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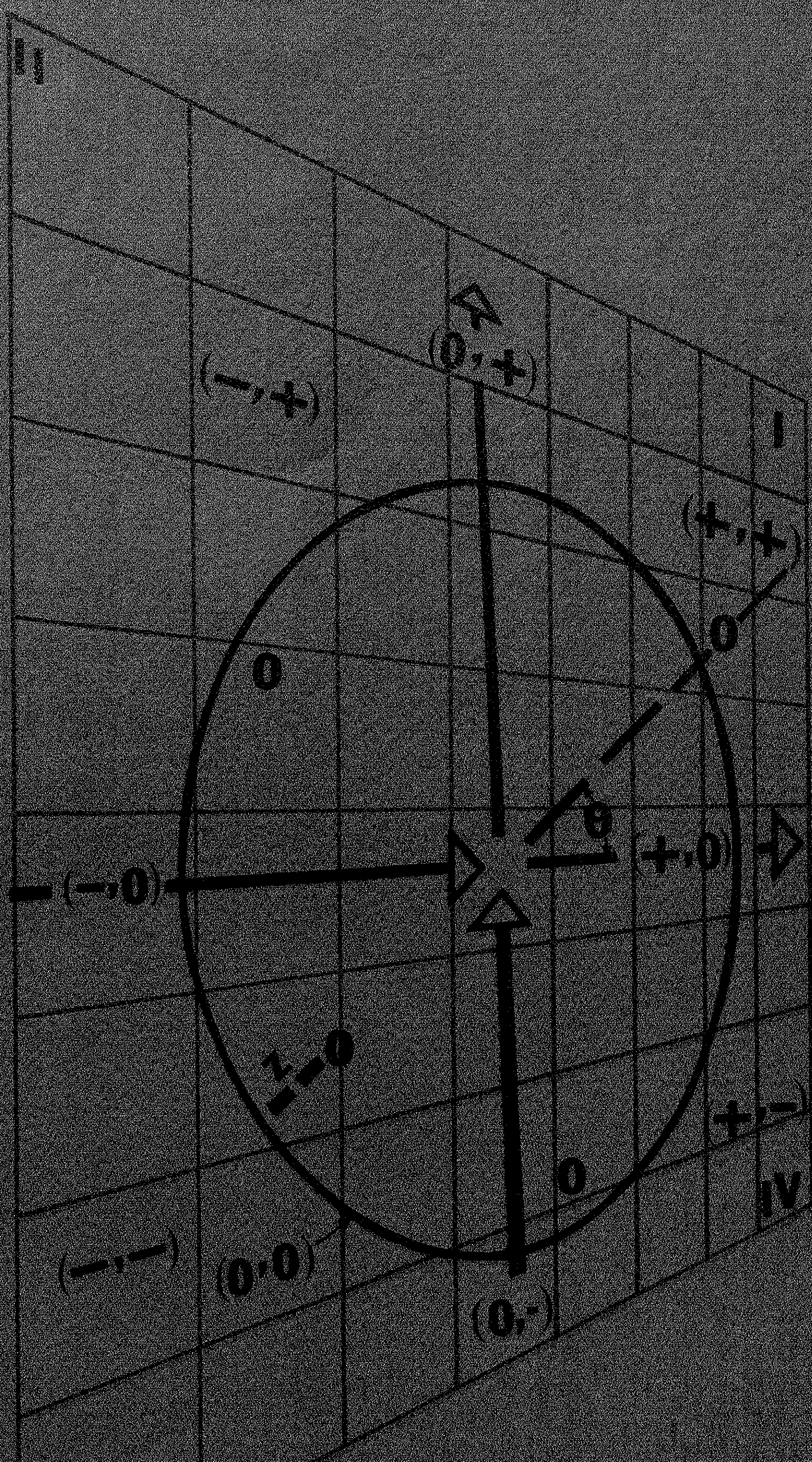

INTERACTION GEOMETRY: AN ECOLOGICAL PERSPECTIVE

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FOREST SERVICE • U.S. DEPARTMENT OF AGRICULTURE

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Manuscript approved for publication August 13, 1975

1976

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The study of interactions has long been an interest of ecologists. Indeed, interaction is now included in the definition of ecology as a science; e.g., "Ecology is the scientific study of the interactions which determine the distribution and abundance of organisms" (Krebs 1972). It is fundamental that studies of biological interactions involve comparisons of entities under two conditions--roughly, separate and together. The earmark of interacting entities is that they are different when developing together than when separate (Williamson 1972, Odum 1971, Malcolm 1966). Although the experimental apparatus used to study interactions are entity-dependent, there has evolved a limited number of mathematical methods for their analysis. Generally speaking these may be grouped in two classes--analysis (mathematical equations) and geometry (coordinate systems). Within the geometric class, the only one of concern here, there are two types of study, relational and metric.

The relational characterization of interactions has been oriented primarily to the coaction cross-tabulation (fig. 1A). It is based on an ordinal sign given by a comparison of process rates for a standard (the "separate" condition) and an experimental situation (the "together" condition). Several authors use the cross-tabulation, or variations of it, to classify types of interactions and to orient discussions of entity systems that possess particular types of interactions. This is the coaction cross-tabulation's primary strength--for broad groupings by type of interaction. It does not have discriminating power within the class and thus functions much as a first approximation, pigeonholing, classification scheme.

The simplest metric method is the time series; a graph of entity attributes plotted over time for the two conditions, separate and together. The method is considered metric because entity attributes are expressed on a cardinal scale as opposed to the comparative relational scale in the coaction cross-tabulation. Surprisingly, many interaction studies stop with this step. It is left to the reader to determine the type and intensity of interactions by making appropriate comparisons of entity attributes under the two conditions.

An extension of the time series is the phase plane (fig. 1B). When used to describe several experiments with different (0,0) equilibrium points, the phase plane is primarily useful for determining intensity of interaction. The natural grouping of points, (0,0) and $(\overline{0},\overline{0})$, in the phase plane is by magnitude of numerical values associated with $(\overline{0},\overline{0})$ or (0,0) conditions, not by type of interaction.

Haskell (1970) recently introduced a new coordinate system (fig. 2) that combines the metric (phase plane) and relational (coaction cross-tabulation) methods of studying interactions. It is called the Periodic coordinate system (PCS). This paper is concerned with methods of calculation involved in the rationale and use of this new coordinate system. For a discussion of other properties and uses, see Haskell (1972).

The initial steps toward development of the PCS were taken by Haskell in the 1940's. One of the first steps was to convert the coaction cross-tabulation into a

[1]*I thank Edward Haskell and Harold Cassidy for introducing me to the Periodic coordinate system and Egolfs Bakuzis who called my attention to Haskell's work.*

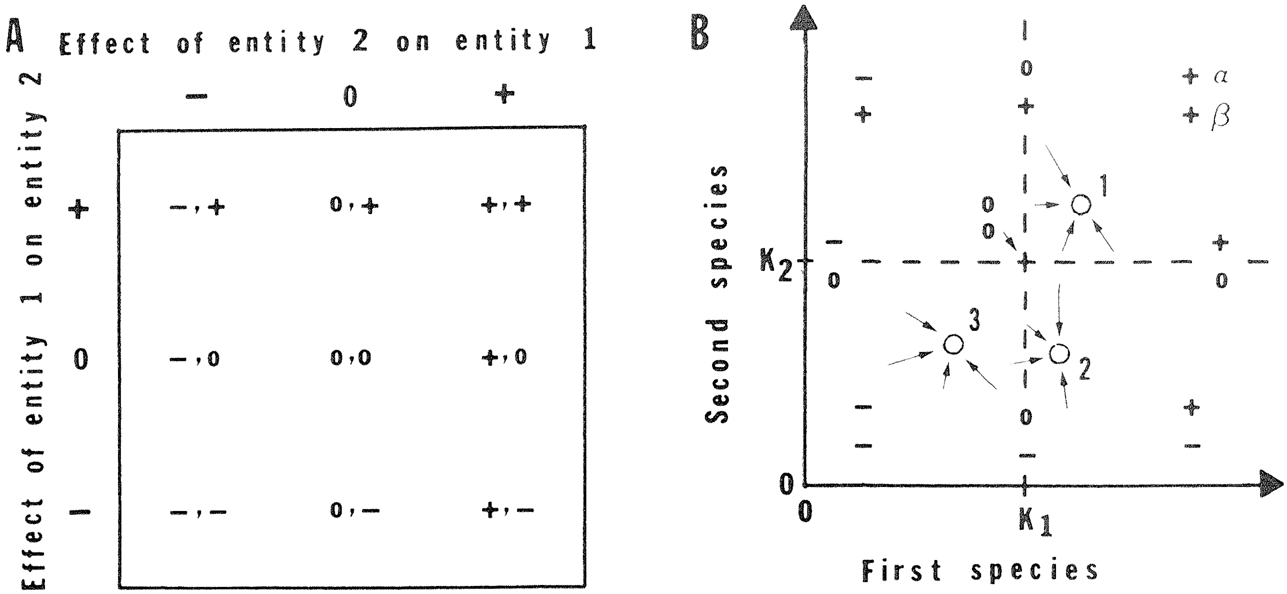

Figure 1.--*(Left.) The coaction cross-tabulation (Haskell 1947). The sign + at the column head indicates that some process rate for entity 1 is greater in the presence of entity 2 than in its absence; - that it is less; 0 that it is the same. The "separate" experimental condition is henceforth called the (0,0) interaction, and the "together" condition, $(\overline{0,0})$. (Right.) Phase plane for analyzing two-species interactions. The point K_1,K_2 represents equilibrium species population attributes when developing separately. The phase space is partitioned into four regions around the point K_1, K_2, four lines and the point itself, using all possible combinations of signs of the coefficients of struggle in the Volterra-Lotka equations. The three small circles represent equilibrium points for interacting species as analyzed by Gause and Witt (1935).*

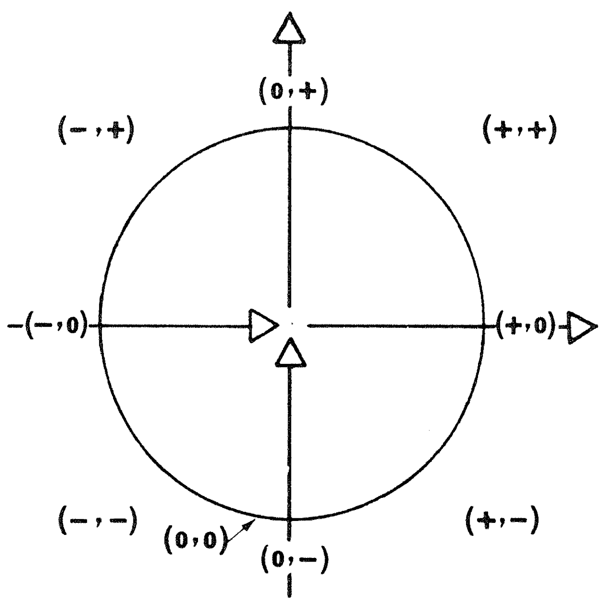

Figure 2.--*The Periodic coordinate system invented by Edward Haskell (Haskell 1970).*

relational coordinate system (RCS) (fig. 3A). This was accomplished by making each bi-ordinal relation in the coaction cross-tabulation a quadrant (2-dimensional region) in the coordinate system, each interaction involving one 0 (neutral) effect an axis of the system and the (0,0) interaction the point of convergence of the four axes. In retrospect it is apparent that Gause and Witt had done a similar thing.[2] However, theirs was based on coefficients in the Volterra-Lotka equations and they apparently did not consider it to be a coordinate system in its own right; rather, as a basis for partitioning the phase plane.

The second step was to embed the phase plane into the RCS. The method of embedding placed the three separate experiments in figure 1B into figure 3A. Experiment 1 was placed in quadrant I, figure 3A, by placing metric axes on relational axes. Experiment

[2] *Personal communication with G. F. Gause, 1974.*

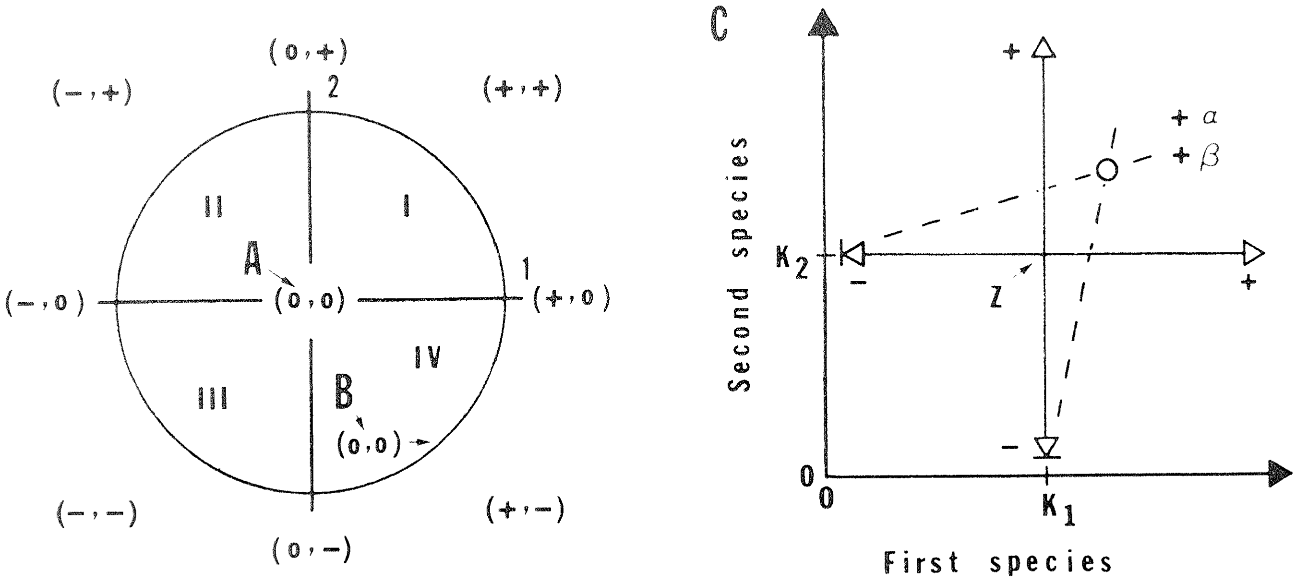

Figure 3.--*(Left.) (A) Relational coordinate system evolved from the coaction cross-tabulation. (Left.) (B) The relational coordinate system with the (0,0) relation represented by a circle rather than a point. The other relations are collectively called (0,0) interactions. (Right.) , (C) Metric coordinate systems. The absolute axes have solid arrowheads, the relative axes have open heads. There are four relative metric axes; two of increase (+) and two of decrease (-). The relative axes of decrease are of finite length, ending at the appropriate absolute axis. They intersect at the point Z, where* α*=0=*β.

2 was placed in quadrant II, figure 3A, metric axes on relational axes, after the horizontal metric axis had been reflected about the vertical axis. Experiment 3 was placed in quadrant III, figure 3A, but only after reflecting each metric axis about its accompanying axis. In this way it was seen that the (0,0) relation could be a circle (fig. 3B) or a point, depending on the numerical magnitude of the equilibrium values.

The result of this embedding procedure is a coordinate system that has four axes of increase, all directed outward from the center in the direction of increasing positive numbers (fig. 4). On the other hand, the coordinate system introduced by Haskell (1970) has four relative axes, two of increase from the (0,0) circle that are directed outward and two of decrease from the (0,0) circle, directed inward (fig. 2). The two major differences between these two coordinate systems are the reversed direction of two of the axes and the change from four absolute axes of increase to two of relative

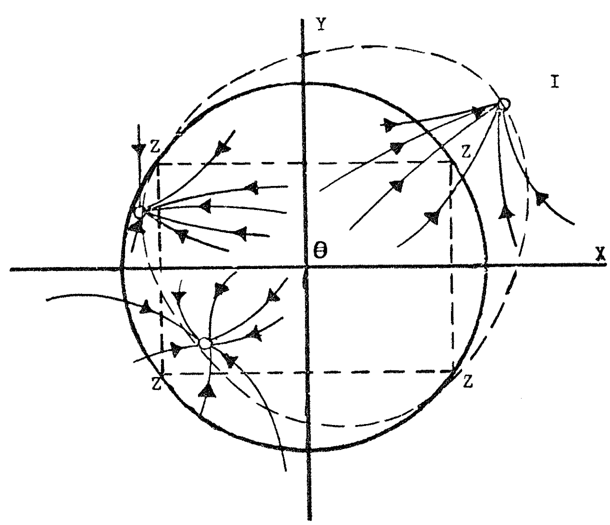

Figure 4.--*Mapping of three Gause and Witt examples (figure 1B) into the relational coordinate system (figure 3A). (From Haskell and Cassidy 1961.) (Reproduced with the permission of Edward Haskell.)*

increase and two of relative decrease. In Part I of this paper I develop an ecological rationale for the type of axes (absolute/relative) and direction of axes (outward/inward).

In Part II I present a method of computing that can be used in all quadrants of the PCS (Leary 1972). The need for this is seen as follows:

> ...the method of calculation appropriate to the Cartesian coordinate system does not suffice for the Periodic coordinate system. The methods appropriate to the latter include the former, but go beyond it.--One method, developed by H. G. Cassidy...[is in (Haskell 1972)] ...Another method, which is still incomplete, was developed by Gause and Witt,...However, while their equation works in quadrants 1 and 3, Cassidy and I have not succeeded in adapting it to quadrants 2 and 4 [of the PCS]. (Haskell 1972).

The method of computation is then applied to an illustrative example of coordinate system use on a famous experiment of Gause (1934).[3]

RATIONALE FOR COORDINATE SYSTEM FORM

An alternative method of combining coordinate systems is to embed the phase plane in figure 3C into figure 3B. They have but one property in common: the relation of reciprocal neutrality (0,0) in 3B and Z (α=0=β) in 3C. Thus, an embedding of 3C into 3B begins by bringing into coincidence Z and the (0,0) circle. But where on the (0,0) circle should the Z point be located? A logical rule for placement is shown in figure 5A: Place 3C in 3B so that a radius from the center of 3B connects first the point Z and then the point for the experiment in question (see fig. 1B, points 1, 2, 3).[4]

The examples in quadrants I, III, and IV are from Gause and Witt (1935); the one in II is hypothetical, for purposes of completeness. Notice that all experimental points are located outside the (0,0) circle. An argument can be made that the region outside the circle should be reserved for enhancing interactions, hence axes of relative increase should be directed outside the circle and, contrarily, that relative decrease axes should be directed inside the circle. The argument is based on three considerations: (1) that the radius of the (0,0) circle is in some way proportional to the numerical magnitude of K_1 and K_2 (e.g., their sum), (2) the existence of mutual obligate enhancing interactions (where K_1,K_2 is numerically 0,0) and, (3) the nonexistence of mutual obligate negative interactions.

Figure 5A may be simplified by discarding the absolute metric axes (solid arrows) and the two inward-directed relative metric axes (see fig. 5B, quadrant I). Other steps produce figure 5B. The final step to the Periodic coordinate system is to notice in figure 5B that each axis of the relational coordinate system separates two similarly directed relative metric axes, and to allow the former to "carry" the latter. This produces the coordinate system, figure 5C, invented by Edward Haskell.

Figure 5C is a construct that combines aspects of both the relational and metric methods of studying interactions. It is a quantification of the coaction cross-tabulation long used by ecologists to orient and classify organisms by their type of interaction. The coaction cross-tabulation, on the other hand, is a mathematization (but not quantification) of the concept "interaction" because it is based only on ordinal relations (>,<,=). The Periodic coordinate system quantifies the concept but still retains the ordinal framework.

Inclusion of the relative metric axes in the cross-tabulation allows cardinal specification of type of interaction using the angle θ, and because of an entirely new dimension it allows quantitative statements about intensity of interaction (fig. 5C). Thus, it appears to combine the classifying power of the cross-tabulation and the discriminating power of the phase plane.

EXAMPLE OF COORDINATE SYSTEM USE

Use of the Periodic coordinate system for interaction analysis may be shown in a simple example. The experiment is that of Gause (1934).[3]

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[3]*I analyzed the* Paramecium aurelia *and* P. caudatum *experiments discussed on pages 98 to 103, with experimental data given in Appendix I, Table 3, columns head "mean."*

[4]*Notice that my placement rule puts experiment 2 (fig. 1B) in quadrant IV instead of quadrant II. This is a slight correction in Haskell's mapping.*

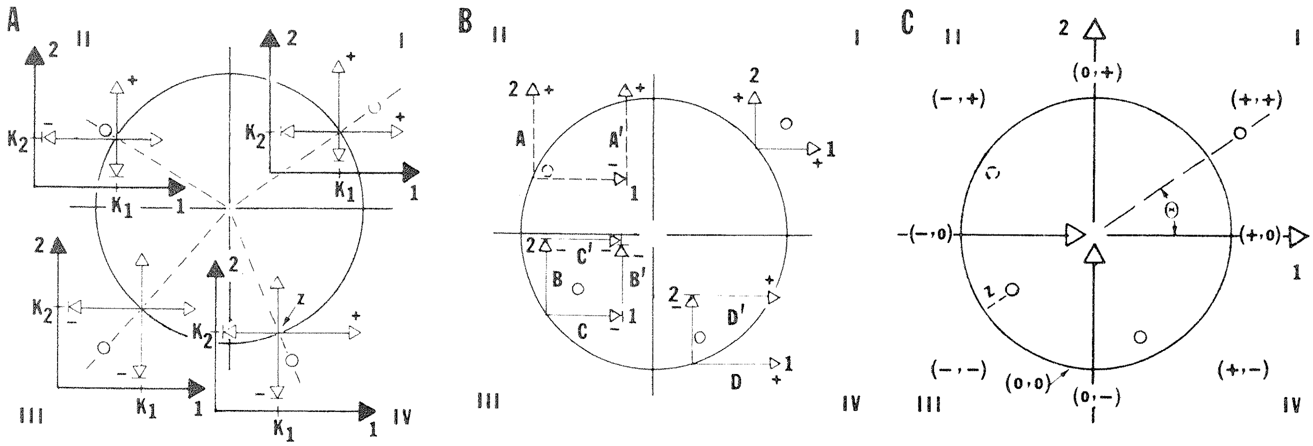

Figure 5.--*(Left.) My method of embedding metric into relational coordinate systems. Placement rules are three: put Z point on (0,0) circle, position so common radius connects Z and experimental points, and maintain conventional directions for Cartesian axes. (Middle.) Intermediate steps in transition from 5A to 5C. Step 1 is to drop both absolute and the two inward directed relative metric axes (see quadrant I). Step two is to reflect each relative axis of decrease about its accompanying axis (necessary once in II and IV, twice in III). Step 3 is to translate axes A,B,C,D to positions A',B',C',D'. (Right.) The Periodic coordinate system produced by allowing each relational axis to "carry" the relative axes it separates in B. Experimental situations are located by their type of interaction (θ) and their intensity (z), given by the distance from the (0,0) circle.*

The first forward difference equation form of the logistic equation was fit to the (0,0) data using a method wherein the (0,0) data are considered boundary conditions in a multi-point boundary-value problem (Leary and Skog 1972). The procedure was adjusted to reflect removal of 1/10th of the population each day except day 1. The r_i and K_i values were r_1 = 0.9701, K_1 = 203.64 (*P. caudatum*), and r_2 = 1.188, K_2 = 535.19 (*P. aurelia*). The Volterra-Lotka equations, modified as suggested by Hutchinson (1947), fit to the $\overline{(0,0)}$ data were:

$$\Delta Y1/\Delta t = 0.9701\ Y1 \left[\frac{203.64 - Y1 + (a_{11} e^{+a_{12} Y2} - 0.5)Y2}{203.64}\right] \qquad (1)$$

$$\Delta Y2/\Delta t = 1.188\ Y2 \left[\frac{535.19 - Y2 + (a_{21} + a_{22} t)Y1}{535.19}\right]$$

Analysis showed the a_{ij} to have values a_{11} = 4.54, a_{12} = -0.0287, a_{21} = 0.1844, a_{22} = -0.2651. The solution of equation (1) at selected times is shown in figure 6A.

The phase plane analysis is shown in figure 6B. This involves a continuous comparison of two trajectories--(0,0) and $\overline{(0,0)}$. The comparison is based on a direction (θ) and distance (z) from (0,0) (the standard) to $\overline{(0,0)}$. Theta is easily determined. However, a question exists about the appropriate measure of interaction intensity. In terms of figure 6B this means, how does one determine the length of z, the hypotenuse of the right triangle? Cassidy (1972) used the standard Pythagorean measure: $z^2 = x^2 + y^2$. I have used the simple measure $z = |x + y|$ (Leary 1972).[5] There appears to be no a priori reason to prefer one over the other, although as greater experience is gained with the coordinate system there may be clues as to which, including others, is preferred. One clue that would, for example, favor $(x^2 + y^2)^{1/2}$ and $|x + y|$ over $(x^2 + y^2)^{-1/2}$ is a natural tendency for x and y to become small as they approach the same

[5] *The value z (the absolute value of the algebraic sum) has value zero when $x = y = 0$ and when $\pm x = \mp y$.*

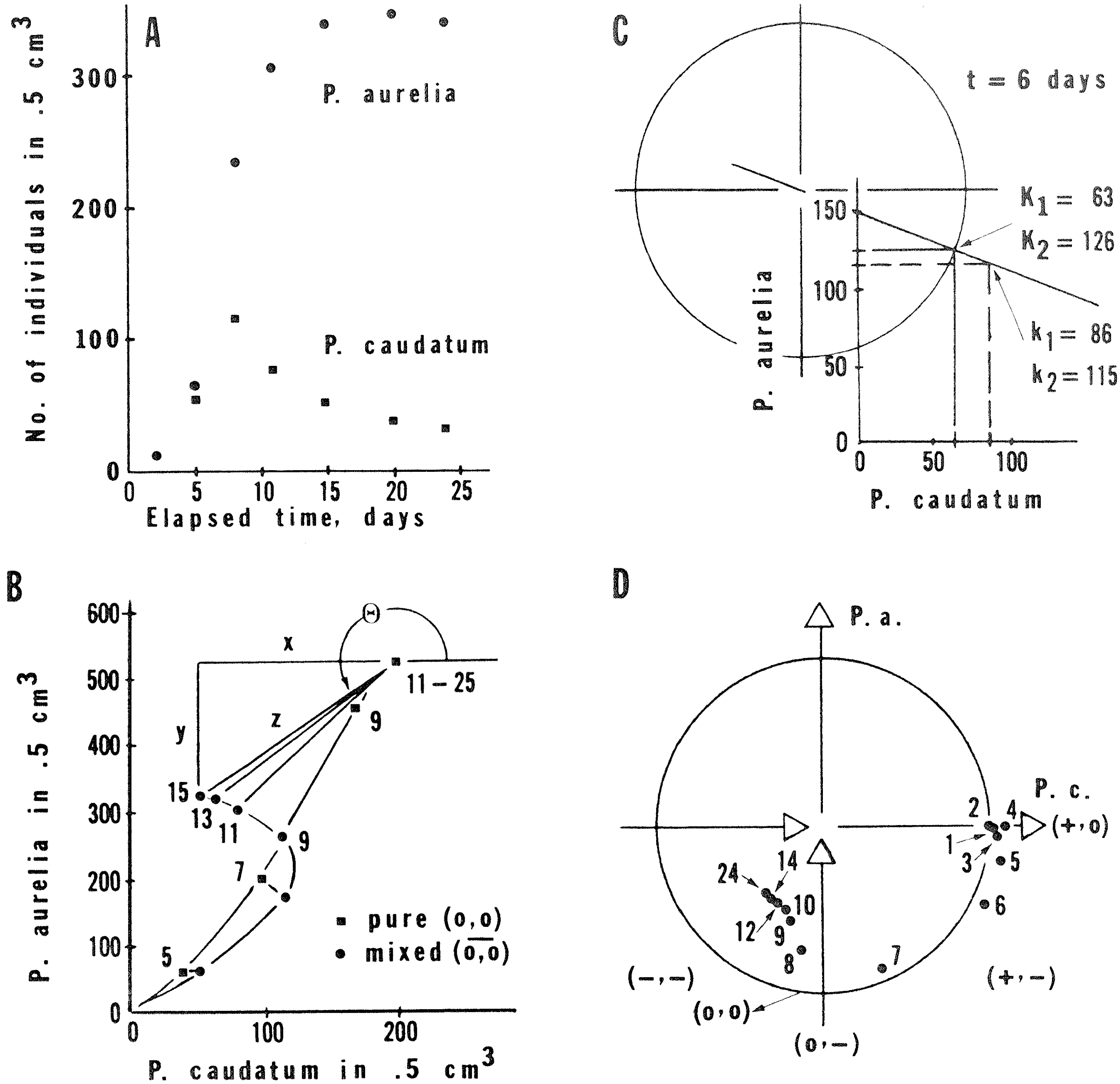

Figure 6.--*(Upper left.) (A) Time series form of Gause experiment*[3] *with mixed population showing predicted values. (Lower left.) (B) Phase plane form of analysis showing that trajectory comparisons form the basis for computing type and intensity of interaction. (Upper right.) (C) Positioning of an observation at day 6 into the relational coordinate system. (Lower right.) (D) Periodic coordinate system representation of Gause experiment.*

absolute value; that is, when gain to one nearly equals loss to another, both gain and loss tend to be small. Of course, $|x + y|$ does not differentiate between situations when $\pm x = \mp y$.

Figure 6C shows the placement of experimental results at day 6, given by solution to my prediction equations, into the relational coordinate system. Table 1 shows the computations required to determine θ

Table 1.--*Example of interaction computations for analysis of paramecium data of Gause (1934)*[1]

Elapsed time (days)	Pure r_1 P. c.	Pure r_1 P. a.	Mixed r_2 P. c.	Mixed r_2 P. a.	$\theta = \tan^{-1}(\frac{y}{x})$	z = x + y	$\frac{\lvert z \rvert}{\lVert r_1 \rVert}$
1	3.9	4.4	4.0	4.4	0°47'	0.073	0.008795
2	7.7	9.5	8.1	9.5	0° 0'	.4	.02326
3	13.3	18.6	15.0	18.5	[2]356°38'	1.7	.05329
4	23.0	35.6	28.2	35.6	0° 0'	5.2	.08874
5	38.7	68.5	52.0	66.2	[3]348°30'	9.3	.08675
6	62.8	126.4	86.0	115.4	[3]335°12'	12.8	.06765
7	96.2	220.2	113.6	178.2	[3]292°30'	-24.6	.07775
8	134.8	346.5	116.1	233.0	260°39'	-132.2	.2747
9	168.9	466.4	102.8	267.0	251°40'	-265.5	.4179
10	189.4	527.3	89.0	289.0	247°09'	-338.7	.4726
12	199.7	539.0	69.0	316.6	239°34'	-353.1	.4780
14	200.3	539.0	56.2	332.2	235°08'	-350.9	.4746
24	200.4	539.0	33.1	341.3	229°45'	-365.0	.4936

[1]Columns 2-5 are the pure and mixed culture coordinates obtained by solving the appropriate difference equation(s). Following Cassidy (1972), the position vectors r_2 and r_1 have two components (X_2, Y_2) and (X_1, Y_1), where X refers to *P. caudatum* and Y to *P. aurelia*. Figure 6B makes clear the meaning of x and y.

[2]The position for time 3 must be corrected by 45' for axis reflection, so θ_c = 357°23'.

[3]The position for time 5 must be corrected by 2°38', so θ_c = 351°8', for time 6 by 12°3', so θ_3 = 347°15', and for time 7 by 5°4', so θ_c = 297°34'

and z. Because of the reflection of the axis of decrease, an adjustment must be made to all points in quadrant IV (and II) for correct positioning of the experiment in figure 6D. Appendix I contains the correction formula. The latter figure shows the pattern of type and intensity of interaction that occurred at selected days in the 25-day experiment. Clearly, intensity, given by z = |x + y|, did not deviate materially from z = 0 for the first 7 days of the experiment. However, after day 7, intensity increased abruptly and type changed less rapidly toward a near equilibrium near the center of (-,-).

Figure 6D shows how the PCS separates experimental results by their components of interaction: type and intensity. It groups interactions with the same bi-ordinal type (e.g., (+,-)) into the same quadrant just as the coaction cross-tabulation does. Within each type, however, it differentiates with angular precision so that questions, for example, how close a (+,-) interaction is to (+,0), can be answered. The addition of the phase plane to RCS makes this possible. It also brings with it the dimension needed for measuring interaction intensity. This makes possible two-dimensional groupings of interactions in the quadrants. It also allows classification of interactions by their trajectories in PCS. For example, (+,-) interactions which begin strong and evolve toward weak would have a trajectory directed toward the (0,0) circle. Those that begin weak, strengthen, and then subside would have a different trajectory (Mattson and Addy 1975). In these respects the PCS has discriminating power that the coaction cross-tabulation does not have, plus it retains the grouping (pigeonholing) asset of the cross-tabulation.

THE PERIODIC COORDINATE SYSTEM IN SYNTHESIS

The example illustrates one manner of using the Periodic coordinate system, i.e., for analysis. In an analysis mode, the coordinate axes are labeled with specific entities. Another use of the coordinate system is for synthesis; for assembling large quantities of experimental results into a single coordinate system. In this mode, the axes are not labeled with specific entities and the map symbols, circles in figure 6D, are replaced with symbols that identify the entities that bear the appropriate relation one to another. For example, the "•" for day 7 might be replaced by a symbol combination (Pc,Pa) denoting that *P. caudatum* and *P. aurelia* bear that relation to each other on day 7.

No doubt other uses can be found for this new coordinate system in ecology and other disciplines where interactions are of interest.

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APPENDIX

When an experimental result falls in quadrants II or IV of the RCS, e.g., figure 6C, a correction must be made to the angle θ before the point is located in the PCS. The necessary information for computing this correction is shown in figure 7.

The objective is to find the angle α that is to be added to θ . Consider the triangle formed by the sides r_1, r_2, and w following reflection about the horizontal axis. The angles opposite the sides r_1, r_2, and w are ρ, γ, and α, respectively. The law of sines for the Euclidean plane shows their relation to be

$$\frac{\sin\rho}{r_1} = \frac{\sin\gamma}{r_2} = \frac{\sin\alpha}{w}.$$

In our case we know r_1, r_2, and γ. Thus we can easily determine ρ and, knowing γ and ρ, also determine α.

Clearly,

$$\rho = \arcsin\left[\frac{r_1 \sin\gamma}{r_2}\right]$$

where $\gamma=\pi-2 \arctan (y/x)$, or $\pi-2\kappa$. Thus, α is given by

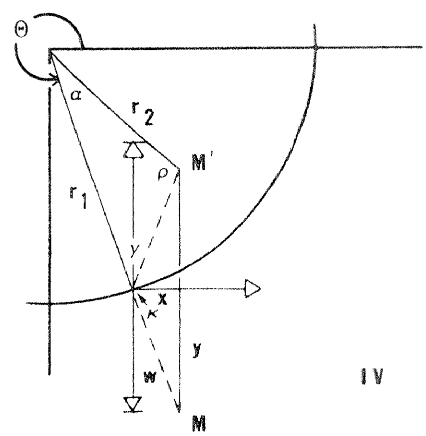

Figure 7.--*Details for locating the position of experimental situation M in quadrant IV before (M) and after (M') correction for reflection of the axis of decrease.*

$$\alpha = \pi - \left[\pi - 2\kappa + \arcsin\left[\frac{r_1 \sin\gamma}{r_2}\right]\right]$$

Note that w is not used in determining the correction angle. Thus, the correction angle determination is not confounded with the question of the geometry of interaction space.

☆U.S. GOVERNMENT PRINTING OFFICE: 1976—669-078/112

Leary, Rolfe A.
1976. Interaction geometry: an ecological perspective. USDA For. Serv. Gen. Tech. Rep. NC-22, 8 p., illus. North Cent. For. Exp. Stn., St. Paul, Minn.

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OXFORD: 228.2/.3:182:181.41--015.5. KEY WORDS: biological interactions, phase plane, coordinate systems.

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