Biological Similarity and Group Theory

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The fact that group theory can be used to advantage in biology has often been ignored. It is shown how biological similarity analysis can be understood in terms of group theory. In particular, the so-called allometric equations used in comparative physiometry and morphometry are analyzed, and a generalization of such allometric relations is given.

1. Introduction

Group theory has played a central role in the development of modern mathematics. More recently, physicists have made great use of group theory (the systematic study of symmetry) in the construction of some of their most successful models, particularly in high-energy physics. Not only have new models been inspired, if not entirely created from symmetry arguments, but also in some instances it has been found necessary to reinterpret old ideas or beliefs in the light of these fundamental relational principles. For instance, in a careful study of the Galilei group, Levy-Leblond (1965) has shown that the existence of non-integral values of the spin is not a relativistic effect, but comes out of non-relativistic (i.e., Galilei-relativistic) quantum mechanics in a very natural way. Thus, in addition to its very practical use in constructing or analyzing models, group theory can also play an important pedagogical or epistemological role, by telling us what properties of a system are specifically due to its symmetry properties under certain transformations.

In biology, very restricted use has been made of group theory and it is certainly not a familiar tool of the average theoretical scientist in the natural sciences. However, there is no *a priori* reason why the exploitation of symmetry could not be as fruitful in biology as it has been in physics; in fact, there are reasons to believe that it may even be more useful in biology. In

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physics, group theory has been a powerful practical tool when, for various reasons, a complete model (or theory) of a physical phenomenon was lacking, and also in situations where a good, albeit complex model was available, but the calculations were hopelessly difficult to perform. In the first situation, one could use group theory in order to obtain as much information as possible which depended on the symmetry of the system only. This is analogous to considering a simplified, but suitable subsystem of a whole system too complex to be studied directly. In the second situation, the calculations are made less difficult to perform by introducing more "natural" variables or co-ordinates. Group theory is, by no means, limited to the above situations.

The applications of group theory can be considered to arise in the following general situations. Let S be a set of objects and let R be a set of relations on S. An example of a relation on S would be an equivalence relation which specifies, for any pair a, b in S, whether or not they are equivalent in some sense. However, a relation on S can be more general and can be mathematically defined as a subset of a cartesian power of S. A one-one transformation T of S onto S, which leaves each relation of R invariant is said to be an automorphism of S for R. One shows that the set of all such automorphisms form a group $G = \text{Aut}\,(S, R)$. Clearly, group theory can be used in very diverse fields, depending on the nature of the set S of objects under study, and the set R of relations or properties being kept invariant. Also, group theory can help relate structurally two different phenomena which are analogous (isomorphic mathematically), their differences being expressed in the different concrete realizations of the abstract sets S and R.

In this paper, we shall sketch a group theoretical approach to the theories of biological similarity which, we believe, are in need of a more solid foundation. Traditionally, the idea of similarity or of dimensional analysis is related to the operation of changing units. However, as will be seen below, the idea of similarity can be pursued much farther, and the tool for doing that is group theory. This was recognized by Birkhoff (1960), Michal (1952), Morgan (1952) and Moran & Gaggioli (1969), in the context of differential equations arising in engineering problems. In recent review papers on theories of biological similarity, Günther (1975a,b) and McMahon (1973, 1975) attempt to relate quantitatively, using allometric equations, various functional or anatomical parameters of animals belonging to the same "model". These allometric relations are based on the traditional approach to similarity, and, although the agreement with the observations seem very good, it is not always clear why they are so good. We believe a group theoretical analysis can shed some light on this problem. Also, a critical analysis of the data would be most useful, and this can best be done in the context of a better understood theory.

2. Dimensional Analysis

The traditional approach to dimensional analysis starts by noticing that natural or physical phenomena should be independent of the units being used in measuring the quantities of interest. When it is realized that "changes of units" are not sufficient, more general transformations are considered and this leads to *similarity analysis* which goes beyond strict dimensional analysis. Here, one must exercise some care: intuition, together with experience, usually is necessary to make the right decision (a) on what type of similarity (mechanical, hydrodynamical, biological,...) is involved, and (b) to what extent it applies to the given situation. In some cases, one is guided by a set of differential equations which describe the phenomenon, and these can be tested for their invariance under the similarity transformations, as well as under the changes of units. In other cases, one must rely entirely on previous experience and intuition to see what invariance is present. Always, extrapolation outside the domain of known validity of the invariances must be done very cautiously. The usefulness of dimensional and similarity analysis is well known to hydrodynamics engineers. Among other things, they use the method to do experimental work on small-scale models, too expensive or impossible to perform on a prototype. They also use the method for reducing the number of variables or parameters in a given study, experimental or theoretical. This traditional approach has its limits. First, it is not general enough, and it does not lend itself to a straightforward generalization. Also, there is often some confusion on the dual role of a "change of unit" type of transformation and the transformation from a model to its prototype. Finally, some of the hypotheses are often hidden or at best not very clear. G. Birkhoff (1960) stressed that the correct approach to dimensional analysis should rely on group theory, and he went on to apply this idea to the solution of differential equations arising in hydrodynamics. More recently, Moran & Marshek (1972) used group theory and matrix methods in their generalized dimensional analysis of differential equations. However, it is well known that the use of group theory in differential equations can be traced to the early works of Lie (1875).

The traditional approach to dimensional analysis may be summarized in the following way. Suppose the system being studied is described by a set of variables $\{x_i\}$, where $i = 1, 2, \ldots, n$. To fix ideas, suppose further that the units of each variable x_i can be written as $M^\alpha L^\beta T^\delta$, where M, L, T are the "fundamental" units of mass, length and time, respectively, and where α, β, δ are real numbers. Usually, one is given a set of constraints on the set $\{x_i\}$ which may take the form of a set of differential equations with initial-boundary conditions. Suppose the constraints can be written in the

form $C_j(x_1, x_2, \ldots, x_n) = 0$, where $j = 1, 2, \ldots, m$. One then considers the effect on C_j of making a change of units

$$M' = \mu M$$
$$L' = \lambda L \tag{1}$$
$$T' = \tau T.$$

This means that each variable x_i of units $M^\alpha L^\beta T^\delta$ is to be transformed according to

$$x_i' = \mu^\alpha \lambda^\beta \tau^\delta x_i. \tag{2}$$

If the constraints have the same form in the transformed variables; i.e., $C_j(x_1', x_2' \ldots, x_n') = 0$, they are said to be invariant under a change of units. In such a case, one shows that the constraints can be reformulated in terms of dimensionless variables, $(n-3)$ in number if the three transformations μ, λ, τ are essential. Being able to express the constraints in fewer variables can be of considerable help if, for instance, they are given as differential equations. In some cases, a partial differential equation is, in this way, transformed into an ordinary differential equation which is then solved numerically or analytically.

These "change of unit" transformations are nothing but special cases of transformations on the variables $\{x_i\}$, which leave dimensionless variables invariant. Moran & Marshek (1972), in the context of differential equations, have shown how to treat the more general transformations

$$x_i' = \lambda_1^{\alpha_{1i}} \lambda_2^{\alpha_{2i}} \ldots \lambda_r^{\alpha_{ri}} x_i \tag{3}$$

for an r-parameter (abelian) Lie group. In this context, the transformation (1) may be considered as arising from a three-parameter group of transformations.

3. Group Theory and Similarity Analysis

Dimensional analysis and its generalizations become more transparent when considered from a group-theoretical standpoint. This is due to the fact that in dimensional or similarity analysis, we focus our attention on properties or parameters which are invariant under a group of transformations. Since invariance implies symmetry, we are then led to group theory if a systematic approach is required.

Suppose we are given a system which is in one of many possible states, and a set of variables $\{x_i \mid i = 1, 2, \ldots, n\}$, whose values partly characterize the state of the system. Each variable is assumed to be a real-valued function defined on the states. It is not always evident how a set of variables is to be chosen in the description of a system; in fact, such a choice already pre-

supposes some knowledge of the system and of the particular phenomenon or behavior which is being looked at. We suppose here, that a choice of variables $\{x_i\}$ has already been made. One of the objects of science is to find, among such a set of variables, relations which may be suggested by experimental results or by a model to be eventually submitted to experimental verification. Loosely speaking, the stronger and the simpler these relations, the better we know the system. Such a set of relations among the variables $\{x_i\}$ can be considered as a constraint on the states. Let S be the set of all states for the system. A constraint will partition S into two subsets $S = S' \cup S''$, whereon S' the constraint (or the relations) is satisfied, and on S'' it is not. Of course, the function of the constraint is to restrict our attention to states belonging to S'; i.e., to states to which the system has access.

We now consider the group Aut(S) of all automorphisms of S onto S. Let G be a subgroup of Aut(S) which leaves the constraint invariant, by which we mean that the action of G on S do not mix states of S' with states of S''; i.e., the subsets S' and S'' are stable under G. This can be formulated in the language of G-orbits in S: a G-orbit in S is a set $\{gs|g \in G\}$. Clearly, each $s \in S$ belongs to exactly one orbit. The invariance of a constraint under G can now be defined as follows: a constraint C, which is satisfied on the set $S' \subset S$, is invariant under G, if and only if S' is a union of G-orbits in S. On any variable $x: S \to R$, the group G induces the following transformation

$$x'(s) = (gx)(s) = x(gs). \tag{4}$$

The mapping $I: S \to R$ is said to be invariant under G (or an invariant), if $I(gs) = I(s)$ for $g \in G$, $s \in S$, that is if I is constant on each G-orbit in S. A set of invariants $\{I_j|j = 1, 2, \ldots, m\}$ is said to be complete if it is sufficient to label the G-orbits in S, that is if the set of values $\{I_j(s)\}$ determines unambiguously the (unique) orbit to which s belongs and this for every $s \in S$.

If a constraint C is invariant under the group G, then it is possible to express this constraint in terms of a complete set of invariants. This can be seen as follows: let S' be the subset of S on which C is satisfied. Then S' is a union of G-orbits. Now, the values of a complete set of invariants determine the orbits, and it follows that, for a given s, the values of $I_j(s)$, $j = 1, 2, \ldots, m$ are sufficient to determine whether s satisfies the constraint or not. This means that, if a G-invariant constraint is given in terms of a set of variables $\{x_i\}$, this constraint can be expressed in terms of a complete set of G-invariants on S. The constraint expressed in terms of invariants partitions the set of all G-orbits in two subsets. The advantage of formulating the constraint in terms of invariants lies mainly in the hope that the form of the constraint will look simpler in terms of invariants. The number of invariants will usually be smaller than the number of original variables.

It often happens that invariants are constructed from a set of variables $\{x_i\}$ which, it will be assumed here, completely describe the state of the system. That is, we have invariants of the form

$$I_j = I_j(x_1, x_2, \ldots, x_n) = I_j(x_1', x_2', \ldots, x_n'), \tag{5}$$

where $\{x_i'\} = g\{x_i\}$, and $j = 1, 2, \ldots, m$. We now consider a change of variables from $\{x_i\}$ to an equivalent set $\{I_j, y_k | j = 1, 2, \ldots, m; k = 1, 2, \ldots, p\}$, where the I_j are invariant. The new set is equivalent in the sense that there is a one-one relation between the two sets of variables. The set $\{I_j, y_k\}$ is chosen to be maximal in the sense that we cannot form, from the y_k's, invariants which would be independent of the I_j's. This new set of variables is useful because any G-invariant constraint on $\{x_i\}$ is translated into a constraint involving only the I_j; i.e., it is independent of the y_k's. How these invariants are formed depends on the specific group under which the constraint is invariant, and also on the specific way that the group acts on the variables $\{x_i\}$. In dimensional or similarity analysis, the groups are abelian Lie groups and they act in a simple way on the variables so that the invariants are easy to construct.

4. The Allometric Equations

Various authors (e.g., Günther, 1975; Stahl, 1963), using the allometric equation of Huxley (1932), have correlated a vast amount of biometrical data in comparative physiometry and morphometry. This allometric equation takes the form

$$x = aW^b, \tag{6}$$

where W represents the weight, x is a variable of anatomical or physiological interest, a and b are constants for a given series of animals belonging to the same group. The constant a, of course, is nothing but the value of x for unit weight. These authors obtain the value of b from dimensional analysis, after making a series of dimensional assumptions. Our objective at this time is not to look critically into the agreement of this equation with the data available, but rather to state what postulates must be made in order to obtain such a representation, and also to show what would be the resulting representation if some of these postulates were relaxed. First, it must be realized that the weight is used for convenience and plays no fundamental role. For suppose two variables x_1 and x_2 are given in allometric form as a function of weight

$$\begin{aligned} x_1 &= a_1 W^{b_1} \\ x_2 &= a_2 W^{b_2}. \end{aligned} \tag{7}$$

Then clearly

$$x_1 = ax_2^b, \qquad (8)$$

where $b = b_1/b_2$ and $a = a_1 a_2^{-b_1/b_2}$, so that x_1 is expressed in allometric form in terms of x_2. Also, we remark that, if the allometric representation were strictly correct, then one anatomical or physiological variable (e.g., the weight) would be sufficient to determine all the others, or at least those subject to allometric representation.

The system that we have to consider here is a series of animals being compared, and a particular state s represents one given animal in the series. Let x_1 and x_2 be two anatomical or physiological variables which belong to the animals in the series, and between which it is hoped to obtain an allometric relation as in equation (8). Of course, the first postulate which must be made if such a relation is to hold is that *there is a one-one relation between* x_1 *and* x_2. In other words, a necessary condition for the existence of an allometric relation between two variables x_1 and x_2 pertaining to a group of animals is that *there exists a constraint C between* x_1 *and* x_2 *so strong that each variable is a function of the other.* States (or animals) must satisfy this constraint to belong to the series of animals being compared. We now suppose that such a constraint exists. In order to obtain the allometric relation (8), it is now sufficient to make the following second postulate: *the constraint C is invariant under a continuous one-parameter group of linear homogeneous transformations G.* More explicitly: if x_1 and x_2 satisfy the constraint, then so do x_1' and x_2', where

$$x_1' = \lambda^{\alpha_1} x_1, \qquad x_2' = \lambda^{\alpha_2} x_2 \qquad (\lambda > 0). \qquad (9)$$

The group G, represented by its parameter λ, acts on the states $s \in S$ (it is implicitly assumed here that there is a continuum of animals in the series), and induces on the variables x_1, x_2 the transformations (9). If the constraint C is invariant, it can be expressed in terms of G-invariants formed from x_1 and x_2. Here, there is only one (independent) invariant and it can be taken as

$$I(x_1, x_2) = x_1^{\alpha_2} x_2^{-\alpha_1},$$

for then $I(x_1', x_2') = I(x_1, x_2)$. Thus $I(x_1, x_2)$ being a constant for the whole series of animals, we obtain

$$x_1 = ax_2^b,$$

where $b = \alpha_1/\alpha_2$.

In the literature, the first postulate is usually implicit, which is understandable because it is somewhat trivial. However, it must be realized that it is a very strong assumption indeed. As for the second postulate, we must enquire about the nature of this one-parameter group of transformations and how it arises. First consider the simple derivation (von Bertalanffy, 1968) of the

Huxley allometric equation in a growth process, where the weight of an organ w is related to the weight W of the whole animal at different times in a growth process. It is assumed that the organ grows in such a way that the relative growth rate dw/wdt is constant, and similarly for the whole body, $dW/Wdt = $ constant. Then one deduces

$$w = w_0\, e^{At}$$

$$W = W_0\, e^{Bt}$$

from which it follows that

$$w = aW^b,$$

where $b = A/B$ and $a = w_0/W_0^{A/B}$. Clearly, in this case, the one-parameter group can be identified with time translation (with $\lambda = e^t$); i.e., it is given by the assumed dynamics of the growth process.

Let us now look at the use of allometric equations in comparative physiometry and morphometry. The group of transformation, in this case, arises from a similarity type of argument. First, it is assumed that the group acts in the same way on all variables representing linear spacial dimensions; this is a simple geometric similarity, and means that the animals belonging to a given series have the same shape. Second, when needed, the density is assumed invariant. And finally, it is sometimes necessary to assume that other quantities, such as velocity or acceleration are invariant under the group. This can be understood by considering three different cases. In the first case, the units of x_1 and x_2 are powers α_1, α_2 of a common basic unit, for instance, x_1 could be a surface and x_2 a volume. Then, it is sufficient to assume that x_1 and x_2 transform according to equation (9). In the second case, there are two independent units, and, if they were transformed independently, a two-parameter group of transformations would be obtained. In order to reduce the number of essential parameters to one only, it must be assumed that a certain quantity is invariant under the group, which is equivalent to introducing another constraint. For instance, if x_1 and x_2 involve units of mass and length in such a way that they have no common multiple (i.e., they are independent dimensionally), then imposing the invariance of density will force each mass to transform in the same way as a volume; i.e., length cubed. Finally, if there are three independent units, such as mass, length and time, then it is necessary to impose invariance of two quantities in order to reduce the number of essential parameters to one. Similarly for more than three independent units. Obviously, the allometric representation can only make sense if the invariance assumptions are valid, and if the invariants being used to reduce the number of essential parameters are relevant to the variables concerned x_1 and x_2.

5. The Generalized Allometric Equation

Suppose we now relax the (very strong) first postulate; i.e., suppose that instead of two, there are now three variables x_1, x_2, x_3, which are linked by a constraint C. The constraint is assumed to be so strong that any one of the three variables is a function of the other two. Let the series of animals being compared (or the constraint) be invariant under the two-parameter abelian group of linear homogeneous transformations G, with

$$x_i' = \lambda^{\alpha_i}\sigma^{\beta_i}x_i, \qquad i = 1, 2, 3, \tag{10}$$

where λ and σ are the two essential parameters $(\lambda, \sigma > 0)$. Then the constraint can be expressed in terms of the G-invariant formed from x_1, x_2, x_3, namely

$$I(x_1, x_2, x_3) = x_1^{\delta_1}x_2^{\delta_2}x_3^{\delta_3}, \tag{11}$$

where $\delta = \alpha \times \beta$. It is easily verified that $I(x_1', x_2', x_3') = I(x_1, x_2, x_3)$. We then deduce from equation (11)

$$x_1 = ax_2^b x_3^d, \tag{12}$$

where the three constants a, b, d are given by $a = I^{1/\delta_1}$, $b = -\delta_2/\delta_1$, $d = -\delta_3/\delta_1$. This two-parameter group of transformations can be considered as arising from geometric, dynamic, or biological similarity in the same way as the one-parameter group considered in the previous section. However, here since there are two parameters, this gives us more freedom, and variables which had to be invariant before may now vary under this larger group. This generalized allometric equation could be used, for instance, in comparing two different series of animals, which were compared separately with the usual allometric equation. This could be useful in taxonomy. Of course, one could go on to more than three variables, but before going into such a program of classification, it is essential to have a very close look at the available data. The allometric representations may just be a very crude approximation, without too much deep significance. However, if there are reasons to take such representations seriously, then it is important to find out exactly what invariants are involved and what role they play. In fact, a more general problem in biology consists in looking for invariants and identifying their meaning. We believe that group theory is one of the essential tools necessary to carry out such a program.

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