7.2	0.25	0.4	N_1	43	15.094

TABLE VI (Continued)

N_1	N_2	r_1	r_2	Winner	Sat.Time	Distance
40	7.2	0.25	0.5	N_1	40	15.094
40	7.2	0.25	0.65	N_1	39	15.094
40	7.2	0.25	1.0	N_1	39	15.094
40	7.2	0.25	2.0	N_2	62	15.094
31	21.6	0.25	0.25	N_2	89	1.887
31	21.6	0.3	0.25	N_2	100	1.887
31	21.6	0.4	0.25	N_1	89	1.887
31	21.6	0.5	0.25	N_1	75	1.887
31	21.6	0.65	0.25	N_1	65	1.887
31	21.6	1.0	0.25	N_1	57	1.887
31	21.6	2.0	0.25	N_1	50	1.887
30	23.2	0.25	0.25	N_2	77	3.774
30	23.2	0.3	0.25	N_2	76	3.774
30	23.2	0.4	0.25	N_2	89	3.774
30	23.2	0.5	0.25	N_1	91	3.774
30	23.2	0.65	0.25	N_1	73	3.774
30	23.2	1.0	0.25	N_1	61	3.774
30	23.2	2.0	0.25	N_1	53	3.774
27	28	0.25	0.25	N_2	61	9.434
27	28	0.3	0.25	N_2	57	9.434
27	28	0.4	0.25	N_2	53	9.434
27	28	0.5	0.25	N_2	52	9.434
27	28	0.65	0.25	N_2	52	9.434

TABLE VI (Continued)

N_1	N_2	r_1	r_2	Winner	Sat. Time	Distance
27	28	1.0	0.25	N_2	59	9.434
27	28	2.0	0.25	N_1	68	9.434
21	37.6	0.25	0.25	N_2	48	20.755
21	37.6	0.3	0.25	N_2	44	20.755
21	37.6	0.4	0.25	N_2	39	20.755
21	37.6	0.5	0.25	N_2	36	20.755
21	37.6	0.65	0.25	N_2	34	20.755
21	37.6	1.0	0.25	N_2	32	20.755
21	37.6	2.0	0.25	N_2	31	20.755

VITA

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Thesis: EFFECTS OF INITIAL NUMBERS AND INTRINSIC RATES OF INCREASE ON
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