listeners ($P < .025$ across subjects and $P < .001$ across stimuli). These differences were numerically consistent for both melodic and rearranged sequences. Most of the differences between naive and experienced listeners can be attributed to the superior performance of the right ear in experienced listeners ($P < .025$ across subjects and $P < .025$ across stimuli); performance in the left ear does not differ significantly between the two groups of subjects.

Confirming the results of previous studies, the musically naive subjects have a left ear superiority for melody recognition. However, the subjects who are musically sophisticated have a right ear superiority. Our interpretation is that musically sophisticated subjects can organize a melodic sequence in terms of the internal relation of its components. This is supported by the fact that only the experienced listeners could accurately recognize the two-note excerpts as part of the complete stimuli. Dominance of the left hemisphere for such analytic functions would explain dominance of the right ear for melody recognition in experienced listeners: as their capacity for musical analysis increases, the left hemisphere becomes increasingly involved in the processing of music. This raises the possibility that being musically sophisticated has real neurological concomitants, permitting the utilization of a different strategy of musical apprehension that calls on left hemisphere functions.

We did not find a significant right ear superiority in excerpt recognition among experienced listeners. This may be due to the overall difficulty of the task and insensitivity of excerpt recognition as a response measure. Support for this interpretation comes from a more recent study in which we compared the response time for excerpt recognition in boys aged 9 to 13 who sing in a church choir (*19*) with the response time in musically naive boys. In this study, recognition accuracy did not differ by ear, but response times were faster in the right ear than the left for the choirboys. Furthermore, the relative superiority of the right ear in choirboys compared with other boys of the same age increased progressively with experience in the choir.

In sum, our subjects have demonstrated that it is the kind of processing applied to a musical stimulus that can determine which hemisphere is dominant. This means that music perception is now consistent with the generalization suggested initially by Jackson that the left hemisphere is specialized for internal stimulus analysis and the right hemisphere for holistic processing.

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10. D. Kimura, *Cortex* **3**, 163 (1967).
11. This modality view is explored by D. Kimura (*10*); *Sci. Am.* **229**, 70 (March 1973).
12. For a similar differentiation of hemispheric function in vision and language, see J. Levy *et al.* (*5*) and B. Milner (*3*).
13. Melody perception is a classic gestalt demonstration [C. von Ehrenfels, *Vierteljahrsschr. Wiss. Philos.* (1890), vol. 14; H. Werner, *Leistungsknechte* **4**, 182 (1917); *Z. Angew. Psychol.* **26**, 101 (1926); H. Meissner, *Zur Entwicklung Des Musikalischen Sinns Beim Kind Waehrend Des Schulalters* (Trorvitzsch, Berlin, 1914); F. Brehmer, *Beih. Z. Angew. Psychol.* (1925), pp. 36 and 37; H. Werner, *J. Psychol.* **10**, 149 (1940)]. For recent investigations, see: W. J. Dowling, *Percept. Psychophys.* **9**, 348 (1971); D. Deutsch, *ibid.* **11**, 411 (1972).
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16. H. W. Gordon (*6*). The subjects in this study were probably intermediate in musical sophistication; accordingly, they did not show a consistent left or right ear superiority. We would expect individual differences in such a population to be quite large.
17. Right-handedness was checked by a modified questionnaire from H. Hecaen and J. Ajuriaguerra, *Left-Handedness: Manual Superiority and Cerebral Dominance* (Grune & Stratton, New York, 1964).
18. The formula used was

$$\frac{\text{True positives (\%)} - \text{False positives (\%)}}{1 - \text{False positives (\%)}}$$

The results are tested nonparametrically across subjects and stimuli separately for reasons outlined by H. Clark [*J. Verb. Learn. Verb. Behav.* **12**, 4 (1973)]. In each case, the by-subject test is a Fisher exact test, and the by-stimulus test is a Wilcoxon matched-pairs, signed-ranks, two-tailed test. There were no significant differences between ears in guessing rates by either measure.
19. The 20 choirboys were in the choir of the Cathedral of Saint John the Divine in New York City. The choir is of professional quality: the boys sing and rehearse about 14 hours a week. The nonchoir, nonmusical boys were drawn from the same school (the Cathedral School) and matched the choirboys in age and school grade (T. Bever, R. Chiarello, L. Kellar, in preparation).
20. We thank A. Handel of Columbia University, J. Barlow and A. Strong of Wesleyan University, and S. Neff of Barnard College for their assistance. Supported by grants from the Grant Foundation and the National Institutes of Health.

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Competition: A Theory Based on Realistic, General Equations of Population Growth

Abstract. *Realistic equations of population growth, separately representing scarcity of renewed material resources and scarcity of fixed resources related to space, show the differential impact of these two factors on competitive coexistence. The equations suggest a general theory of competition covering any number or kind of resources, consumers, and intraspecific and interspecific interactions.*

Some limitations of the logistic growth equation are recognized in at least one recent treatment of general competition theory (*1*), but the most serious defects are neither noted nor corrected. These are: (i) the maximum specific rate of increase is achieved only at zero density and (ii) the maxi-

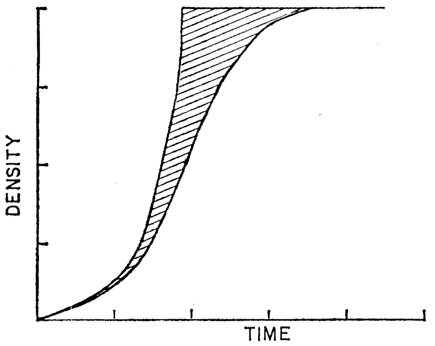

Fig. 1. Curves showing the upper and lower boundaries of growth for any populations with identical maximum growth rates and maximum maintenance densities.

mum density (carrying capacity) must incorporate both the effects of scarcity of renewed material resources and the effects of scarcity of space or any other fixed resource.

In this report the first defect is removed by writing a general equation incorporating threshold effects, with the logistic as a special limiting case, and the second defect is remedied by separating thresholds and minima of competition for material resources from thresholds and maxima characterizing competition for available space. The resultant equations are used in place of the Lotka-Volterra equations to propose a general theory of competition.

Consider first the logistic equation in its differential form (*2*)

$$\frac{dx_j}{dt} = r_jx_j\left(\frac{\gamma_j - x_j}{\gamma_j}\right) \qquad (1)$$

where x_j is population density (the units may be organisms, biomass, energy, and so forth), t is time, r_j is the maximum (or intrinsic) specific rate of increase of j, and γ_j is the maximum density of j that can be maintained at equilibrium for a specific level of material resources and a fixed amount of space. The rate r_j is approached as x_j approaches zero.

An exponential growth equation, on the other hand, permits the maximum rate of growth to be achieved until the population reaches the limit γ_j at which time growth ceases instantly. Thus

$$\begin{aligned} dx_j/dt &= r_jx_j \text{ for } x_j < \gamma_j \\ dx_j/dt &= 0 \quad \text{for} \quad x_j = \gamma_j \end{aligned} \qquad (2)$$

The curves defined by Eqs. 1 and 2 are graphed in Fig. 1. The logistic represents the lower boundary or slowest approach to the limit γ_j; the exponential curve represents the maximum rate of approach to this limit. For given r_j and γ_j a species would not usually be expected to grow more slowly than predicted by the logistic, since in that model feedback control begins as soon as x_j is greater than zero. Similarly, every population has a maximum specific rate of growth (r_j). The realized growth curve of a population with specified r_j and γ_j then lies somewhere within the hatched area of Fig. 1. A general growth equation specifying this family of curves with the same feedback characteristics as the logistic (*3*) is given by

$$\frac{dx_j}{dt} = r_jx_j\left[\left(1 - f_j + \frac{\lambda_j}{r_j}\right)_+ - \frac{\lambda_j}{r_i}\right] \qquad (3)$$

and

$$f_j = \left(\frac{x_j - \alpha_j}{\gamma_j - \alpha_j}\right)_+ \qquad (4)$$

where λ_j is the sum of those specific rates of loss (respiration, excretion, and nonpredatory mortality) experienced even under optimal conditions and α_j is a density of population j below which the realized rate of growth equals the maximum (r_j). By definition

$$(\cdot)_+ \begin{cases} = 0 \text{ if } (\cdot) \leq 0 \\ = (\cdot) \text{ if } (\cdot) > 0 \end{cases}$$

If $x_j \leq \alpha_j$, $f_j = 0$ and Eq. 3 reduces to Eq. 2 with population j growing at the maximum specific rate. When $x_j \geq \gamma_j$, $f_j \geq 1$ and the realized growth rate is ≤ 0, the lower limit (from Eq. 3) being $-\lambda_j$.

When $\alpha_j = 0$—that is, when there is no threshold density below which population j can grow at rate r_j—then Eq. 3 reduces to Eq. 1, the logistic, forming the lower boundary of growth in Fig. 1. As $\alpha_j \rightarrow \gamma_j$, Eq. 3 approaches the form of Eq. 2, the exponential, forming the upper boundary of growth in Fig. 1. Clearly, α_j is an important biological parameter determining the curve of population growth and should be included in the generalization of the logistic equation. This generalization is next extended to the case of competition between two species.

Lotka-Volterra competition equations. In any system where species 2 and 3 are competing for both space and common material resources, Eq. 3 can be used to develop a set of competition equations of which the Lotka-Volterra model is a special case. Let β_k represent the proportional effect of a unit of species k on the growth of its competitor, species j. Then Eq. 4 becomes

$$f_j = \left(\frac{x_j + \beta_kx_k - \alpha_j}{\gamma_j - \alpha_j}\right)_+ \qquad (5)$$

and the set of competition equations governing the interactions of species 2 and 3 is:

$$\frac{dx_2}{dt} = r_2x_2\left[\left(1 - f_2 + \frac{\lambda_2}{r_2}\right)_+ - \frac{\lambda_2}{r_2}\right] \qquad (6)$$

$$\frac{dx_3}{dt} = r_3x_3\left[\left(1 - f_3 + \frac{\lambda_3}{r_3}\right)_+ - \frac{\lambda_3}{r_3}\right] \qquad (7)$$

Table 1. Nine possible steady state cases for two species potentially competing, both intra- and interspecifically, for space and material resources. A + entry indicates limitation of the growth of the species by scarcity of the particular resource.

Case	Species 2		Species 3	
	Material limit (f_{12})	Space limit (f_{22})	Material limit (f_{13})	Space limit (f_{33})
1	+	0	+	0
2	0	+	0	+
3	+	+	+	+
4	+	0	0	+
5	0	+	+	0
6	+	+	+	0
7	+	0	+	+
8	0	+	+	+
9	+	+	0	+

At equilibrium the feedback control (f) terms of Eqs. 6 and 7 must each equal 1. When we remove the subscripts +, set each equation equal to zero, and simplify, the equations reduce to the classical Lotka-Volterra equations for the equilibrium case, where the question of coexistence depends on the β and γ values (*4*) and is independent of the shape of the growth curves as determined by the α values.

Generalized competition equations. However, the generalization of the Lotka-Volterra model represented by Eqs. 6 and 7 answered only the first criticism of the logistic equation, the problem of setting a threshold density below which growth can equal the maximum or intrinsic specific rate. There remains a serious biological deficiency of the logistic model, the Lotka-Volterra model, and the model represented by Eqs. 6 and 7. Each of the parameters α, β, and γ combines characteristics of two quite different ecological processes: (i) direct physical, chemical, or behavioral interactions between individuals (that is, competition for space) and (ii) indirect interaction through the medium of material resources commonly shared. Thus, the degree of competition for space, a fixed resource, is a function of the density of competitors, whereas competition for a material resource is a function of the density of that resource. The competition model given by Eqs.

6 and 7 makes no provision for explicitly separating these effects, nor does it allow their realistic combination in cases where the material resource and the living space may be related (saprophagans utilizing the surface of detritus, for example).

A general model capable of resolving these criticisms is proposed, based on a splitting of α_j and γ_j into two new parameters each and a redefinition of β. Let α_{ij} be the density of a material resource i at or above which growth by the consumer j is still maximum (the saturation density), γ_{ij} be the density of a material resource i at or below which ingestion by the consumer j is prevented (the refuge density) (*5*), α_{jj} be the density of a consumer j at or below which growth by j is maximum (the threshold response density), γ_{jj} be the density of a consumer j at which growth is zero (the asymptotic density), and β_k be the proportional effect of a unit of population k on the space requirements of its competitor j, and vice versa for β_j.

Now two kinds of feedback control terms may be defined, one representing competition for space (f_{jj}) and the other representing the status of a particular limiting material resource for a particular consumer (f_{ij}). Thus

$$f_{jj} = \left(\frac{x_j + \beta_k x_k - \alpha_{jj}}{\gamma_{jj} - \alpha_{jj}}\right)_+ \qquad (8)$$

$$f_{ij} = \left(\frac{\alpha_{ij} - x_i}{\alpha_{ij} - \gamma_{ij}}\right)_+ \qquad (9)$$

The general model for populations 2 and 3 competing for space and for a limiting material resource (x_1) is given by

$$\frac{dx_2}{dt} = r_2x_2\left\{\left[1 - f_{12}\left(1 + \frac{\lambda_2}{r_2}\right) - f_{22} + \frac{\lambda_2}{r_2}\right]_+ - \frac{\lambda_2}{r_2}\right\} \qquad (10)$$

$$\frac{dx_3}{dt} = r_3x_3\left\{\left[1 - f_{13}\left(1 + \frac{\lambda_3}{r_3}\right) - f_{33} + \frac{\lambda_3}{r_3}\right]_+ - \frac{\lambda_3}{r_3}\right\} \qquad (11)$$

Setting Eqs. 10 and 11 equal to zero, removing the subscripts +, which are superfluous at steady state, and simplifying, we obtain the equations

$$f_{12}\left(1 + \frac{\lambda_2}{r_2}\right) + f_{22} = 1 \qquad (12)$$

$$f_{13}\left(1 + \frac{\lambda_3}{r_3}\right) + f_{33} = 1 \qquad (13)$$

There are nine ecologically possible different sets of steady state equations (*6*), depending on the values of f_{ij} and f_{jj} (positive or zero, Table 1). For particular values of the biological parameters, the possibility of a solution (coexistence) can be evaluated for each case.

In case 1 the two populations at steady state would be limited solely by competition for x_1, the common material resources; f_{22} and f_{33} are zero. Substituting Eq. 9 into Eqs. 10 and 11, we find the steady state value of the resource x_1. Coexistence is possible if and only if

$$\frac{\lambda_2(\alpha_{12} - \gamma_{12})}{r_2 + \lambda_2} + \gamma_{12} = \frac{\lambda_3(\alpha_{13} - \gamma_{13})}{r_3 + \lambda_3} + \gamma_{13} \qquad (14)$$

That this condition could be fulfilled is highly improbable, and Eq. 14 represents a quantitative restatement of the conditions under which the Gaussian dictum holds; that is, no two species can coexist competing solely for a limiting material resource. Even if Eq. 14 is satisfied, the number of steady state solutions for x_2 and x_3, given x_1, is infinite. For random fluctuations in the level of x_1, the population with the competitive advantage will be the one for which losses relative to its competitor when x_1 decreases below the steady state value will be more than made up by gains relative to its competitor when x_1 increases above the steady state value. Although it would never disappear in a mathematical sense, the competitor with the disadvantage would be reduced eventually to some nonviable density. Interestingly, the only exception to this would be if Eq. 14 were satisfied by complete identity of the α, γ, λ, and r values. In this case, however, the competitors would be identical species.

Case 2, involving space limitation alone, is analogous in form to the generalized Lotka-Volterra model (Eqs. 6 and 7), but there is no shortage of any material resource. If no equilibrium solution is possible, x_2 or x_3 will always survive. If an equilibrium is possible but unstable, either x_2 or x_3 will win depending on the direction of the perturbation, and if equilibrium is stable, coexistence at a unique density ratio is assured (*4*).

The remaining seven cases, 3 to 9, require, at equilibrium, that both scarcity of material resources and scarcity of space exert limiting effects on at least one of the competing species. Each of these intermediate situations, provided α, β, and γ are constant, will move toward a case 1 or a case 2 situation according to whether the available limiting material resource is decreased or increased. Continued decrease of x_1 would eventually result in a case 1 situation with the elimination of one species. Continued increase of x_1 would eventually result in a case 2 situation where the stability characteristics would depend on the β_j and γ_{jj} parameters alone, that is, direct intra- and interspecific competition for space.

Recently some controversy has arisen over the possibility of destabilization of ecological systems by enrichment (*7*). The competition equations developed in this report predict that the effects on stability of continued enrichment would not be the same for all systems, but would depend on the α, β, and γ values for the species groups involved, as well as on the level of enrichment.

The model utilizes parameters with precise biological definitions that can be measured by appropriate observation and experimentation. Additional parameters or functions that may be needed to describe other competitive interactions can be easily incorporated into the theory. Although only the two-species case is analyzed in this report, the theory is easily generalized to n species, including more than one trophic level and variable material resources, themselves represented by realistic growth equations (*8*). Although the number of possible sets of equilibrium equations becomes very large when more than a few competitive pathways are considered, coexistence and stability properties are easily assessed by simulation on digital or analog computers.

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3. The self-control feedback characteristic of the logistic is that the effect of an additional unit added to the population is constant, that is, independent of the density at the time of addition. Although most population control may be of this type, the general equational structure presented here admits of any other types. See, for example, R. G. Wiegert, in *Occasional Papers of the Ecological Society of Australia*, vol. 1, *Insects: Studies in Population Management*, P. W. Geier, L. R. Clark, D. J. Anderson, H. A. Nix, Eds. (Ecological Society of Australia, Canberra, 1973), pp. 85–102; R. G. Wiegert, in *Proc. 6th Southeast Syst. Symp. I.E.E. Conf., Baton Rouge, La.*, in press.
4. L. B. Slobodkin, *Growth and Regulation of Animal Populations* (Holt, Rinehart & Winston, New York, 1961).
5. There is a limit to the rate of negative growth

achieved when no material resources are available, equivalent to the constant losses by respiration and mortality. Making these rates functions of the levels of space and material resources complicates the equations but does not alter the conclusions.
6. An ecologically possible solution requires positive values for x_1, x_2, and x_3. No such solution is possible for either $f_{12} = f_{22} = 0$ or $f_{13} = f_{33} = 0$.
7. M. L. Rosenzweig, *Science* **171**, 385 (1971); C. D. McAllister, R. J. LeBrasseur, T. R. Parsons, *ibid.* **175**, 562 (1972); M. L. Rosenzweig, *ibid.*, p. 564.
8. R. G. Wiegert, in preparation.
9. The development of the ideas in this report has been aided by NSF grants GB-21255 and GB-7683. I am indebted to many students and colleagues for helping shape these ideas. Some comments by W. Anderson prompted the direct comparison with the logistic.

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Origin of the 260-Day Cycle in Mesoamerica

Malmstrom (*1*) has recently attempted to account for the origins of the Mesoamerican 260-day cycle, or sacred almanac, in terms of the interval between zenithal transits of the sun. His hypothesis is that the 260-day cycle originated in the narrow latitudinal band (14°42′N to 15°N) in which the sun is vertically overhead about 12–13 August and again 260 days later about 30 April–1 May. Although this is one of the more stimulating hypotheses on the origins of the sacred almanac, there are serious objections which ought to be raised. It is not a new explanation; Malmstrom was anticipated by several earlier investigators (*2*).

The most serious objection to explaining the origin of the sacred almanac in terms of the interval between zenithal sun positions has been forcefully expressed by Thompson (*3*, pp. 98–99). Although there is a 260-day interval between the autumn and spring zenithal transits of the sun (within the critical latitudinal band), there is a complementary 105-day interval between the spring and autumn positions. The sacred almanac, on the other hand, ran continuously; the spring position would fall on or near the same day in the sacred almanac as the preceding autumn position, but the subsequent autumn position would not correspond. One of the most striking aspects of Mayan calendrics is the importance of reconciling cycles; the Venus table in the Dresden Codex is perhaps the best example of this pervasive concern with the days on which the beginning points of cycles of varying length, all running simultaneously, would coincide (*3*, pp. 208–229). It is extremely unlikely that the 260-day cycle could have been based upon any natural phenomenon that was not continuously repetitive and that was not observable in the greater part of the area in which the sacred almanac was in use.

The nature of the 260-day cycle does not force the conclusion that it was based upon a natural phenomenon. It could simply have resulted from the permutation of its subcycles (13 and 20, both important numbers in Mesoamerican thought), in the same way that the 52-year cycle resulted from the permutation of the 260-day cycle against the solar year (*4*). Thus, any argument for a correspondence with some natural phenomenon must be not merely plausible but compelling.

Malmstrom calls attention to the fact that the lowland site of Izapa is located within the critical latitudinal band, and to the fact that much of the earliest evidence for the use of the Long Count occurs in Late Preclassic contexts which are in some sense Izapan (at least stylistically). As he notes, however, this evidence occurs outside the critical zone, not at Izapa itself; moreover, it is by no means certain that Izapa was the center of this "culture." Malmstrom mentions but does not deal with the fact that the earliest presently known Mesoamerican calendar system—probably (but not unequivocally) involving a typical 260-day cycle—is that of Monte Albán I and II of highland Oaxaca, which is considerably earlier than the Izapan evidence (*5*).

Malmstrom, citing Thompson's (*6*) observations about the distribution of the fauna which lend their names to days in the sacred almanac, rejects the possibility of a highland origin. Although a strong case can be made for a lowland origin, the question is complex and cannot be resolved on the basis of this category of evidence alone. Thompson (*7*) has in fact recently reversed himself, arguing for a highland origin precisely on the basis of the day names.

Although it does not affect his arguments, Malmstrom's misuse of native terms is likely to add confusion to Mesoamerican calendrical studies and should be corrected. He refers to the 260-day cycle as the *tzolkin* or *tonalámatl*, and to the 52-year cycle as the *tonalpohualli*. Actually, *tonalpohualli* ("count of the days") refers to the 260-day cycle, and *tonalámatl* ("book of the days") refers to the books in which it was depicted; *xiuhmolpilli* ("binding of the years") was the Náhuatl word for the 52-year cycle (*8*). The term used by the Maya for the 260-day cycle is unknown; *tzolkin*, which would mean "count of the days" in Yucatec Maya, is a creation of modern Mayanists (*3*, p. 97).

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4. The same suggestion has been made by Thompson (*3*, pp. 98–99), Broda de Casas (*2*), and Prem (*5*, p. 115).
5. A. Caso, in *Handbook of Middle American Indians*, R. Wauchope, Ed. (Univ. of Texas Press, Austin, 1965), vol. 3, pp. 931–947; H. J. Prem, *Contrib. Univ. Calif. Archaeol. Res. Fac.* **11**, 112 (1971).
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7. ———, *Maya Hieroglyphs without Tears* (British Museum, London, 1972), pp. 21–23.
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Perhaps Malmstrom (*1*) can resolve what seems to be a conflict regarding the precedence of the hypothesis describing the correlation of the Mayan *tzolkin* 260-day calendar with zenithal transits of the sun near latitude 15°N. I refer to a theory apparently overlooked by Coe (*2*, p. 55) and others in the field and cited by Peterson (*3*, pp. 186–187) in a discussion on the origin of the *tonalpohualli* or Aztecan version of the *tzolkin*. The pertinent comment is quoted here in its entirety:

> We do not know why a 260-day religious period was chosen, nor what 260 is intended to count. It may have been based on some important astronomical observation of the ancient Mexicans which we have not taken into account, or it may refer to certain cycles of the sun, moon, Venus, or the solstices. Ola Apenes explained it by certain observations made in the Maya region, in the following manner: the difference between the 260-day religious cycle and the 365-day solar cycle