A DYNAMICAL THEORY OF HETEROCHRONY: TIME-SEQUENCING CHANGES IN ECOLOGY, DEVELOPMENT AND EVOLUTION

P. ANTONELLI

*Department of Mathematics, University of Alberta, Edmonton,
Alberta, Canada T6G 2G1*

R. BRADBURY

National Resource Information Center, Canberra A.C.T. 2600 Australia

V. KŘIVAN

Biol. Research Center, Branišovska 31, 370 05 České Budejovice, Czech Republic

H. SHIMADA

Department of Mathematics, Hokkaido Tokai Univ., Sapporo, 005, Japan

ABSTRACT

This work provides a foundation for a quantitative dynamical theory of heterochronic processes in the evolution of colonial invertebrate animals including Bryozoans, Siphonophores and Ants. These processes are environmentally induced changes in the time-sequencing of growth and development which can produce alterations in the morphotypes or castes within an individual colony. Motivation comes from Křivan's theory of environmentally induced constraints on population densities for ecological interactions, but the present theory is second order with allometric production variables x^i and population densities for morphotypes, N^i. We are able to unite ecological theory and the allometric form of the Wilson Ergonomic Theory via projective differential geometry and Wagner spaces which provide a natural description of environmentally induced time-sequencing changes altering the allometric curve of a species. Such changes define a model of heterochronic processes important in paleontology.

Keywords : Colonial animal, heterochrony, ergonomics.

1. Křivan's Growth Rate Transformation Defined by Ecological Constraints

Many model ecological populations assume that per capita growth rate (i.e., intrinsic growth rate) m, is a positive constant. The classical models of Volterra, Gause and Witt, and Lotka tacitly assume this, for example. However, in the presence of constraints on the population densities due to environmental stress or physical stress, m must be variable, because these stresses will act differently in different

age classes and in different parts of their range, in general. Therefore, we wish to explore in this paper the idea of m being a function of the population densities which can then respond to external constraints.

Let us start with a detailed example. Suppose two exponentially growing population densities $N^1(t)$ and $N^2(t)$ are subject to an environmental constraint resulting, say, from *overlap in a common habitat*. Let's represent this as*

$$\frac{dN^i}{dt} = \lambda_{(i)}N^i \ , \quad i = 1, 2 \tag{1.1}$$

subject to the *constraint relation*

$$cN^1 + dN^2 \leq 1 \ . \tag{1.2}$$

In [16], Křivan asks what alteration of λ_i will result from this constraint relation (1.2). He writes

$$\frac{dN^i}{dt} = \lambda_{(i)}N^i - mN^i \tag{1.3}$$

and interprets m as the unbiased "mortality rate" resulting from overcrowding.

Figure 1 illustrates exponential growth of each of the populations resulting from (1.1), until the constraint boundary is reached. On this line we have from (1.2) that

$$c\left(\frac{dN^1}{dt}\right) + d\left(\frac{dN^2}{dt}\right) = 0 \ . \tag{1.4}$$

From which it follows that

$$m = \frac{c\lambda_1 N^1 + d\lambda_2 N^2}{cN^1 + dN^2} = c\lambda_1 N^1 + d\lambda_2 N^2 \ . \tag{1.5}$$
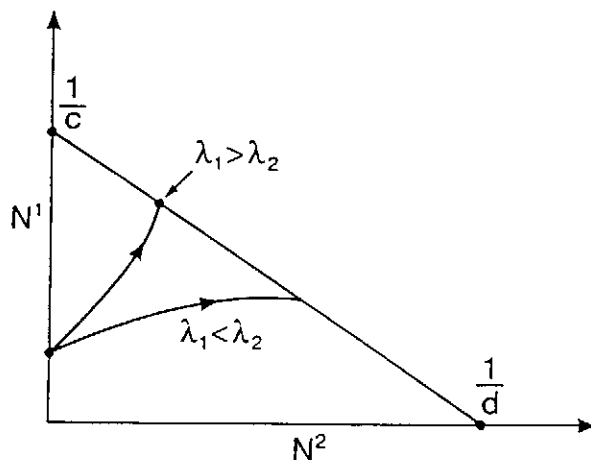

Fig. 1. $N^1(t) = De^{(\lambda_1 - \lambda_2)t} \cdot N^2(t)$

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*Parenthesis means *not* summed.

Consequently, life in the overlap region is described by the *dynamics on the constraint curve*. It is

$$\frac{dN^1}{dt} = N^1(\lambda_1 - c\lambda_1 N^1 - d\lambda_2 N^2)$$

$$\frac{dN^2}{dt} = N^2(\lambda_2 - c\lambda_1 N^1 - d\lambda_2 N^2) \; . \tag{1.6}$$

But, this system has *no positive equilibria*, if $\lambda_1 \neq \lambda_2$. Indeed, this *result holds* for *any form of constraint curve* $F(N^1, N^2) = 1$ *which allows a unique solution for m* because of the form of (1.3). Hence, *the constrained life-style for two exponentially growing population densities in the overlap region must have the same growth rate* $(\lambda_1 = \lambda_2)$ *if they are both to survive*. We call this the *pre-symbiant condition* and we shall have occasion to use it in what is to follow, which concerns evolution of symbiant organisms from previously separate species [19, 20].

Let's consider two logistic populations subject to the *linear constraint* (1.2). The Křivan system is then

$$\left. \begin{array}{l} \dfrac{dN^i}{dt} = N^i(\lambda_{(i)} - \alpha_{(i)}N^i) - mN^i \\[2mm] m = \dfrac{cN^1(\lambda_1 - \alpha_1 N^1) + dN^2(\lambda_2 - \alpha_2 N^2)}{cN^1 + dN^2} \\[2mm] cN^1 + dN^2 = 1 \end{array} \right\} \; . \tag{1.7}$$

In Fig. 2 we see that the separate logistic populations will follow a trajectory intersecting the shortest constraint line. This means the populations will never reach their logistic equilibria. But, for the case of the longer constraint curve, that equilibrium is below the line so that eventually the logistic equilibria will be reached. Note that there is a discontinuity in the 1st derivative of the trajectory as it hits the shortest curve, because from that point on the state is confined to the constraint line. *Note the constraint is not enforced until the boundary is reached.*

Let's suppose that for $cN^1 + dN^2 = 1$, c and d have been chosen so that a trajectory must hit it (i.e., $c \cdot \frac{\lambda_1}{\alpha_1} + d \cdot \frac{\lambda_2}{\alpha_2} \geq 1$). The *constrained dynamics* is 1-dimensional and has steady-state

$$\left. \begin{array}{l} N_0^1 = \dfrac{\alpha_2 + (\lambda_1 - \lambda_2)d}{c\alpha_2 + d\alpha_1} \\[3mm] N_0^2 = \dfrac{\alpha_1 + (\lambda_2 - \lambda_1)c}{c\alpha_2 + d\alpha_1} \end{array} \right\} \tag{1.8}$$

as is easily deduced. One can show this is a (linearly) *stable point* relative to other points on the constraint line, simply by computing the first partial derivative of the right-hand side of $dN^1/dt = Q(N^1)$, which results from dimensional reduction, at equilibrium (1.8). It is negative when all other parameters are positive.
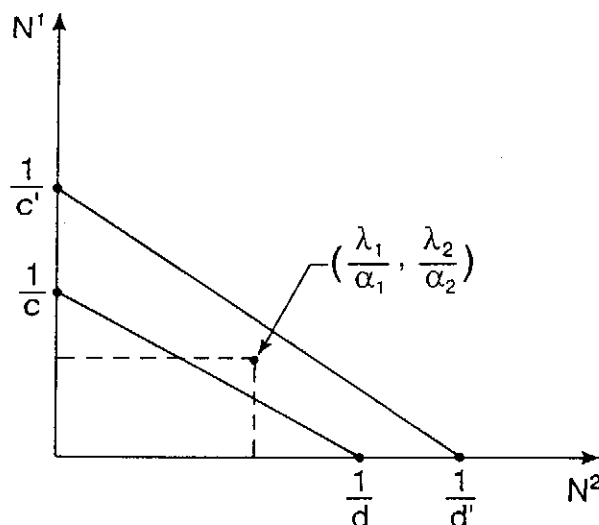
Fig. 2. Linear constraint curves and separate logistic equilibria.

If we choose $c = \alpha_1/\lambda_1$, $d = \alpha_2/\lambda_2$, then $\lambda_1 = \lambda_2 = \lambda$ implies $N_0^1/N_0^2 = \alpha_2/\alpha_1$, the same ratio as before external constraint had been imposed. Thus, the *steady-state direction* N_0^1/N_0^2 is preserved under Křivan transformation, if $\lambda_1 = \lambda_2$ (see Fig. 3 below). This holds for any constraint $F(N^1, N^2)$.
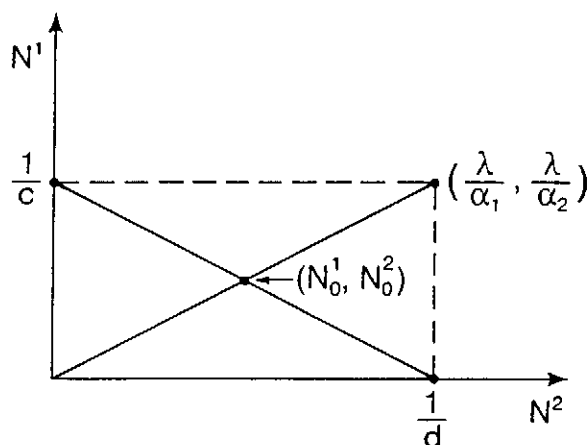

Fig. 3. $\alpha_1 N^1 + \alpha_2 N^2 = \lambda$, Linear contraint and constraint equilibrium. Preservation of steady-state direction N_0^2/N_0^1.

The necessity for these differently shaped constraints has been argued for by Tilman [22] and Křivan [16]. We now investigate two more examples below.

A. For the separate logistic system with *elliptical constraint* we have taken

$$\left.\begin{aligned}
\frac{dN^i}{dt} &= N^i(\lambda - \alpha_{(i)}N^i) - mN^i \\
F^2 &= c(N^1)^2 + d(N^2)^2 \leq 1 \\
\sqrt{c} &= \frac{\alpha_1}{\lambda}, \quad \sqrt{d} = \frac{\alpha_2}{\lambda}
\end{aligned}\right\} \qquad i = 1, 2 .$$
(1.9)

In the overlap region represented by the boundary of the constraint region we have

$$cN^1\left(\frac{dN^1}{dt}\right) + dN^2\left(\frac{dN^2}{dt}\right) = 0$$
(1.10)

from which it follows that

$$m = \lambda - \frac{(\alpha_1 N^1)^3 + (\alpha_2 N^2)^3}{(\alpha_1 N^1)^2 + (\alpha_2 N^2)^2}$$
(1.11)

with $(\alpha_1 N^1)^2 + (\alpha_2 N^2)^2 = \lambda^2$. The constrained dynamics is represented by

$$\frac{dN^1}{dt} = -\alpha_1(N^1)^2 + \frac{1}{\lambda^2}\{(\alpha_1 N^1)^3 + [\lambda^2 - (\alpha_1 N^1)^2]^{3/2}\}N^1 .$$
(1.12)

Furthermore, there is a unique positive equilibrium (N_0^1, N_0^2) which satisfies $N_0^2/N_0^1 = \alpha_1/\alpha_2$ so that the steady-state direction of the separate logistic system is preserved under Křivan transformation. Consequently, there is exactly one point on the constraint curve with this direction. It is

$$N_0^1 = \frac{\lambda}{\alpha_1\sqrt{2}}, \quad N_0^2 = \frac{\lambda}{\alpha_2\sqrt{2}} .$$
(1.13)

If χ denotes the right-hand side of (1.12) then

$$\frac{\partial\chi}{\partial N^1}\Big|_{N_0^1} = -\frac{\lambda}{\sqrt{2}} < 0$$
(1.14)

so that (1.13) is (linearly) stable on the constraint curve (but not in the whole space). This example can be extended to any number n of separate logistics, but the $(n-1)$-dimensional constrained dynamics on the corresponding ellipsoidal surface is complicated and would have to be analyzed, numerically.

B. For two separate logistic populations with pre-symbiant condition we now consider a *hyperbolic constraint relation*

$$(N^1 + c_1)(N^2 + c_2) \leq \frac{1}{Q} ,$$
(1.15)

where $Q > 0$ and c_1, c_2 are certain constants. The boundary curve is a hyperbola and we suppose it defines a certain set of states (N^1, N^2) which are of *unit length,*

just as $\sqrt{c(N^1)^2 + d(N^2)^2} = 1$ and $cN^1 + dN^2 = 1$, do in the previous two examples. The positive first degree homogeniety of these examples is basic to our present method. We wish to find L an positively homogeneous function of degree one in N^1 and N^2, such that $L = 1$ will be equivalent to $(N^1 + c_1)(N^2 + c_2) = \frac{1}{Q}$, i.e., so that the solution sets are the same. To do this we apply the well-known Okubo's Trick and merely substitute N^i/L directly into the boundary relation and obtain

$$cL^2 + 2(b_i N^i)L + (b_{ij} N^i N^j) = 0 \tag{1.16}$$

with $c = c_1 c_2 - \frac{1}{Q}$, $b_1 = -\frac{c_2}{c}$, $b_2 = -\frac{c_1}{c}$ and $(b_{ij}) = \begin{pmatrix} 0 & 1/2 \\ 1/2 & 0 \end{pmatrix}$. Thus,

$$L \equiv \beta \pm \alpha \equiv -\frac{c_2 N^1 + c_1 N^2}{2c}$$

$$\pm \frac{1}{2c}\sqrt{\left[(c_2 N^1)^2 + (c_1 N^2)^2 + \left(\frac{4}{Q} - 2c_1 c_2\right) N^1 N^2\right]} . \tag{1.17}$$

This is clearly positively first degree homogeneous in N^i, as required. This functional L is an example of a Minkowski (α, β)-metric [21] called a *Rander's metric.* One usually needs such *norms* L to be *positive-valued.*

Proposition:

$$L = \alpha + \beta > 0 \quad \text{if} \quad \frac{1}{Q} < c_1 c_2 < \frac{4}{Q} .$$

Proof:
It will suffice to show $2cL > 0$ if $c_1 c_2 < \frac{4}{Q}$. First we show α^2 is a positive definite quadratic form. By definition, the matrix $a_{ij} \equiv \frac{1}{2}\dot{\partial}_i \dot{\partial}_j (\alpha^2)$ is just

$$(\alpha_{ij}) = \begin{pmatrix} c_2^2 & \frac{2}{Q} - c_1 c_2 \\ \frac{2}{Q} - c_1 c_2 & c_1^2 \end{pmatrix}$$

whose trace is positive and whose determinant is $\det(\alpha_{ij}) = -\frac{4}{Q^2} + \frac{4c_1 c_2}{Q}$. Here, $\dot{\partial}_i$ denotes the partial derivatives with respect to N^i. Hence, $\det(\alpha_{ij}) > 0 \Longleftrightarrow c_1 c_2 > \frac{1}{Q}$. Using [5], Prop. 3.1, Chapter 1, we only need to show $(\alpha_{ij} - b_i b_j)$ is positive definite. This matrix is symmetric with entries

$$\begin{pmatrix} \frac{3}{4}c_2^2 & \left[\frac{2}{Q} - \frac{5}{4}c_1 c_2\right] \\ * & \frac{3}{4}c_1^2 \end{pmatrix} .$$

The trace is positive and the determinant equals the expression

$$-c_1^2 c_2^2 + \frac{5}{Q}c_1 c_2 - \frac{4}{Q^2} .$$

This expression vanishes at $c_1 c_2 = \frac{4}{Q}$ and at $c_1 c_2 = \frac{1}{Q}$. The graph of $c_1 c_2$ versus the determinant is concave down and positive at the midpoint of $\left[\frac{1}{Q}, \frac{4}{Q}\right]$. This concludes the proof.

The hyperbolic constraint curve is asymptotic to $N^1 = c_1$ and $N^2 = c_2$ and passes through the separate logistic equilibria. This curve is identical with the indicatrix $L = 1$ from (1.17). The Křivan transformation function m is not simple in this case. But, because Křivan transformations of pre-symbiant systems must preserve the steady-state directions, we can obtain the steady-state (N_0^1, N_0^2) geometrically from Fig. 4 by computing the intersection of the straight-line with slope α_1/α_2 through $(0, 0)$ with the hyperbola. We have

$$
\left.
\begin{aligned}
(N_0^1, N_0^2) &= \left(-\frac{(c_1\alpha_1 + c_2\alpha_2) + \sqrt{[(c_1\alpha_1 + c_2\alpha_2)^2 - 4\alpha_1\alpha_2 c]}}{2\alpha_1}, \frac{\alpha_1}{\alpha_2}N_0^1 \right) \\
(c_1, c_2) &= \left(\frac{-\lambda}{2\alpha_1} - \frac{1}{2\alpha_1}\sqrt{\left(\lambda^2 + \frac{4\alpha_1\alpha_2}{Q}\right)} , \frac{-\lambda}{2\alpha_2} - \frac{1}{2\alpha_2}\sqrt{\left(\lambda^2 + \frac{4\alpha_1\alpha_2}{Q}\right)} \right) ,
\end{aligned}
\right\}
$$

$$(1.18)$$

where $\frac{\lambda}{\alpha_1} = \frac{1}{c_2 Q} - c_1$ and $\frac{\lambda}{\alpha_2} = \frac{1}{c_1 Q} - c_2$. Linear stability at (N_0^1, N_0^2) on the constraint curve can be implemented with a computer.
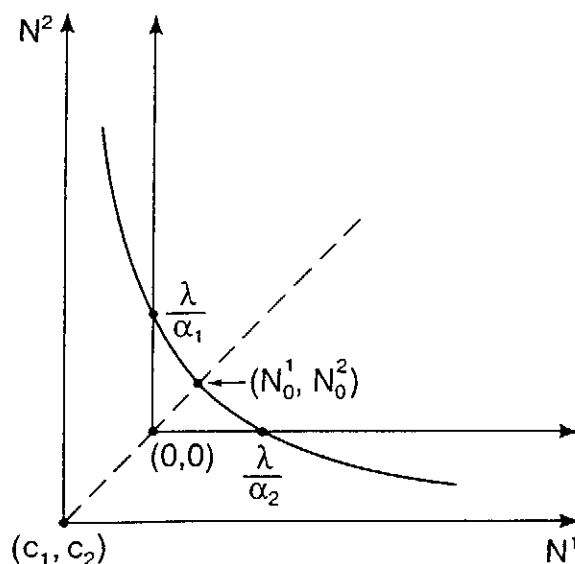

Fig. 4. Hyperbolic constraint curve $(N^1 + c_1)(N^2 + c_2) = \frac{1}{Q} > 0$, $c_1 < 0$, $c_2 < 0$.

2. Constraints on Production and the Projective Geometry of Sprays and The Adaptation Theorem

Our perspective now switches from population densities and their ecological dynamics to biomass production. The ith type population is assumed to produce organic material in characteristic forms which accumulate in the local environment (at least a *net* accumulation accounting for bioerosion etc.) For example $x^i(t)$ could be a measure of aragonite produced up to time t by coral of type i, $i = 1, \ldots, n$, on the Great Barrier Reef [3,4,5,6,8].

Let us consider the n-dimensional Volterra-Hamilton system (Passive, i.e., Constant Coefficients) [2]

subject to constraint
$$\left.\begin{aligned}
\frac{dx^i}{dt} &= k_{(i)} N^i \\
\frac{dN^i}{dt} &= \lambda N^i - \alpha_{(i)} (N^i)^2 - m N^i, \\
F &= \{c_i (N^i)^2\}^{1/2} = 1 \\
\sqrt{c_i} &= \frac{\alpha_i}{\lambda}
\end{aligned}\right\} \quad i = 1, 2, \ldots, n. \quad (2.1)$$

This is a variation of Example **A** above. Here, $k_{(i)}$ denotes the per capita production rate of the ith type producer. We will set them all equal to *one* in what follows.

It is easy to compute the Křivan function for (2.1). It is

$$m = \lambda - \frac{c_i \alpha_i (N^i)^3}{c_i (N^i)^2} \qquad (2.2)$$

with the *constrained dynamics of production*

$$\frac{d^2 x^i}{dt^2} = -\alpha_{(i)} \left(\frac{dx^i}{dt}\right)^2 + \frac{c_j \alpha_j \left(\dfrac{dx^j}{dt}\right)^3}{c_l \left(\dfrac{dx^l}{dt}\right)^2} \cdot \frac{dx^i}{dt} . \qquad (2.3)$$

Let us consider the *geometry of constraint*.

If we compute $a_{ij} \equiv \frac{1}{2} \dot{\partial}_i \dot{\partial}_j F^2$, as in the previous section we obtain a positive definite diagonal matrix with $a_{ii} = c_i > 0$. The constraint boundary surface is written

$$\left[c_i \left(\frac{dx^i}{dt}\right)^2 \right]^{1/2} = 1 \qquad (2.4)$$

and implies (Riemannian metric tensor arc-length)

$$a_{ij}dx^i dx^j \equiv c_i(dx^i)^2 = l^2(dt^2) \equiv ds^2 \tag{2.5}$$

where $l > 0$ is factor depending on the specific time units employed (seconds, years, etc.) Of course, there are units for the x^i as well and these may be absorbed in the coefficients c_i. The infinitesimal quantity ds is the *Riemannian arc-length*. That is to say, if $\gamma(s)$ is a smooth curve in the space of $x^1, \ldots, x^n$, then $\int_\gamma ds$ is its arc-length, i.e.,

$$s = \int_{\bar{t}_0}^{\bar{t}_1} \left[c_i \left(\frac{dx^i}{d\bar{t}} \right)^2 \right]^{1/2} d\bar{t} , \tag{2.6}$$

where γ is given by a parameter $\bar{t}$ along γ and $x^i = x^i(\bar{t})$. Clearly, it does not matter which parameter $\bar{t}$ is used, the answer is the same because of the chain rule. We see that for the Riemannian arc-length.

$$ds = l \cdot dt , \tag{2.7}$$

whereas (2.5) suggests ds^2 is a weighted average of all $dx^i \cdot dx^j$.

Since t is real time, it seems therefore natural to interpret s as some measure of total production, say, *size*. In this case (2.7) tells us that size increments are directly proportional to time (age) increments where the dynamics of size s is defined by (2.1) and (2.5). To make this clearer, set $d\bar{s} = Be^{\lambda t}dt$ and substitute into separate logistic dynamics,

$$\frac{d^2 x^i}{dt^2} = \lambda \frac{dx^i}{dt} - \alpha_{(i)} \left(\frac{dx^i}{dt} \right)^2 . \tag{2.8}$$

Thus,

$$\frac{d^2 x^i}{d\bar{s}^2} = -\alpha_{(i)} \left(\frac{dx^i}{d\bar{s}} \right)^2 . \tag{2.9}$$

From the *general theory of sprays* [5,11] it is possible to show that $s = b\bar{s} + \text{const}$, and that (2.9) is a special case of spray dynamics

$$\frac{d^2 x^i}{ds^2} = H^i_{(2)} \left(x, \frac{dx}{ds} \right) . \tag{2.10}$$

If F is conserved under the flow of this spray, then $b = 1$. Here the (2) indicates that H^i is *positively homogeneous in* dx^i/ds *of degree* 2 [i.e., for any fixed constant $q > 0$, $H^i_{(2)} \left(x, q \cdot \frac{dx}{ds} \right) = q^2 \cdot H^i_{(2)} \left(x, \frac{dx}{ds} \right)$]. Such a system is called a *spray*, because its solutions are such that there is a unique one joining *any* two close points and one in *any* direction through a fixed point [5,11]. We shall have need of Euler's Theorem on homogeneous (C^∞) functions: If $f(y^1, \ldots, y^n)$ is positively homogenous of degree, r, then $(\partial f/\partial y^i) \cdot y^i = rf$.

The *spray equations in affine form* are written

$$\frac{\dfrac{d^2 x^i}{dt^2} - \underset{(2)}{H^i}\left(x, \dfrac{dx}{dt}\right)}{\dfrac{dx^i}{dt}} = \frac{\dfrac{d^2 x^j}{dt^2} - \underset{(2)}{H^j}\left(x, \dfrac{dx}{dt}\right)}{\dfrac{dx^j}{dt}} \qquad (2.11)$$

for all i, j running 1 through n. The *natural parameter s* for this spray is determined completely by the spray by solving

$$\frac{\dfrac{d^2 s}{dt^2}}{\dfrac{ds}{dt}} = \frac{\dfrac{d^2 x^i}{dt^2} - \underset{(2)}{H^i}\left(x, \dfrac{dx}{dt}\right)}{\dfrac{dx^i}{dt}} \ . \qquad (2.12)$$

Thus, $s = A + B \int e^{\int \rho(t)dt}$ for arbitrary constants A and B. The advantage is that with s as parameter along trajectories, (2.11) becomes (2.10) and the latter is *invariant under arbitrary transformations* (smooth) *of the coordinate functions*. The spray equations have the same form in any coordinate patch on the underlying smooth manifold.

In the case (2.8) above $\rho(t) = \lambda$ and $ds/dt = B \cdot e^{\lambda t}$.

If we write (2.3) in terms of an arbitrary parameter τ we obtain

$$\frac{d^2 x^i}{d\tau^2} = -\alpha_{(i)}\left(\frac{dx^i}{d\tau}\right)^2 + \left[\frac{c_i \alpha_i \left(\dfrac{dx^i}{d\tau}\right)^3}{c_i \left(\dfrac{dx^i}{d\tau}\right)^2} + \rho(\tau)\right]\frac{dx^i}{d\tau} \ . \qquad (2.13)$$

In this instance, $c_i \left(\frac{dx^i}{d\tau}\right)^2$ is *not constant*, but the terms other than $\rho(\tau)\frac{dx^i}{d\tau}$ are 2nd degree homogeneous.

One of the most interesting facts about a Křivan transformation in the present context of production modelled by Volterra-Hamilton systems is that it leads to the projective differential geometry of sprays.

Let us now discuss this at length. The function $m - \lambda$ is (positively) *first degree homogeneous* in dx^i/dt and denoting it by ψ, defines a "time-sequence change" by introducing along trajectories a new (*projective*) *parameter*,

$$p = B \int e^{-\int_\gamma \varphi(x, dx)} ds + A \ , \qquad (2.14)$$

where γ is a solution of (2.10) and A and B are arbitrary constants. Now (2.10) becomes, after two applications of the chain rule,

$$\frac{d^2 x^i}{dp^2} = \underset{(2)}{H^i}\left(x, \frac{dx}{dp}\right) + \psi\left(x, \frac{dx}{dp}\right) \cdot \frac{dx^i}{dp} \tag{2.15}$$

which is again a spray. Thus, *projective change preserves the spray properties.*

Returning to the Křivan problem in our context, we would like to ask if, *given a spray and a constraint relation* (i.e., *its boundary*) *or indicatrix of a norm F uniquely defined by Okubo's method, can we find a new (projective) parameter p so that (2.15) holds, p is defined by (2.14) and $F\left(x, \frac{dx}{dp}\right) = 1$?* The latter amounts to saying $dp = F(x, dx)$ or that the projective parameter p is the arc-length. But, we are *not* asking that (2.15) be geodesics of the F-geometry defined by $g_{ij} = \frac{1}{2}\dot{\partial}_i\dot{\partial}_j F^2$. (We reserve the symbol a_{ij} for Riemannian cases only, as in (2.5) and the hyperbolic constraint example in Sec. 1.) The geodesic property will not hold generally, even though $F = 1$ along all γ. See an example in Sec. 6.

We now prove the interesting

Theorem (Adaptation of Křivan Type):
Given a local spray with natural parameter s, and

$$\frac{dx^i}{ds} = y^i , \quad \frac{dy^i}{ds} = -2G^i(y^1, \dots, y^n) , \quad i = 1, 2, \dots, n \tag{2.16}$$

such that G^i are independent of coordinates x^i, there exists exactly one projective transformation function $\psi(x, y)$ for each fixed choice of a (Minkowski) norm F, assumed independent of x^i, and whose projectively related spray is locally given by

$$\frac{d^2 x^i}{dp^2} = -2G^i\left(\frac{dx^1}{dp}, \dots, \frac{dx^n}{dp}\right) + \psi\left(\frac{dx^1}{dp}, \dots, \frac{dx^n}{dp}\right) \cdot \frac{dx^i}{dp} . \tag{2.17}$$

Here, there is no x-dependence on the right-hand side. Furthermore, all solutions of (2.17) satisfy

$$F\left(\frac{dx^1}{dp}, \dots, \frac{dx^n}{dp}\right) = 1 \tag{2.18}$$

and

$$\psi(y) = \frac{dp}{ds} \cdot \psi\left(\frac{dx}{dp}\right) = \frac{2g_{ij}(y)G^i(y)y^j}{[F(y)]^2} . \tag{2.19}$$

We shall first prove a

Lemma:
If $F = 1$ along solutions γ of a spray as (2.16) then

$$g_{ij}\frac{dy^i}{ds}y^j = 0 \ ,$$

along γ where

$$g_{ij} \equiv \frac{1}{2}\dot{\partial}_i\dot{\partial}_j F^2 \ .$$

The proof uses that F is independent of x^i.

Proof: Along any solution γ we have for the total derivative d/ds that

$$0 = \frac{dF^2}{ds} = \frac{dg_{ij}}{ds}y^i y^j + 2g_{ij}\frac{dy^i}{ds}y^j$$

$$= (\partial_k g_{ij})\frac{dx^k}{ds}y^i y^j + (\dot{\partial}_l g_{ij})\frac{dy^l}{ds}y^i y^j + 2g_{ij}\frac{dy^i}{ds}y^j \ .$$

But, $\partial_k g_{ij} = 0$ because $\partial_k F = 0$ and $g_{ij} = \frac{1}{2}\dot{\partial}_i\dot{\partial}_j F^2$.

Also, g_{ij} is of degree zero in y^i, so that Euler's Theorem on homogeneous functions gives

$$(\dot{\partial}_l g_{ij})y^i\frac{dy^l}{ds}y^j = (C_{lij}y^i)\frac{dy^l}{ds}y^j = (C_{jl\,i}y^i)\frac{dy^l}{ds}y^j$$

which vanishes identically because $C_{jl\,i}y^i = \dot{\partial}_i(g_{il})y^i \equiv 0$ and

$$C_{ijk} = \frac{1}{4}\dot{\partial}_k\dot{\partial}_j\dot{\partial}_i F^2$$

is completely symmetric (see [5]). This completes the proof of the lemma.

We now apply the lemma to solutions of (2.17). Recall that $\psi(y)$ is smooth and is positively homogeneous of first degree in y^i. Obviously, since $F\left(\frac{dx^1}{dp}, \ldots, \frac{dx^n}{dp}\right) = 1$ holds along γ,

$$0 = g_{ij}\frac{dx^j}{dp}\left(-2G^i\left(\frac{dx^1}{dp}, \ldots, \frac{dx^n}{dp}\right) + \psi\left(\frac{dx}{dp}\right) \cdot \frac{dx^i}{dp}\right)$$

so that we have uniquely

$$\psi(y) = \frac{2g_{ij}(y)G^i(y^1, \ldots, y^n)y^j}{F^2} \tag{2.20}$$

and the proof is complete.

Remark:

The adaptation theorem holds even when G^i and F depend on x^i. The same proof works and the form of $\psi(x, y)$ is similar (but is now dependent on x), the only difference is that $2G^i$ is to be replaced by $2G^i - H_F^i = c^i$ where H_F^i denotes the right-hand side of the geodesics of g_{ij} being given by $-\gamma_{jk}^i y^j y^k$ where

$$\gamma_{jk}^i = \frac{1}{2} g^{il} (\partial_k g_{jl} + \partial_j g_{kl} - \partial_l g_{jk})$$

are the so-called Levi-Cività symbols [18].

Let us further discuss the projectively transformed spray (2.17). What is the structure of this new spray? We answer this question now with a view towards ecological interactions. Let us denote dx^i/dp by ξ^i and differentiate the right-hand side of (2.17) by $\partial^2/\partial \xi^j \partial \xi^k$. Denoting the result by $\bar{\Gamma}_{jk}^i(x, \xi)$ we find

$$\bar{\Gamma}_{jk}^i = \Gamma_{jk}^i + \delta_j^i \psi_k + \delta_k^i \psi_j + \xi^i \psi_{jk} \tag{2.21}$$

where $\Gamma_{jk}^i = \partial^2 H^i / \partial \xi^j \partial \xi^k$, $\psi_j = \frac{1}{2} \frac{\partial \psi}{\partial \xi^j}$ and $\psi_{kj} = \partial \psi_j / \partial \xi^k$. These are the *new interaction coefficients, the old ones being the n^3 quantities,* Γ_{jk}^i; ψ_i and ψ_{il} have degrees zero and minus one in ξ, respectively, by Euler's Theorem on homogeneous functions. *In fact,* Γ_{jk}^i *and* $\bar{\Gamma}_{jk}^i$ *have degree zero in* ξ.

Let us examine our findings with more concrete ideas. *First,* we start with a Volterra-Hamilton system ($k_{(i)} = 1$ for each i for convenience)

$$\left. \begin{aligned} \frac{dx^i}{dt} &= N^i \\ \frac{dN^i}{dt} &= -\Gamma_{jk}^i N^j N^k + \lambda N^i \; . \end{aligned} \right\} \tag{2.22}$$

Here, the ecological interactions are given by n^3 coefficients Γ_{jk}^i which are often constants but may depend on what is produced, i.e., x^i (often x^i is taken as a log biomass (i.e., $x^i = \ln m^i$, as in Sec. 7 below) and hence $\nu \cdot x^i$ is allometrically related to biomass and can be usefully interpreted as a secondary compound, or toxin, see [8,3,7], for more information). Using $s = Be^{\lambda t}$ we transform to the natural parameter of this spray, obtaining the form (2.16) with $\Gamma_{jk}^i N^j N^k \equiv 2G$. *Second,* we have chosen a (Minkowski) norm F as a *constraint functional* in the sense of Křivan: $F(y^1, \dots, y^n) \leq 1$ is the constraint relation. (Its boundary $\bar{F} = 1$ is uniquely determined by Okubo's trick given any quadratic hypersurface description). F can depend on x^i. According to our theorem there is exactly one projective transformation ψ_F and its associated parameter p from (2.20) and (2.14). The new spray has coefficients of interaction given by (2.21). The trajectories of the transformed dynamics are identical with the original in x-space. But, reparametrization via (2.14) gives "new ecology." We could think of p as a "non-linear tick" relative to s or to t. Instead, it is thought of as a transformation of production, non-linearly changing

the size parameter s of the original system. We use $p = D\bar{e}^{\lambda t}$ to return to *real time* to obtain

$$\frac{dx^i}{dt} = N^i$$

$$\frac{dN^i}{dt} = -\bar{\Gamma}^i_{jk} N^j N^k + \bar{\lambda} N^i \; . \tag{2.23}$$

The $\bar{\lambda}$ is freely chosen, it *could* be taken as $\bar{\lambda} = \lambda$, $D = B$. In any case, this last transformation may or may not be biologically appropriate depending on the model considered.

Let's be very specific and go through this process once again with

$$\frac{dx^i}{dt} = N^i$$

$$\frac{dN^i}{dt} = \lambda N^i - \alpha_{(i)} (N^i)^2$$

$$F = \{c_i (N^i)^2\}^{1/2} \; , \quad \sqrt{c_i} = \frac{\alpha_i}{\lambda} \; .$$

Use of $\bar{s} = Be^{\lambda t}$ yields (2.9), for some constant B.

Then, by the theorem above

$$\psi(x, \xi) = \frac{[c_i \alpha_i (\xi^i)^2] \xi^i}{c_i (\xi^i)^2} \; , \tag{2.24}$$

and our resulting spray has the form

$$\frac{d^2 x^i}{dp^2} = -\alpha_i (\xi^i)^2 + \frac{c_i \alpha_i (\xi^i)^3}{c_i (\xi^i)^2} \cdot \xi^i \tag{2.25}$$

which is the *same as (2.3) obtained by Křivan's method except t is replaced by p in the above. This is an extremely important distinction, however.* In this theory not only is it true as with Křivan that the constraint is now satisfied, it is satisfied by a transformation of the parameter along the original spray, i.e.,

$$F(\xi^1, \dots, \xi^n) = 1 \; ,$$

not $F(N^1, \dots, N^n) = 1$, as in the Křivan Method. Thus, $dp = F(dx^1, \dots, dx^n)$ not $dt = F(dx^1, \dots, dx^n)$. Also, the above 2nd order theory (Křivan's is first order) is *continuous*. There is no discontinuity of the partial derivatives in the transformed dynamics when a trajectory hits the constraining surface. In fact, N^i-space, trajectories are *never* off this surface. This is the nature of production in our colonial animal model.

On the other hand, we can use the full projective theory above as a *formal* generalization of Křivan's by ignoring the distinction between t and p in (2.3) and (2.25) and implementing the auxillary variable x^i only as a device, as done originally

by Volterra in a somewhat more simple approach to ecology than the present theory (see Chapter 9 of [2]).

The differential geometry of sprays and the associated projective theory are useful because their transformation behaviour is well-known and convenient. We are saying that even from Křivan's perspective it is still of interest to study the 2nd order system projective geometry. For example, (2.3) has the *same solution sets* (i.e., trajectories) as (2.9) *but with a different clock* — given by ψ and (2.14). In this particular case (2.9) is very easy to solve to obtain the trajectories in x-space or their tangent fields in N-space (or ξ-space). Generally, Křivan's method is very complicated for dimension ≥ 2 and the above theory provides considerable conceptual power to settle questions of equilibria stability, etc. Of course we must suppose $\lambda_i = \lambda$, $i = 1, \ldots, n$ and that the constraint surface is a quadratic hypersurface. In any case, in the next section we adopt fully the method of projective geometry to model evolution via time-transformations along growth trajectories, i.e., a model of *heterochrony*, a term coined by biologists [1,13].

3. Division of Labour in Colonial Animals. Wilson's Ergonomics and Allometric Space

The contemporary biologist *L.* Margulis has argued convincingly that the vast array of somatic cells of eukaryotes evolved by symbiosis from separately living bacterial species almost two billion years ago [19,20]. Mathematically, a necessary condition for this evolutionary step is that the proliferation rate of cells in separate populations should be nearly equal to allow their DNA, RNA replication machinery a stable association in which all members of the smaller (e.g., mitochondrian) cell type live inside the larger in a one-to-one fashion. This has been expressed as the *pre-symbiant condition* on growth rates in the previous sections. We have seen that environmental constraints on exponential populations must subscribe to this condition if they are to survive in an overlap region of their ranges. Herein, we wish to further require conditions on two separately living pre-symbiant populations to satisfy the fundamentals of *Ergonomic Theory of Colonial Animals* due to E. O. Wilson and N. Beklemeshev. We intend to describe evolution of fossil invertebrates like polymorphic Bryozoans, as well as eusocial insect colonies and Siphonophores. For this, x^i represents log biomasses of morphological characters of fossils or of living biomass of the ith caste of a social insect colony like an ant colony. The *Principle of Division of Labor* means that the total energy of growth of a polymorphic (i.e., at least two castes) colonial individual must be apportioned between all the constituent morphotypes until sexual maturity is attained [10,23]. Each morphotype is designed to perform a different task for the colony as a whole. There is wide agreement that Natural Selection in colonial animals is operating at the level of the colony-as-whole. Rarely, is it true that there are allelic (i.e., genetic) differences among the castes. Indeed, they are determined almost entirely by the environment, and "are usefully interpretted as a consequence of variations among species on *growth transformation*

during larval development," [24]. This colonial growth and development has been described by Oster and Wilson in terms of a curve in *allometric space* (see [24]) as in the caption to the figure below.

Let us consider the 2-dimensional (i.e., 2 castes) pre-symbiant system

$$\frac{dx^i}{dt} = k_{(i)}N^i$$

$$\frac{dN^i}{dt} = \lambda N^i - \alpha_{(i)}(N^i)^2 \ . \tag{3.1}$$

Again, the x^i are Volterra auxiliary variables which measure accumulation of biomass of the ith caste or morphotype, with $k_{(i)}$ the per capita rate of production. Is Eq. (3.1) consistent with Ergonomics? Is it in agreement with division of labour? Well, Eq. (3.1) becomes

$$\frac{d^2x^i}{dt^2} + \frac{\alpha_i}{k_i}\left(\frac{dx^i}{dt}\right)^2 - \lambda\frac{dx^i}{dt} = 0 \tag{3.2}$$

upon substitution, and this is the Euler-Lagrange equation of the variational problem (fixed endpoints)

$$\delta \int_0^t \left[\exp\left(2\frac{\alpha_i}{k_i}x^i - \lambda t\right)\right] \cdot \left(\frac{dx^i}{dt}\right)^2 dt = 0 \ . \tag{3.3}$$

But, (3.1) is not truly coupled, as symbiants must be. We need a more general form to capture the essence of symbiosis.

We write

$$\left. \begin{array}{l} \dfrac{dx^i}{dt} = k_{(i)}N^i \\[2mm] \dfrac{dN^i}{dt} = -\Gamma^i_{jk}N^jN^k + \lambda N^i \end{array} \right\} \tag{3.4}$$

to replace (3.1). Here, the 8 constants must surely satisfy

$$\Gamma^i_{ii} = \frac{\alpha_i}{k_i}, \quad \Gamma^i_{ji} = \Gamma^i_{ij} \neq 0 \quad \text{for} \quad i \neq j \ , \tag{3.5}$$

as well as the requirement that (3.4) are Euler-Lagrange equations for

$$\delta \int_0^t \mathcal{L}\left(x, \frac{dx}{dt}, t\right) dt = 0 \ , \tag{3.6}$$

a regular variational problem with fixed endpoints for some C^∞ *convex* Lagrangian $\mathcal{L}$. The coefficients Γ are uniquely determined, but $\mathcal{L}$ is, only up to a fixed multiplicative constant. Here, they are

$$\Gamma^i_{ji} = \frac{\alpha_j}{k_j}(i \neq j) \quad \text{and} \quad \Gamma^i_{jj} = \frac{-\alpha_i}{k_i} \quad (i \neq j) \tag{3.7}$$
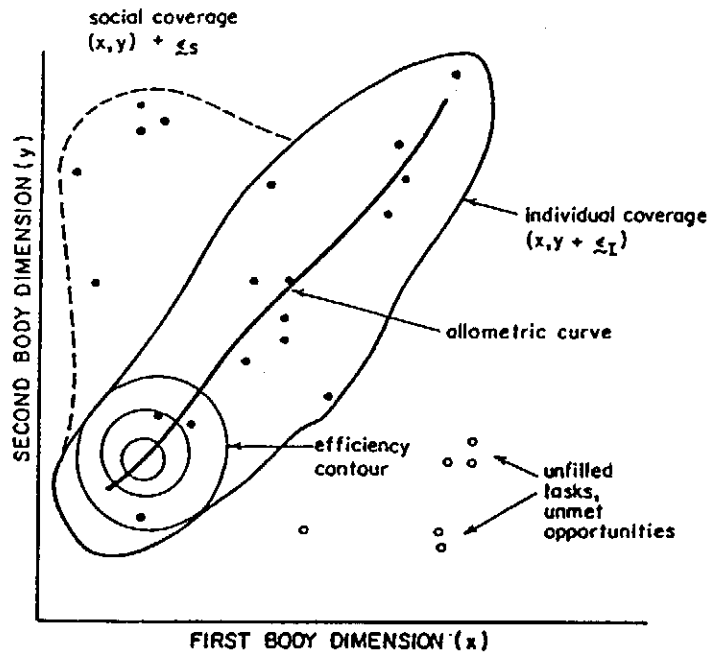
Fig. 5. Egonomic Allometric Space of Oster and Wilson for Two Characters of a Colony (Log-log Plot). "The worker caste of each ant species has a characteristic allometric curve drawn here for two anatomical dimensions only (for example, thorax width and head width). The allometric curve exists within the broader allometric space of all possible physical forms. In the local environment where the colonies live there exists a set of contingencies, consisting of opportunities such as food items and nest sites and perils such as predators and cave-ins. It is postulated [in Ergonomic Theory] that for each task by which the colony meets the contingency there is a point in the allometric space that corresponds to the physical caste ideally suited to perform the task. There is also a zone of the allometric space, with radius ε, within which the task is performed with at least adequate proficiency. The *species can cover a greater number of task points by altering the allometric curve, by increasing individual coverage, or by increasing social coverage through cooperative efforts* (Oster and Wilson, 1978)."

and

$$\mathcal{L}\left(x, \frac{dx}{dt}, t\right) = \exp\left(2\frac{\alpha_i}{k_i}x^i - \lambda t\right)\left[\left(\frac{dx^1}{dt}\right)^2 + \left(\frac{dx^2}{dt}\right)^2\right] \qquad (3.8)$$

(see [5], Chapter 5). Therefore, the *true symbiant* has its growth given by

$$\left.\begin{aligned}
\frac{dx^i}{dt} &= k_{(i)}N^i, \quad i = 1, 2, \\
\frac{dN^1}{dt} &= \lambda N^1\left(1 - 2\alpha_2 N^2 - \alpha_1 N^1 + \alpha_1\left(\tfrac{N^2}{N^1}\right)N^2\right) \\
\frac{dN^2}{dt} &= \lambda N^2\left(1 - 2\alpha_1 N^1 - \alpha_2 N^2 + \alpha_2\left(\tfrac{N^1}{N^2}\right)\cdot N^1\right).
\end{aligned}\right\} \qquad (3.9)$$

This *model of a dimorphic colonial organism* exhibits *a unique positive stable* (linearly) *steady-state,*

$$N_0^i = \frac{\lambda \alpha_i}{\alpha_1^2 + \alpha_2^2} \ . \tag{3.10}$$

These steady-states are to be regarded as populations of mature, adult sized, polyp-persons, castes or morphotypes within the colony. At this point all production is directed to maintenance and repair. Accordingly, we define the *real growth* variables by

$$y^i(t) = \int_0^t (N^i(\tau) - N_0^i)d\tau + D^i \ . \tag{3.11}$$

At $t = 0$, $y^i(0) = D^i > 0$ and $x^i(0) = k_{(i)}C^i$ and at or near adult sizes $y^i \approx 0$ and $dy^i/dt \approx 0$. Thus, after transforming to y-coordinates, the *total energy* (2.8) at adult sizes is (taking $k_1 = k_2 = 1$)

$$\mathcal{L}_0 = \frac{\lambda^2}{\alpha_1^2 + \alpha_2^2} e^{\lambda t} \tag{3.12a}$$

while that available for so-called *real growth* is

$$\tilde{\mathcal{L}} = \exp\left(2\frac{\alpha_i}{k_i}y^i + \lambda t\right)\left[\left(\frac{dy^1}{dt}\right)^2 + \left(\frac{dy^2}{dt}\right)^2\right] \tag{3.12b}$$

and is *negligibly small.*

Now substitution of (3.11) into (3.9) yields

$$\frac{d^2y^1}{dt^2} + 2\frac{\alpha_2}{k_2}\frac{dy^1}{dt}\frac{dy^2}{dt} + \frac{\alpha_1}{k_1}\left[\left(\frac{dy^1}{dt}\right)^2 - \left(\frac{dy^2}{dt}\right)^2\right] + \lambda\frac{dy^1}{dt} = 0$$

$$\frac{d^2y^2}{dt^2} + 2\frac{\alpha_1}{k_1}\frac{dy^1}{dt}\frac{dy^2}{dt} + \frac{\alpha_2}{k_2}\left[\left(\frac{dy^2}{dt}\right)^2 - \left(\frac{dy^1}{dt}\right)^2\right] + \lambda\frac{dy^1}{dt} = 0 \ . \tag{3.13}$$

If we set $\alpha_1 = \alpha_2 = 0$ in (3.13), then the solution $y^i(t)$ with positive value at $t = 0$ and which is decreasing at $t = 0$, is $y^i(t) = B^i \cdot e^{-\lambda t}$, where there is an $A^i = \ln a^i$ s.t. $A^i - y^i(0) = B^i$ and $\ln a^i - B^i e^{-\lambda} = \ln \eta^i(t)$ where

$$\eta^i(t) = a^i e^{-B^i e^{-\lambda t}}$$

is a Gompertz growth curve, with predetermined upper asymptote. Thus, real growth dynamics generalizes Gompertz growth ($\alpha_1 = \alpha_2 = 0$).
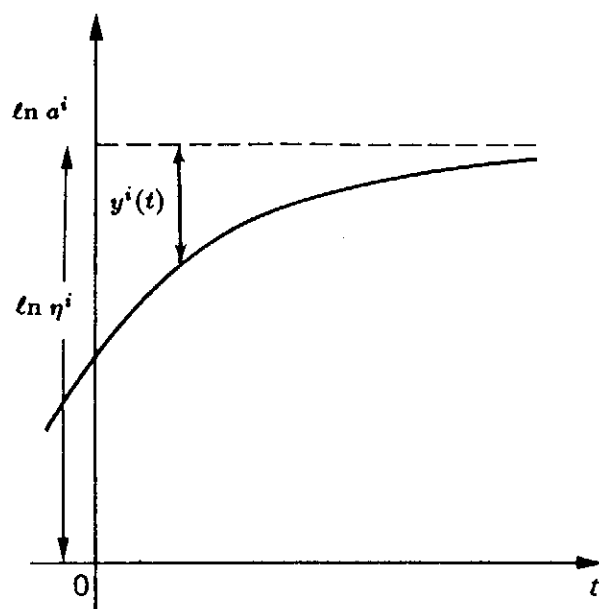
$y^i(t)$-Real Growth Variable for Log-Gompertz Curve
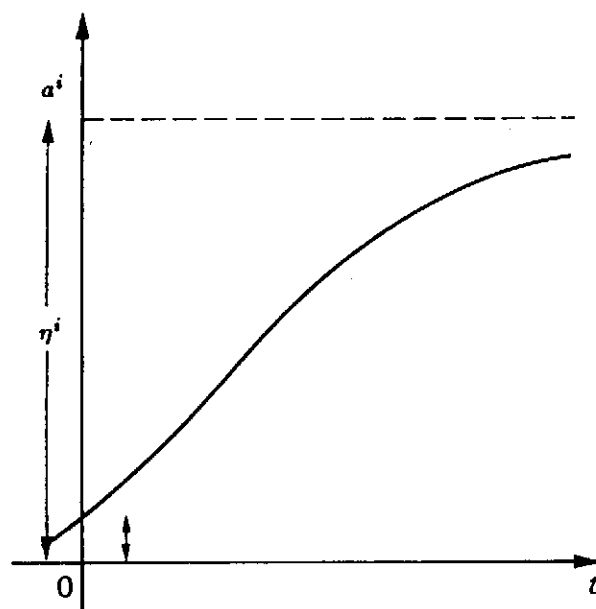
Gompertz Growth Curve

Fig. 6

The existence of $A^i = \ln a^i$ amounts to a statement of determinant final adult size.
Extensive laboratory measurements, performed with statistical precision indicate
large numbers of individual animals display Gompertz growth for the *same* λ for
their organ growth (hearts, livers, etc.) [17]. Here we are pointing out that (3.13)
is a well-founded generalizations of Gompertz growth in multi-organ individuals.
Note that *real growth* (3.11) generalizes Gompertz growth to the situation where α_i
are not zero (i.e., equilibrium (3.10) exists). We dub (3.13) *the growth equation for
a dimorphic symbiant* (or colonial) *organism.* It remains to be verified using field
data.

Note that the *natural parameter* of (3.13) can be expressed as $s = A - Be^{-\lambda\tau}$.
This is because, the spray associated with (3.13) can be written for general param-
eter τ

$$\frac{d^2y^i}{d\tau^2} + \Gamma^i_{jk}\frac{dy^j}{d\tau}\frac{dy^k}{d\tau} = \frac{\frac{d^2s}{d\tau^2}}{\frac{ds}{d\tau}} \cdot \frac{dy^i}{d\tau} \, , \tag{3.14}$$

with Γ given in (3.5) and (3.7), $k_{(i)} = 1$, and s, as defined above, solves

$$\frac{d^2s}{d\tau^2} + \lambda\frac{ds}{d\tau} = 0 \, , \tag{3.15}$$

uniquely for $A - B > 0$ and $ds/d\tau]_{\tau=0} > 0$. Thus, if $\tau = t$, then s is none other
than a *log-Gompertz variable.* This is a strong reason for interpretation of s as
size. There will always be an arbitrary multiplicative positive constant to relate
the natural parameter (which is some cases is true arc-length) to size based on
allometric methods.

4. Social Interactions, Curvature and Complexity, Kwang Jeon's Experiment

Following Douglas [11] and Matsumoto [21] the *curvature of a spray* as (2.10) is
defined simply as

$$\mathcal{D}^i_{jkl} = \dot{\partial}_j \dot{\partial}_k \dot{\partial}_l \underset{(2)}{H^i} \, . \tag{4.1}$$

This is a tensor so that if it vanishes in some coordinate system $\bar{x}^i$ it vanishes
in every coordinate system. Vanishing of the spray curvature is equivalent to $\underset{(2)}{H^i}$
being quadratic in $y^i = dx^i/ds$. Thus, the spray associated with (3.13) has $\mathcal{D} \equiv$
0, while $\mathcal{D} \neq 0$ for the spray (2.3) or (2.25). The point is the *Douglas tensor
detects density-dependence, in the ecological sense,* in interactions. We define *social
interactions* to be present in a Volterra-Hamilton (pre-symbiant) system if and
only if the associated spray has *non-zero spray curvature tensor,* $\mathcal{D}^i_{jkl}$. Such social
interactions are *intrinsic* in the sense that it is not an accidental choice of production
variables x^i which cause density-dependent interactions to occur, rather there is
no choice possible which would eliminate them, rendering the Volterra-Hamilton
system quadratic.

But, it may be possible to reparametrize the spray curves when $\mathcal{D} \neq 0$ to obtain the classical quadratic interaction patterns. This is possible for the spray (2.3), because it is projectively equivalent to (2.9). Let us look at the general situation.

Given a spray as (2.10) with natural parameter s and coordinates x^i and interaction coefficients $\Gamma^i_{jk} = \partial_j \partial_k H^i_{(2)}$, the n^3 quantities

$$\pi^i_{jk} = \Gamma^i_{jk} - \frac{1}{n+1} \delta^i_j \Gamma^a_{ak} - \frac{1}{n+1} \delta^i_k \Gamma^a_{aj} - \frac{1}{n+1} \xi^i \mathcal{D}^a_{jka} \tag{4.2}$$

have the same values before and after application of any projective transformation ψ. They are called the *projective connection coefficients* (in coordinate x^i) and are *projectively invariant. This means that π describes structures of the given spray that do not depend on parameterization of the spray curves.* The n^3 coefficients π^i_{jk} constitute neither an affine connection nor a tensor under arbitrary coordinate transformations, only under the so-called *projective group* [11]. Now, just as

$$\mathcal{D}^i_{jkl} = \dot{\partial}_l \Gamma^i_{jk} \ , \tag{4.3}$$

we define the (Douglas) *tensor*

$$\mathcal{K}^i_{jkl} \equiv \dot{\partial}_l \pi^i_{jk} \ , \tag{4.4}$$

and find that, $\mathcal{K} \equiv 0 \iff$ there is a projective transformation to a quadratic dynamics and generally

$$\mathcal{K}^i_{jkl} = \mathcal{D}^i_{jkl} - P\left(\frac{1}{n+1} \delta^i_j \mathcal{D}^a_{akl} \right) - \frac{1}{n+1} \xi^i \dot{\partial}_a \mathcal{D}^a_{jkl} \ , \tag{4.5}$$

where P indicates a sum of three terms obtained by cyclic permutation of j, k, l and $\dot{\partial}_a$ indicates the partial derivative with respect to ξ^a. Thus, $\mathcal{D} = 0 \Longrightarrow \mathcal{K} = 0$, but not, conversely. In fact, any projective transformation of a quadratic spray will result in a spray with $\mathcal{K} = 0$ but usually *not* $\mathcal{D} = 0$. This implies that a Křivan transformation m of a pre-symbiotic ecological interaction results in

$$\bar{\Gamma}^i_{jk} = \Gamma^i_{jk} + \delta^i_j m_k + \delta^i_k m_j + \xi^i m_{jk} \tag{4.6}$$

as in (2.21), but that from projective invariance,

$$\bar{\pi}^i_{jk} = \pi^i_{jk} \ , \tag{4.7}$$

for the projective connections associated to $\bar{\Gamma}$ and Γ. Therefore, if $\Gamma^i_{jk} = 0$ whenever $i \neq j \neq k$ (naturally $n \geq 3$), then

$$\left. \begin{array}{l} \bar{\Gamma}^i_{jk} = \xi^i m_{jk} \quad (i \neq j \neq k) \\[2mm] \bar{\Gamma}^i_{jk} \bar{y}^j \bar{y}^k = \xi^i m_{jk} \xi^j \xi^k \cdot \left(\dfrac{ds}{d\bar{s}}\right)^2 \cdot \end{array} \right\} \tag{4.8}$$

But m is 1st degree positively homogeneous in y so by Euler's Theorem, the right-hand side vanishes. That is, in

$$\left. \begin{array}{l} \dfrac{dx^i}{d\bar{s}} = \bar{y}^i \\[3mm] \dfrac{d\bar{y}^i}{d\bar{s}} = -\bar{\Gamma}^i_{jk} \bar{y}^j \bar{y}^k \end{array} \right\} \tag{4.9}$$

there are *no 3-way interaction terms* (i.e., $i \neq j \neq k$) *if before projective transformation by* m, *there were none.* [Note that $(\xi^i \equiv y^i \equiv dx^i/ds)\, \xi^i m_{jk}\xi^j\xi^k \equiv 0$ always holds.] *Therefore, projective transformation does not allow higher-order interactions to emerge. But, in considering how social interactions arise, one naturally begins with classical models which are quadratic. From these, Křivan transformation induced by any environmental constraint F (homogeneous in ξ) we like, cannot result in n-way interactions,* $n \geq 3$. We may paraphrase this by saying that *projective transformations do not increase complexity.* We are able to rectify this problem with use of *semi-projective transformations* in the next section, (see [12]). But, let us now demonstrate the utility of projective theory in a classical (i.e., quadratic) setting.

Consider the Volterra-Hamilton system

$$\left. \begin{array}{l} \dfrac{dx^1}{dt} = N^1 \;, \quad \dfrac{dx^2}{dt} = N^2 \\[3mm] \dfrac{dN^1}{dt} = \lambda N^1 - \alpha_1 (N^1)^2 - 2\alpha_2 N^1 N^2 \\[3mm] \dfrac{dN^2}{dt} = \lambda N^2 - \beta_1 (N^2)^2 - 2\beta_2 N^1 N^2 \;. \end{array} \right\} \tag{4.10}$$

This describes production in a 2-species Gause-Witt *competition* if $\alpha_1 > 0$, $\alpha_2 > 0$, $\beta_1 > 0$, $\beta_2 > 0$ or *parasitism* if $\alpha_1 > 0$, $\alpha_2 < 0$, $\beta_1 > 0$, $\beta_2 > 0$. Converting to the natural parameter by $s = Ae^{\lambda t}$ we readily compute the non-zero projective connection coefficients to be (use (4.10) in the form (3.14), obtain Γ^i_{jk} and then use (4.2))

$$\left. \begin{array}{ll} \pi^1_{11} = \dfrac{1}{3}(\alpha_1 - 2\beta_2) \;, & \pi^2_{22} = \dfrac{1}{3}(\beta_1 - 2\alpha_2) \\[3mm] \pi^1_{12} = \dfrac{1}{3}(2\alpha_2 - \beta_1) \;, & \pi^2_{21} = \dfrac{1}{3}(2\beta_2 - \alpha_1) \;. \end{array} \right\} \tag{4.11}$$

Please note that $\pi^i_{jk} = \pi^i_{kj}$ and $\pi^a_{ak} = 0$, always hold, as follows directly from (4.2) and homogeneity of $\mathcal{D}$ (degree minus one) via Euler's Theorem. Returning to real time t, we have the ecological equations

$$\left.\begin{array}{l} \dfrac{dN^1}{dt} = -\bar{\lambda}N^1 - \dfrac{1}{3}(\alpha_1 - 2\beta_2)(N^1)^2 + \dfrac{2}{3}(\beta_1 - 2\alpha_2)N^1N^2 \\[3mm] \dfrac{dN^2}{dt} = -\bar{\lambda}N^2 - \dfrac{1}{3}(\beta_1 - 2\alpha_2)(N^2)^2 + \dfrac{2}{3}(\alpha_1 - 2\beta_2)N^1N^2 \end{array}\right\} \qquad (4.12)$$

where $\bar{\lambda} > 0$, but is otherwise arbitrarily chosen. If $\alpha_1 \ll \beta_1$ and $\beta_2 \ll \alpha_1$, then $\alpha_1 - 2\beta_2$ and $\beta_1 - 2\alpha_2$ are both positive and the system is classical *symbiosis* with positive steady-state $\left(\frac{\bar{\lambda}}{\alpha_1 - 2\beta_2}, \frac{\bar{\lambda}}{\beta_1 - 2\alpha_2}\right) = (N^1_0, N^2_0)$. This holds even if $\alpha_2 < 0$ and the original system ecology was *parasitic*. But, note that the N^1N^2 cooperative terms cannot be neglected, by an order-of-magnitude argument, by comparison to the $(N^1)^2$ and $(N^2)^2$ terms. Nevertheless, it is true that the system goes extinct if cooperation is negligible (then only $-\bar{\lambda}N^i$ terms remain). This reminds us of Kwang Jeon's *experiment in which an originally destructive interaction of amoeba and a bacterial pathogen evolved to a symbiotic state in which neither could survive without the other.* The above method shows that this *evolution can occur by a time-sequencing change in production,* that is by a projective transformation. More generally, mitochondria in eukaryotic cells of plants and animals are described with this model via the symbiosis theory of cellular evolution of L. Margulis [19,20]. Note that complexity does not change, here.

In this model, π^i_{jk} result from a projective transformation $\psi_k = \frac{1}{n+1}\Gamma^a_{ak} = \partial_k\psi$ applied to the spray (2.10). Generally, only a covariant vector field is needed to define such a time-sequencing change, but on many occasions $\psi_k = \partial\psi/\partial x^k = \partial_k\psi$ holds, as it does in the present case as is easily seen from (4.2) and (2.21). In the case (4.10) $\psi = (\alpha_1 + \beta_2)x^1 + (\beta_1 + \alpha_2)x^2$, thus π^i_{jk} results from a special projective transformation which does not depend on $\xi^i \left(\equiv y^i \equiv \frac{dx^i}{ds}\right)$, only on x^i. But, what of the projective invariance of π^i_{jk}? Generally, π^i_{jk} do not behave like Γ^i_{jk} under changes of coordinates. Indeed,

$$\frac{\partial\bar{x}^r}{\partial x^j}\frac{\partial\bar{x}^s}{\partial x^k}\bar{\Gamma}^i_{rs} = \frac{\partial\bar{x}^i}{\partial x^r}\Gamma^r_{jk} - \frac{\partial^2\bar{x}^i}{\partial x^j\partial x^k} \qquad (4.13)$$

$$\frac{\partial\bar{x}^r}{\partial x^j}\frac{\partial\bar{x}^s}{\partial x^k}\bar{\pi}^i_{rs} = \frac{\partial\bar{x}^i}{\partial x^h}\pi^h_{jk} - \frac{\partial^2\bar{x}^i}{\partial x^j\partial x^k} + \frac{\partial\bar{x}^i}{\partial x^j}\frac{\partial\theta}{\partial x^k} + \frac{\partial\bar{x}^i}{\partial x^k}\frac{\partial\theta}{\partial x^j} , \qquad (4.14)$$

where $\theta = \frac{1}{n+1}\log\left[\det\left(\frac{\partial\bar{x}^i}{\partial x^j}\right)\right]$. Thus, π transforms like Γ if and only the transformation has constant determinant, so is essentially "special linear". Nevertheless, the *interaction coefficients of a spray* Γ *determine a unique projective connection;* by $\psi_k = \frac{1}{n+1}\Gamma^a_{ak}$ even without the gradient condition $\psi_k = \partial_k\psi$. But, the resulting *projective quantities* π^i_{jk} *define an entire class of interaction patterns* because these quantities are projectively invariant. But, π^i_{jk} are not examples of any Γ^i_{jk} as (4.13)

and (4.14) show. But, π^i_{jk} has a representative called the *normal connection*, and this is a Γ^i_{jk} and has the identical components of π. This *normal* representative of π is what defines (4.12) as an ordinary interaction dynamics. We have seen that it is projectively related to (4.10).

$$\pi \quad \text{(Normal form)}$$

$$\ldots \Gamma_{(t)} \ldots \Gamma_{(p)} \ldots \Gamma_{(q)} \ldots \Gamma_{(r)} \ldots \Gamma_{(s)} \ldots$$
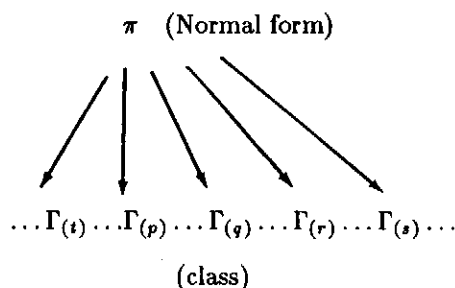
$$\text{(class)}$$

$$\frac{dN^i}{dt} + \Gamma^i_{(l)jk} N^j N^k \pm \lambda N^i = 0 \quad \text{(Typical Ecology)}$$

Fig. 7. *The $\Gamma_{(l)}$ are all time-sequence transformation (i.e., projectively) related to each other, and π given by (4.2) applied to any $\Gamma_{(l)}$ in the class, is always the same,* provided the coordinates x^i are fixed once and for all.

Applied to (4.12) we see that *classical Gause-Witt competition or parasitism are members of a class of $\Gamma_{(l)}$ whose projective class π has a symbiotic dynamics for its normal representative π^i_{jk}.* We show this is the figure below.

$$\text{Symbiant} \quad (\pi)$$

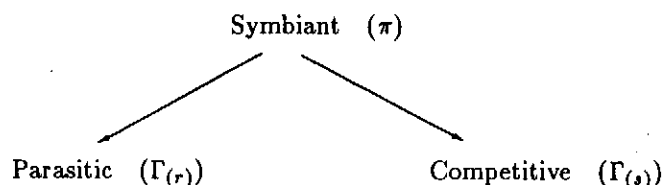$$\text{Parasitic} \quad (\Gamma_{(r)}) \qquad\qquad \text{Competitive} \quad (\Gamma_{(s)})$$

Fig. 8

At the level of separate species, N^1 and N^2 may interact competitively or symbiotically, but if they are to constitute, in addition a colonial individual, (an emergent form at a higher level), then these interactions must be subsumed under a normal form which is symbiotic. Generally, the concept of normal form of ecological interactions within a colonial individual gives us an approach to looking at processes both within and between levels in a hierarchy which expresses emergence through time-sequencing changes in growth and development. We shall employ this in the next section on a model of the processes of evolution called *heterochrony*.

5. Heterochrony and Environment in the Evolution of a Colonial Individual

We shall take the view here that time-sequencing changes in growth and development are induced from environmental influences, either somatic internal ones or external ones, to the colony. This is consistent with the Ergonomic Theory of Wilson and Bekhemeshev and its allometric space representation due to Oster and Wilson, as expanded briefly in Sec. 3. The simplest way to include these influences is with a *gradient* of the transformation function ψ. Thus, we define a *heterochonic transformation* of the Volterra-Hamilton system (2.22)

$$\left. \begin{array}{l} \dfrac{dx^i}{dt} = N^i \\[2mm] \dfrac{dN^i}{dt} + \Gamma^i_{jk} N^j N^k \pm \lambda^i = 0 \end{array} \right\} \tag{5.1a}$$

to be defined by application of ψ (1st degree homogeneous in N^i) such that a new Volterra-Hamilton system results:

$$\left. \begin{array}{l} \dfrac{dx^i}{dt} = N^i \\[2mm] \dfrac{dN^i}{dt} + (\Gamma^i_{jk} + \delta^i_j \psi_k + \delta^i_k \psi_j) N^j N^k \pm \bar{\lambda} N^i = F^2 \, \mathrm{grad}^i_F \psi \end{array} \right\} \tag{5.1b}$$

where $\bar{\lambda} > 0$ and

$$\mathrm{grad}^i_F \psi \equiv g^{ij}(\dot{\partial}_j \psi) \equiv g^{ij} \psi_j \equiv \psi^i \ .$$

Note that (5.1b) is the same as (2.23) except for the gradient.

Now since $F^2 = g_{rs} N^r N^s$ and $\bar{F} = e^{\alpha_i x^i} F = d\bar{s}$ we can rewrite (5.1b) so that

$$\dfrac{d^2 x^i}{d\bar{s}^2} + (\Gamma^i_{jk} + \delta^i_j \psi_k + \delta^i_k \psi_j - g_{jk} \psi^i) \dfrac{dx^j}{d\bar{s}} \dfrac{dx^k}{d\bar{s}} = 0 \tag{5.1c}$$

results, after passage to the natural spray parameter $\bar{s}$ is performed via $\bar{s} = A \cdot e^{\lambda t}$.

As an important example, let's take (5.1a) to be

$$\left. \begin{array}{l} \dfrac{dx^i}{dt} = N^i \\[2mm] \dfrac{dN^i}{dt} = \lambda N^i \end{array} \right\} \tag{5.2}$$

for $n = 2$, where $\Gamma^i_{jk} \equiv \gamma^i_{jk} \equiv 0$, the γ being the Levi-Cività symbols of Sec. 2 for the F-metric tensor $g_{ij} = \frac{1}{2} \dot{\partial}_i \dot{\partial}_j F^2$ for

$$F = [(N^1)^m + (N^2)^m]^{1/m} \ , \quad m \geq 2 \tag{5.3}$$

the so-called *m*th-root Minkowski norm. Note that $ds^2 = F^2(x,\, dx)$ or $F\left(x,\, \frac{dx}{ds}\right) = 1$ holds along the solution curves of the spray associated to (5.2). Choosing

$$\psi = \alpha_i N^i \, , \quad i = 1,\, 2 \tag{5.4}$$

we compute to *obtain* $dx^i = N^i dt$ and

$$\left. \begin{array}{l} \dfrac{dN^1}{dt} + \alpha_1 (N^1)^2 + \dfrac{m\alpha_2}{m-1} N^1 N^2 - \bar{\lambda} N^1 = \dfrac{\alpha_1}{m-1} \left(\dfrac{N^2}{N^1}\right)^{m-2} (N^2)^2 \\[4mm] \dfrac{dN^2}{dt} + \alpha_2 (N^2)^2 + \dfrac{m\alpha_1}{m-1} N^1 N^2 - \bar{\lambda} N^2 = \dfrac{\alpha_2}{m-1} \left(\dfrac{N^1}{N^2}\right)^{m-2} (N^1)^2 \end{array} \right\} \tag{5.5}$$

for an arbitrarily chosen $\bar{\lambda} > 0$. We know that (5.5) are geodesics of $d\bar{s} = \bar{F} = e^{\alpha_i x^i} F(x,\, dx)$. This system has deep meaning in the ecological area (see [4]) but was studied from the purely Finsler differential geometric point of view by Antonelli and Shimada [9] who refer to $\bar{F}$ as the *Ecological Finsler Metric*. The solutions to (5.5) are extrema of the variational problem (fixed end points)

$$\delta \int_{t_0}^{t_1} \bar{F}^2 \cdot e^{\bar{\lambda} t} dt = 0 \, , \tag{5.6a}$$

or equivalently,

$$\delta \int_{\bar{s}_0}^{\bar{s}_1} \bar{F}\left(x,\, \frac{dx}{d\bar{s}}\right) d\bar{s} = 0 \tag{5.6b}$$

[Note that absence of the squared exponent in (5.6b)]. We can see, therefore, that $d\bar{s} = F$ holds for trajectories of (5.2) and that $d\bar{s} = \bar{F}$ holds for those of (5.5). Thus, $F = 1$, *before* projective/gradient — change, as well as, $\bar{F} = 1$, *after* it. This brings out a very important point about *our concept of heterochrony*, namely it *preserves division of labour* (i.e., $F = 1$ *along trajectories*). But, (5.3) is only a special case of a more general case.

Theorem (Geodesic Heterochrony):
If Γ^i_{jk} is taken to be γ^i_{jk} for a given *n*-dimensional norm F (independent of x), then (5.1a) has straight lines as solutions to the associated geodesic spray and (5.1c) are the equations of geodesics of $\bar{F} = e^{\alpha_i x^i} F$, provided, $\psi = \alpha_i N^i$.

Note that such γ^i_{jk} are *identically zero*. Applying this theorem to (5.3) with $m = 2 = n$ we see that *real growth* dynamics

$$\frac{d^2 y^i}{dt^2} + \lambda \frac{dy^i}{dt} = 0$$

maps, via geodesic heterochrony, into (3.13), the *growth equation for a dimorphic symbiant*, with $k_i = 1$. For $m \geq 3$, we obtain the growth equations for a *dimorphic symbiant with strong social interactions*. This derives from (5.5) using the definition of the so-called *real growth variables* (3.11). The steady-state necessary for their definition is

$$N_0^i = \frac{\bar{\lambda}\alpha_i^{\frac{1}{m-1}}}{\alpha_1^{\frac{m}{m-1}} + \alpha_2^{\frac{m}{m-1}}} \, . \tag{5.7}$$

The interaction coefficients of (5.5) are given by

$$\bar{\Gamma}_{11}^1 = \alpha_1 - \frac{\alpha_1}{2}(m-2)\left(\frac{N^2}{N^1}\right)^m \; ; \quad \bar{\Gamma}_{12}^1 = \frac{m}{2(m-1)}\left\{\alpha_2 + \alpha_1(m-2)\left(\frac{N^2}{N^1}\right)^{m-1}\right\}$$

$$\bar{\Gamma}_{22}^1 = -\frac{m}{2}\alpha_1\left(\frac{N^2}{N^1}\right)^{m-2} \, .$$

$$\tag{5.8}$$

with $\bar{\Gamma}_{22}^2$, $\bar{\Gamma}_{21}^2$ and $\bar{\Gamma}_{11}^2$ *obtained from these by interchanging 1 and 2 in the indexing.* The spray curvature tensor $\mathcal{D}$ is given by

$$\mathcal{D}_{111}^1 = \frac{\alpha_1}{2}m(m-2)\left(\frac{N^2}{N^1}\right)^m \cdot \frac{1}{N^1} \; ; \qquad \mathcal{D}_{112}^1 = -\frac{\alpha_1}{2}m(m-2)\left(\frac{N^2}{N^1}\right)^{m-1} \cdot \frac{1}{N^1}$$

$$\mathcal{D}_{121}^1 = -\frac{\alpha_1}{2}m(m-2)\left(\frac{N^2}{N^1}\right)^{m-1} \cdot \frac{1}{N^1} \; ; \quad \mathcal{D}_{122}^1 = \frac{\alpha_1}{2}m(m-2)\left(\frac{N^2}{N^1}\right)^{m-2} \cdot \frac{1}{N^1}$$

$$\mathcal{D}_{221}^1 = \frac{\alpha_1}{2}m(m-2)\left(\frac{N^2}{N^1}\right)^{m-2} \cdot \frac{1}{N^1} \; ; \quad \mathcal{D}_{222}^1 = -\frac{\alpha_1}{2}m(m-2)\left(\frac{N^2}{N^1}\right)^{m-3} \cdot \frac{1}{N^1}$$

$$\tag{5.9}$$

All others of the $\mathcal{D}_{jkl}^i$ are obtained from these by the index interchange. Note that *the spray curvature vanishes identically if and only if $m = 2$.* Thus, (5.5) is *intrinsically social.* But, even more interesting is the question of whether or not it is projectively equivalent to (5.2). *Recall, Křivan's method always gives intrinsically social interactions that are time-sequencing equivalent to classical (i.e., quadratic) systems.* We can answer this question by direct calculation. First, we compute the *normal form π* of (5.5)

$$\pi_{11}^1 = -\frac{\alpha_1}{3(m-1)} - \frac{(m+1)(m-2)}{6(m-1)} \left\{ \alpha_1(m-1)\left(\frac{N^2}{N^1}\right)^m + \alpha_2 m \left(\frac{N^1}{N^2}\right)^{m-1} \right\}$$

$$\pi_{12}^1 = -\frac{\alpha_2}{3(m-1)} - \frac{(m+1)(m-2)}{6} \left\{ \frac{\alpha_1 m}{m-1}\left(\frac{N^2}{N^1}\right)^{m-1} + \alpha_2 \left(\frac{N^1}{N^2}\right)^{m} \right\}$$

$$\pi_{22}^1 = -\frac{\alpha_1 m(m+1)}{6}\left(\frac{N^2}{N^1}\right)^{m-2} + \frac{\alpha_2 m(m-2)}{6}\left(\frac{N^1}{N^2}\right)^{m+1} .$$

$$(5.10)$$

The rest of the component of π_{jk}^i are obtained by indexing interchange. Now we compute the *Douglas* (Projective) *tensor* $\mathcal{K}$ of Sec. 4:

$$\mathcal{K}_{111}^1 = \frac{(m-2)m(m+1)}{6} \left\{ \alpha_1\left(\frac{N^2}{N^1}\right)^m \cdot \frac{1}{N^1} - \alpha_2\left(\frac{N^1}{N^2}\right)^{m-2} \cdot \frac{1}{N^2} \right\}$$

$$\mathcal{K}_{112}^1 = \frac{(m-2)m(m+1)}{6} \left\{ \alpha_1\left(\frac{N^2}{N^1}\right)^{m-1} \cdot \frac{1}{N^1} - \alpha_2\left(\frac{N^1}{N^2}\right)^{m-1} \cdot \frac{1}{N^2} \right\}$$

$$\mathcal{K}_{121}^1 = \frac{(m-2)m(m+1)}{6} \left\{ \alpha_1\left(\frac{N^2}{N^1}\right)^{m-1} \cdot \frac{1}{N^1} - \alpha_2(m-1)\left(\frac{N^1}{N^2}\right)^{m-2} \cdot \frac{1}{N^2} \right\}$$

$$(5.11)$$

All others of the components of $\mathcal{K}_{jkl}^i$ are obtained by indexing interchange. We see that $\mathcal{K}$ *is identically zero* if and only if $m = 2$ *and that therefore, there does not exist a projective transformation to the straight-line dynamics of* (5.2) if $m \geq 3$. The reason is, of course, the gradient term on the right-hand side of (5.1b). Moreover, consider that

$$\pi_{jk}^i = \frac{1}{n+1}\delta_j^i \psi_k + \frac{1}{n+1}\delta_k^i \psi_j - g_{jk}\psi^i - \frac{1}{n+1}N^i \mathcal{D}_{jka}^a ,$$

so for $n \geq 3$, with $i \neq j \neq k$,

$$\pi_{jk}^i = -g_{jk}\psi^i - \frac{1}{n+1}N^i \mathcal{D}_{jka}^a , \qquad (5.12)$$

which will not be generally zero.

   Therefore, heterochronic transformation of classical (i.e., quadratic) systems do result in increased complexity (3-way interactions ($n \geq 3$) where there were only 2-way before time-sequencing change) something that is lacking in the Křivan method, but is necessary for a mathematical theory of evolution by heterochrony in colonical individuals. Heterochrony can only occur when a direct environmental influence induces it. The processes we have described creates an emergent hierarchy, due to Antonelli and Bradbury via the theory of the normal form described in the diagram below.
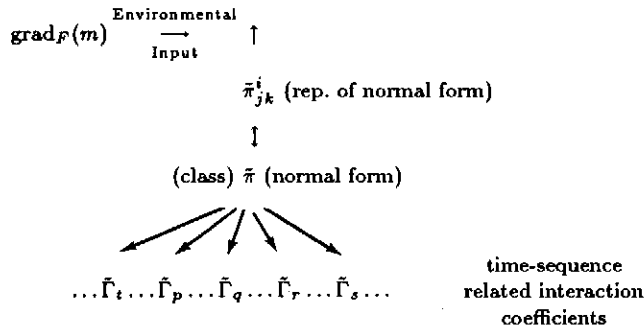
(Level three)

$$\frac{dN^i}{dt} + \tilde{\bar{\Gamma}}^i_{jk} N^j N^i \pm \tilde{\bar{\lambda}} N^i = 0 \left(\tilde{\bar{\Gamma}}^i_{jk} = \pi^i_{jk} + \delta^i_j \tilde{m}_k + \delta^i_k \tilde{m}_j - \bar{g}_{jk} \operatorname{grad}^i_{\tilde{F}}(\tilde{m}) \right)$$
$$+ N^i \tilde{m}_{jk}$$

$$\Updownarrow$$

$$\frac{dN^i}{dt} + \left(\bar{\pi}^i_{jk} + \delta^i_j \tilde{m}_k + \delta^i_k \tilde{m}_j \right) N^j N^k \pm \tilde{\bar{\lambda}} N^i = \tilde{F} \operatorname{grad}^i_{\tilde{F}}(\tilde{m})$$

$$\tilde{F} = 1$$

$$\operatorname{grad}_F(m) \quad \overset{\text{Environmental}}{\underset{\text{Input}}{\longrightarrow}} \quad \uparrow$$

$$\bar{\pi}^i_{jk} \text{ (rep. of normal form)}$$

$$\updownarrow$$

$$\text{(class) } \tilde{\pi} \text{ (normal form)}$$

$$\swarrow \quad \swarrow \quad \downarrow \quad \searrow \quad \searrow$$

$$\dots \tilde{\Gamma}_t \dots \tilde{\Gamma}_p \dots \tilde{\Gamma}_q \dots \tilde{\Gamma}_r \dots \tilde{\Gamma}_s \dots \qquad \begin{array}{c} \text{time-sequence} \\ \text{related interaction} \\ \text{coefficients} \end{array}$$

(Level two)

$$\frac{dN^i}{dt} + \bar{\Gamma}^i_{jk} N^j N^k \pm \bar{\lambda} N^i = 0 \; (\bar{\Gamma}^i_{jk} = \pi^i_{jk} + \delta^i_j m_k + \delta^i_k m_j$$
$$+ N^i m_{jk} - g_{jk} \operatorname{grad}^i_F(m))$$

$$\Updownarrow$$

$$\frac{dN^i}{dt} + (\pi^i_{jk} + \delta^i_j m_k + \delta^i_k m_j) N^j N^k \pm \bar{\lambda} N^i = F^2 \operatorname{grad}^i_F(m)$$

$$\bar{F} = 1$$

$$\operatorname{grad}_F(m) \quad \overset{\text{Environmental}}{\underset{\text{Input}}{\longrightarrow}} \quad \uparrow$$

$$\pi^i_{jk} \text{ (rep. of the normal form)}$$

$$\updownarrow$$

$$\text{(class) } \pi \text{ (normal form)}$$

$$\swarrow \quad \swarrow \quad \downarrow \quad \searrow \quad \searrow$$

$$\dots \Gamma_t \dots \Gamma_p \dots \Gamma_q \dots \Gamma_r \dots \Gamma_s \dots \qquad \begin{array}{c} \text{time-sequence} \\ \text{related interaction} \\ \text{coefficients} \end{array}$$

(Level one)

$$\frac{dN^i}{dt} + \Gamma^i_{jk} N^j N^k \pm \lambda N^i = 0$$

$$F = 1$$

Antonelli-Bradbury Hierarchy for Evolution of Complexity

Here, we begin with (say) a classical (i.e., quadratic) dynamics with division of labour ($F = 1$), for the colonial individual. This Γ defines the normal form π by (4.2) which has an interaction pattern representative, π^i_{jk}. Then a time-sequence function m is applied and the heterochronic transformation is defined at the next level by application of the Minkowski F-gradient to yield, by definition,

$$\frac{dN^i}{dt} + (\pi^i_{jk} + \delta^i_j m_k + \delta^i_k m_j)N^j N^k \pm \tilde{\lambda} N^i = F^2 \, \mathrm{grad}^i_F(m) \; . \tag{5.13}$$

Next, the *proper sort of F and m will allow adaptation to occur* in the sense that

$$\tilde{\Gamma}^i_{jk} = \pi^i_{jk} + \delta^i_j m_k + \delta^i_k m_j + N^i m_{jk} - g_{jk} \, \mathrm{grad}^i_F(m) \tag{5.14}$$

is an interaction pattern for which there exists a Finsler metric function $\bar{F}$ which is conserved along solutions γ of

$$\frac{d^2 x^i}{d\bar{s}^2} + \tilde{\Gamma}^i_{jk} \frac{dx^j}{d\bar{s}} \frac{dx^k}{d\bar{s}} = 0 \; . \tag{5.15}$$

That is, $\frac{d\bar{s}}{dt} = \bar{F}\left(x, \frac{dx}{dt}\right) \iff \bar{F} = 1$ so that division of labour holds along γ. If this adaptation is allowed, the *level two* is defined in the hierarchy. Then, another environment input $\mathrm{grad}\frac{i}{\bar{F}} \, \tilde{m}$ is applied to the normal form of (5.13) and simultaneously a projective (time-sequencing) change is effected. If adaptation is allowed, the result defines the next level in the hierarchy, and so on. Equation (5.12) insures that social complexity increases from level one to two, given it was quadratic to start. But, it remains an *open problem* as to just how complexity behaves going from level two to level three. This is the *Hierarchy Problem*.

6. Allometric Space and Wagner Geometry

In Sec. 3 we briefly described the Oster and Wilson allometric space representation of the Ergonomic Theory of colonial organisms. If we consider n separate Gompertz curves with the same rate parameter λ in terms of *real-growth variables* $y^i(t)$ which solve

$$\frac{d^2 y^i}{dt^2} + \lambda \frac{dy^i}{dt} = 0 \; , \quad i = 1, \ldots, n \tag{6.1}$$

with *initial conditions* $y^i(0) > 0$ and $\frac{dy^i}{dt}\big|_{t=0} < 0$. Conversion to the natural parameter $\hat{s}$ via $\hat{s} = B \cdot e^{-\lambda t}$ leads to

$$\frac{d^2 y^i}{d\hat{s}^2} = 0 \tag{6.2}$$

where $\hat{s} = S_{\max} - s$, $S_{\max}$ being adult size and $ds = F(x, dx)$, being size increment, is assumed independent of x. Thus, Eq. (6.2) has all its solutions constrained by the division of labor principle because $d\hat{s} = -ds$ so that $F\left(\frac{dx^1}{d\hat{s}}, \ldots, \frac{dx^n}{d\hat{s}}\right) = 1$ if and only if $\pm F\left(\frac{dx^1}{d\hat{s}}, \ldots, \frac{dx^n}{d\hat{s}}\right) = 1$. (There is no assumption that $F(-dx) = F(dx)$, here.)

Now let $\phi(x)$ be a scalar function of x^i and define a *semi-projective transformation* of Eq. (6.2) to be

$$\frac{d^2 y^i}{dp^2} + (\delta^i_j \phi_k)\frac{dy^i}{dp}\frac{dy^k}{dp} = 0 \tag{6.3}$$

where $\phi_k \equiv \partial_k \phi$ and

$$\frac{dp}{d\hat{s}} = M \cdot e^{-\int_\gamma \phi(x)d\hat{s}} \tag{6.4}$$

for some constant of integration M. Solutions of Eq. (6.2) are reparametrized to give solutions of (6.3) via (6.4) (see [12]). The *Theory of Wagner Geometry* [14,15] states that Eq. (6.3) has $\bar{F} = e^\phi \cdot F = dp$ along its solutions, that is $\bar{F}\left(x, \frac{dx}{dp}\right) = 1$ along solutions γ of Eq. (6.3). These γ are called *auto parallels of the Wagner geometry*. Clearly, *they exhibit the division of labor principle, but they are (almost) never geodesic of $\bar{F}$!* This is because the geodesics of $\bar{F}$ have "curvature" relative to Wagner autoparallels. That is, according to the geodesic heterochrony theorem in Sec. 5, the geodesics are given as solutions to

$$\left. \begin{array}{l} \dfrac{d^2 y^i}{dp^2} + \delta^i_j \phi_k \dfrac{dy^j}{dp}\dfrac{dy^k}{dp} = C^i \\[2mm] C^i = F^2 \phi^i - \delta^i_k \phi_j \dfrac{dy^k}{dp}\dfrac{dy^j}{dp} \,, \end{array} \right\} \tag{6.5}$$

is the *Wagner geodesic curvature vector*. If we pass to real-time t and use the special case $\phi = \alpha_i x^i$ and F is the mth root norm given in Eq. (5.3), then we obtain Eq. (5.5) with

$$C^2 = \left[\frac{\alpha_2}{m-1}\left(\frac{N^2}{N^1}\right)^{m-2}(N^2)^2 - \frac{\alpha_1}{m-1}N^1 N^2\right]$$

$$C^1 = \left[\frac{\alpha_1}{m-1}\left(\frac{N^1}{N^2}\right)^{m-2}(N^1)^2 - \frac{\alpha_2}{m-1}N^1 N^2\right] \,, \tag{6.6}$$

as the Wagner geodesic curvature vector components. Furthermore, *since the Wagner autoparallels have sets of straight lines in allometric spaces as solution sets* (i.e., semi-projective transformations only reparametize these straight lines), *it is the curvature vector C^i which warps these straight lines into honest curved lines in allometric space*, as required by Oster and Wilson (see quote in the caption of Fig. 5).

The above arguments shows that geodesic heterochronic transformation of Gom-pertz growth in allometric space results generally in new growth curves which are curved because of the presence of the environmental gradient, $\mathrm{grad}_F m$.

Now we shall formulate a *concept of heterochronic transformation more general* than geodesic heterochrony. We will restrict ourselves to

$$\psi \equiv \phi_k(y) \cdot \frac{dy^k}{dt} \tag{6.7}$$

$$\text{where} \qquad \psi_k \equiv \dot{\partial}_k \psi = \phi_k \equiv \partial_k \phi \ .$$

Thus, a *heterochronic transformation* of Eq. (6.2) consists of a pair (ϕ, C^i) with ϕ a scalar function of y^i and C^i depending on y^i and dy^i/dt and positively 2nd order homogeneous in the latter, such that the n equations

$$\frac{d^2 y^i}{dt^2} + (\delta^i_j \phi_k) \frac{dy^j}{dt} \frac{dy^k}{dt} + \bar{\lambda} \frac{dy^i}{dt} = C^i \left(y, \frac{dy}{dt} \right) \tag{6.8}$$

hold in terms of *real growth* variables and *real time* t. We impose the further condition on the curvature vector C^i:

$$\bar{g}_{ij} C^i \frac{dy^i}{dt} = 0 \ , \tag{6.9}$$

along solutions of Eq. (6.8) where

$$\left. \begin{aligned} \bar{g}_{ij} &= e^\phi g_{ij} = \frac{1}{2} e^\phi \dot{\partial}_i \dot{\partial}_j F^2 \\ \text{and} \qquad d\bar{s} &= \bar{F} = e^\phi \cdot F \ . \end{aligned} \right\} \tag{6.10}$$

The equation (6.9) is equivalent to $\bar{F} \left(y, \frac{dy}{dt} \right) = \frac{d\bar{s}}{dt}$ along all solutions of Eq. (6.8) [11]. It is a generalization of the lemma in Sec. 2. (In the remark following the lemma, $C^i = 2G^i - H^i_F$ is the curvature vector of the spray curves relative to norm F). Note that in terms of the natural parameters Eq. (6.8) is just Eq. (6.3) with $C^i \left(y, \frac{dy}{dp} \right)$ affixed to the right-hand side. The point is that *it is possible to have division of labour satisfied and still not have the geodesic condition* (i.e., extremals of the $\bar{F}$ variational problem). For example, consider

$$\left. \begin{aligned} C^i &= F^i_j \frac{dy^j}{dt} \ , & F_{ij} &= g_{ir} F^r_j \\ F_{ij} &= \partial_i A_j - \partial_j A_i \ , & A_i &= (\phi_1 + \phi_2) \cdot g_{ri} \frac{dy^r}{dt} \end{aligned} \right\} \tag{6.11}$$

where ϕ_1 and ϕ_2 are scalar functions of y^i. Then one computes

$$\left. \begin{aligned} C^i &= F^2 \phi^i - \delta^i_k \phi_j \frac{dy^k}{dt} \frac{dy^j}{dt} \\ \phi &= \phi_1 + \phi_2 \end{aligned} \right\} \tag{6.12}$$

Now, if we apply the heterochronic transformation (ϕ, C^i), the result will *not* be geodesics of $e^{\phi_1} \cdot F$, but division or labour (orthogonality relative to $g_{ij} = \frac{1}{2}\dot\partial_i\dot\partial_j F^2$) will still hold. As a concrete example, consider Eq. (5.5) with C^i as in Eq. (6.6) but add B^1 and B^2 to C^1 and C^2 respectively, where

$$\left.\begin{aligned}
B^1 &= -\left(\delta_1 - \tfrac{m\alpha_2}{m-1}\right)\frac{dy^1}{dt}\frac{dy^2}{dt} + \left(\delta_2 - \frac{m\alpha_1}{m-1}\right)\left(\frac{\dot y^2}{\dot y^1}\right)^{m-2}\left(\frac{dy^2}{dt}\right)^2 \\
B^2 &= -\left(\delta_2 - \tfrac{m\alpha_1}{m-1}\right)\frac{dy^1}{dt}\frac{dy^2}{dt} + \left(\delta - \frac{m\alpha_2}{m-1}\right)\left(\frac{\dot y^1}{\dot y^2}\right)^{m-2}\left(\frac{dy^1}{dt}\right)^2 .
\end{aligned}\right\} \tag{6.13}$$

Then we obtain a system whose ecological interactions are in terms of x^i and N^i $(dx^i = k_{(i)}N^i dt,\ i = 1,\ 2)$ are

$$\left.\begin{aligned}
\frac{dN^i}{dt} &= \lambda N^1 - \alpha_1(N^1)^2 - \delta_1 N^1 N^2 + (\delta_2 - \alpha_1)\left(\frac{N^2}{N^1}\right)^{m-2}(N^2)^2 \\
\frac{dN^2}{dt} &= \lambda N^2 - \alpha_2(N^2)^2 - \delta_2 N^1 N^2 + (\delta_1 - \alpha_2)\left(\frac{N^1}{N^2}\right)^{m-2}(N^1)^2 .
\end{aligned}\right\} \tag{6.14a}$$

Just use the reverse of the substitution (3.11) for real growth variables. The steady-state necessary for this is (with $k_i = k = 1$)

$$\left.\begin{aligned}
N_0^1 &= \frac{\lambda(\delta_2 - \alpha_1)^{\frac{1}{m-1}}}{\alpha_1(\delta_2 - \alpha_1)^{\frac{1}{m-1}} + \alpha_2(\delta_1 - \alpha_2)^{\frac{1}{m-1}}} \\
N_0^2 &= \frac{\lambda(\delta_1 - \alpha_2)^{\frac{1}{m-1}}}{\alpha_1(\delta_2 - \alpha_1)^{\frac{1}{m-1}} + \alpha_2(\delta_1 - \alpha_2)^{\frac{1}{m-1}}}
\end{aligned}\right\} . \tag{6.14b}$$

Theorem (Antonelli and Lin).
The system (6.14a) has unique positive solution (6.14b) which is globally asymptotically stable in the positive region of (N^1, N^2)-space. Such a system has geodesic form if and only if, $\delta_i = \frac{m\alpha_j}{m-1}$, $i \neq j$ [4].

We have also the much deeper result:

Theorem (Antonelli and Shimada):
Almost all trajectories of the geodesic version of (6.14) $(m \geq 3)$ are Liapunov stable [9].

The proof of this is to compute the Berwald's Gauss curvature K for $\bar F$, $m \geq 3$. It is almost everywhere positive. *A corollary is that geodesic heterochrony can result in stable caste systems* (Antonelli and Lin) *with stable biomass production* (Antonelli and Shimada) *and yet be highly social* $(m \geq 3)$ (see Sec. 5) *in its interactions.* This is not so for $m = 2$, because production is *unstable* and $\mathcal{D} \equiv 0 \equiv \mathcal{K}$. Yet (6.14b) is still globally asymptotically stable [4].

Let us quote at length the statements of Wilson and Hölldobler [24]:

> An example of social homeostasis is provided by the caste systems of the
> ant genus *Pheidole*. Each species of this large cosmopolitan genus has a
> characteristic ratio of small-headed minor workers to large-headed major
> workers. When the ratio is altered in a particular colony by an excess of
> birth or mortality in one of the castes the colony converges back toward the
> original ratio within one or two worker generations, extending across one
> to three months. The feedback loop is an inhibitory pheromone, so that
> the larvae surrounded by an excess of majors curtails growth and tend to
> become minors. Those present during a shortage of majors become more
> sensitive to juvenile hormone, extend growth, and turn into majors."

7. Allometric Growth and Heterochrony in Paleontology

We have seen how our concept of a heterochronic transformation converts Gompertz
growth of a colonial individual into a growth process with complicated interactions
between the morphotypes as in (6.14). But, how is this system related to classical
heterochrony as used in paleontology? The answer is that when $\phi = \alpha_i y^i$, α^i
constants, the trajectories eventually head in direction, $\tan^{-1} \cdot \left(\frac{\alpha_1}{\alpha_2}\right)^{m/2}$. This is
called the *Landsberg direction*, in Finsler differential geometry. This was first worked
out for $m = 2$, the Riemannian case, but follows from results in [9] for $m \geq 3$.

From a different point of view, the global stability of N_0^i in (6.14) implies that
dx^i/dt, where x^i is log biomass, approaches unique constants as $t \to t_f$, the time of
full growth, while the length of the tangent vector dx^i/dt is preserved along growth
paths and so $\bar{F} \cong 1$ implies size increase dS/dt (S = size) is constant.

Therefore,

$$\frac{dx^i}{dt} = \frac{dx^i}{dS} \cdot \frac{dS}{dt}$$

implies dx^i/dS, at or near t_f, the time of full growth (or adult size, $S = A$) is a
constant times N_0^i. Consequently,

$$x^i = M^i S + D^i \qquad i = 1, 2, \ldots \tag{7.1}$$

for suitable constants M^i, D^i. The Eqs. (6.14) are autoparallels which conserve
lengths and total energy $\bar{F}$. Defining a new time parameter $S = \frac{1}{\lambda} e^{\lambda t}$ with x^i
replacing y^i converts (6.14) into the usual autoparallel form. This transformation
leads to S, the arc length, and should not be confused with the Gompertz equa-
tion. The variable y^i are not used here. Rather x^i is used and so a different time
transformation is needed to obtain standard autoparallel form, because the λ term
switches sign in passing from y^i to x^i variables. So, setting $k_i = k$ in (6.14a)

$$\frac{dx^i}{dS}\rfloor_{S=A} = \frac{dx^i}{dt}\rfloor_{t=t_f} \cdot \frac{dt}{dS}\rfloor_{S=A} = \frac{kN_0^i}{(\bar{g}_{ij} N_0^i N_0^j)_{t=t_f}^{1/2}} \tag{7.2}$$

where

$$
\left.
\begin{aligned}
\tilde{g}_{ij}(x_f) &= e^{2(\alpha_i x_f^i)} \cdot g_{ij}(x_f) \\
[g_{ij}(x_f) N_0^i N_0^j]^{1/2} &= [(N_0^1)^m + (N_0^2)^m]^{1/m} \ .
\end{aligned}
\right\} \tag{7.3}
$$

Then

$$
\left.
\begin{aligned}
\frac{dx^1}{dS}\Big]_{S=A} &= Q \cdot \frac{k}{\left[1 + \left(\dfrac{N_0^2}{N_0^1}\right)^m\right]^{1/m}} \\
Q &= e^{-\alpha_i x_f^i} \ .
\end{aligned}
\right\} \tag{7.4}
$$

Thus, (6.14b) leads to the *Allometry* (approximation), after rescaling $x^i(t)$ with k equal to the mth-root norm of $\left(\alpha_1^{\frac{-1}{m-1}}, \ \alpha_2^{\frac{-1}{m-1}}\right)$,

$$
x^i(t) \approx Q \cdot (\alpha_i)^{1/m-1} \cdot S + D^i \tag{7.5}
$$

between $x^i(t) = \ln m^i(t)$ ($m^i(t)$ being total biomass of ith caste accumulated up to time t) and log of the total size, S (for t *near* t_f). That is,

$$
\ln m^i \approx \frac{1}{(m_f^1)^{\alpha_1}(m_f^2)^{\alpha_2}} \cdot (\alpha_i)^{\frac{1}{m-1}} \cdot S + D^i \ . \tag{7.6}
$$

In Paleontology *normalized adult sizes* can be used so that $m_f^1 = m_f^2 = 1$, and so

$$
\ln m^i \approx (\alpha_i)^{\frac{1}{m-1}} \cdot S + D^i \tag{7.7}
$$

holds *near adult sizes*. The *social aspect* is clear in the parameter m, also.

If we have performed a heterochronic transformation via $\phi = \alpha_i y^i$, we may follow this by another such, $\psi = \alpha_i' y^i$. This amounts to replacing α_i by $\alpha_i + \alpha_i'$ in (7.6) and (7.7). If $\alpha_1' < 0$ but $\alpha_1 + \alpha_1' > 0$, then x_f^1 has experienced a *neotenic change from its ancestral form*. If $\alpha_1' > 0$, then x_f^1 has experienced an *acceleration from its ancestral form* [13]. Thus, the generalization we have here represented does indeed give the usual allometric relations for neoteny and acceleration as they were defined for the Evolution of fossil forms [13,1].

8. Conclusion

The examples we have given are limited, for our work has only just begun. More examples are needed, say, the Minkowski norm of Sec. 1 (The Rander's metric) or certain others, should be worked out in detail in the near future, in order to define the geodesic heterochrony (i.e., perfect adaptation). There is also the comparison

with data on allometric measurements of say, fossil bryozoans. This has been done in part for the above example (mth-root norm) in Sec. 7. On the other hand, such data seem at first to be inadequate for verification of our mathematical theory. Rather, data on development in Ant colonies would seem much more appropriate. For our model is *dynamical* and says a lot more about neoteny and other types of biological heterochrony than mere allometric comparison of x^i at or near adult size (i.e., the stuff of fossil measurements). S. J. Gould has written of the need for a theory like the above [13] and no one to our knowledge has filled this gap until now. There is however, the classic work in the field due to Oster and Gould *et al.* [1], and again we recommend this paper as an excellent introduction to heterochrony modelling.

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