

*Quantitative Methods  
in the Study  
of Animal Behavior*

Edited by

BRIAN A. HAZLETT

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*Division of Biological Sciences  
University of Michigan  
Ann Arbor, Michigan*



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## *Preface*

Most of the chapters in this volume resulted from a symposium, "Quantitative Methods in Behavior," held November 13, 1976, as part of the midwest regional meeting of the Animal Behavior Society. (The methods discussed by Neal Oden in his chapter had not been fully developed at the time of the conference, but are an important addition to this volume and so his paper was included.) The meetings were held at the University of Illinois Chicago Circle campus in the Chicago Circle Center. Doctors Gary Hyatt and Robert B. Willey of the Chicago Circle campus were co-hosts for the meetings and they, along with the many graduate students and other faculty of U.I.C.C., made the meetings a profitable and pleasurable experience for all of us. Our thanks also to the University of Illinois Foundation for the funds that supported the meetings and provided honoraria for the speakers at the symposia.

When Gary Hyatt originally contacted me about chairing a symposium on quantitative methods in the study of animal behavior I was ambivalent. There was no question in my mind that such a gathering would be a good idea and one that was needed, since mathematical methods are used and misused with increasing frequency in the study of behavior. As an extreme empiricist, I have been a reasonably successful parasite of mathematicians but one might expect the chairman of a meeting to be closer to being an expert in a field than just knowing some experts. However, hopefully my level of mathematical expertise is not far below average for ethologists and this may facilitate communication with the intended audience.

While each of the papers in this collection illustrates and comments on the uses of certain mathematical approaches in studying behavior, it should be pointed out that there are several general ways in which mathematics can be an aid in understanding behavior. The most frequent uses of mathematics are attempts to deal with the variability of behaviors by statistical approaches, that is, comparisons of distributions in order to make statements on the probability that the distributions are different from one another or from some hypothesized distribution. The use of mathematics in dealing with behavioral variability allows us to consider all the data we gather. The strategy used in early ethological studies was to deduce the "main patterns" and unconsciously dismiss the variability. This of course was necessary both because of a lack of technical or mathematical tools and because the formulation of ethological principles was based upon the deduction of the "main patterns." With more statistical approaches and the availability of computers, ethologists no longer need to throw out any data—we can look for "main patterns" and the variability around these patterns. To put it another way, with appropriate mathemat-

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QUANTITATIVE STUDIES OF THREE AREAS OF  
CLASSICAL ETHOLOGY: SOCIAL DOMINANCE,  
BEHAVIORAL TAXONOMY, AND BEHAVIORAL VARIABILITY

Marc Bekoff

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*Abstract: Among the areas of classical ethology that still constitute a large portion of current research in behavioral biology are social dominance, the use of behavioral characters in the assessment of taxonomic relationships, and behavioral variability and stereotypy ("fixed" action patterns). Unfortunately, until recently, there have been very few quantitative analyses of these classical areas. In this chapter, I shall consider some ways in which these three topics have been analyzed quantitatively. Specifically, I shall discuss (1) the application of Landau's index to the measurement of social dominance hierarchies, (2) the use of procedures that are commonly employed in numerical taxonomy to assess taxonomic relationships based on non-behavioral characters, and how some of these have recently been applied to behavioral taxonomies, and (3) the way in which behavioral variability and/or stereotypy have been measured, primarily by use of the coefficient of variation.*

*Modern ethology has advanced to a level at which quantitative analyses must be forthcoming in these and other areas of research. Yet, the "realities" of any given behavioral system, organism, and research problem must not be obscured by using techniques for which the underlying assumptions cannot be met. That is, there must be congruence between the problem at hand and the analytical method that is employed.*

...biology is a system that proceeds from biochemistry to the associated subjects of neurophysiology and genetics. All else, as they used to say of the non-physical sciences, is stamp-collecting (de Solla Price, 1960).

All too often ethologists paint a vivid picture of the

behavioral element of an animal without giving a single figure as to its probability of occurrence or duration; psychologists present meticulous quantified results subjected to analyses of variance while giving only the scantiest indications of how the animal behaves (Hutt and Hutt, 1970).

In my own surroundings, I notice that those who are most positive in the matter of (these) difficult questions are those who have seen the least (Fabre, 1916).

In few fields of biological study is it so easy to obtain results and so difficult to explain them as it is in the study of animal behavior (Simpson, 1969).

But we must be wise and careful in applying the theorems and results of communication theory, which are exact for a mathematical ergodic source, to actual communication problems (Pierce, 1961).

## INTRODUCTION

In this paper, I shall consider the following three topics: social dominance, behavioral taxonomy, and behavioral variability (or stereotypy). I do not plan to review each of these fields other than to give a brief background so that the quantitative techniques that are discussed will be understood with respect to the behavior under consideration. For discussions of sampling methods the reader is referred to Altmann (1974) and Dunbar (1976). My purposes are specifically to discuss a variety of ways in which ethologists may analyze some "classical" concepts and to present some recent examples that have approached the above classical concepts using one or another quantitative techniques. I have provided a rather lengthy reference section to allow the reader to see how various analytical procedures have been applied to these behavioral problems among a wide variety of animal species.

In the behavioral sciences, it usually is the case that qualitative descriptions of behavioral phenotypes give rise to quantitative analyses. Certainly, this is a healthy trend. However, quantitative "overkill" may be damaging, and the temptation to make the leap from the initial compilation of descriptive information to the use of highly sophisticated mathematical analyses requires careful consideration. We should choose an analytical procedure with the same degree of care that we exercise when we choose a piece of equipment to increase our powers of observation. With regard to quantitative procedures, we must be very careful since there are often many underlying assumptions that must be met and in many cases the ability of animals to behave in a manner that



would allow the assumptions to be supported is at best tenuous. This is particularly true when sequential variability is the problem under study (see below). As Slater (1973) has stressed, it is a simple matter -- the less valid the assumptions, the more unrealistic are the results. The degree to which researchers choose to overlook certain guidelines for the use of various methods, and the effect of these "oversights" on the validity of their results and conclusions, is difficult to assess (Siegel, 1956). Although "slight" deviations on meeting assumptions may not have radical effects, there seems to be no general agreement as to what constitutes a "slight" deviation (Siegel, 1956, p. 20).

In light of the current interest in quantitative ethology, it is refreshing to see that some researchers (many of whom have equal expertise in the behavioral sciences as well as in mathematics) are professing the use of extreme restraint in the application of various analytical procedures (e.g., discussion of Cane, 1959; Chatfield and Lemon, 1970; Simpson, 1973; Slater, 1973). Just because something has been done before does not mean that it is correct, and the wide availability of "canned" computer programs should not be the factor determining how a problem(s) should be analyzed or in ultimately directing further research. The suggestion that seems to be the most appropriate is, simply, fit the method of analysis to the animal, not the animal to the method. Do not make the animal something that it is not (e.g., a stationary beast; see below); do not "short-circuit" evolution! Lest I lead you to believe that I am going to conclude that quantification of ethological data is impossible and that behavioral research and stamp-collecting are synonymous (an insult to serious philatelists), let me now consider how the problems of social dominance, behavioral taxonomy, and behavioral variability have been analyzed or can be studied using standard quantitative techniques for which the underlying assumptions can be satisfied in many ethological endeavors. I have chosen these three topics because there is a good deal of current research being conducted within these areas, they are truly "classical" concepts, and because of my familiarity with them.

## I. SOCIAL DOMINANCE

The concept of social dominance, or status hierarchies, has received a lot of attention ever since Schjelderup-Ebbe (1922, translated in Schein, 1975) published his work on the social psychology of domestic chickens in which he described the social organization, or pecking orders, of these birds. Within the last decade or so, detailed analyses of "dominance"

and, in particular, the sweeping generalizations that accompany the idea, have been called into question by a number of investigators (e.g., Rowell, 1966, 1974; Brantas, 1968; Gartlan, 1968; Bernstein, 1970; van Kreveld, 1970; Watson and Moss, 1970; Drew, 1973; Kummer, 1973; Spigel and Fraser, 1974; Clutton-Brock, Greenwood, and Powell, 1976; Hanby, 1976; Marler, 1976). The word itself is used in a wide variety of contexts (Gartlan, 1964, 1968; Rowell, 1974), with definitions including information about competitive abilities (e.g., priority of access) and traits that are related to an individual's status, and even going as far as using the terms "aggressive" and "dominant" as synonyms. Aggressive individuals are not necessarily the most dominant in a group, aggression does not necessarily lead to the establishment of dominance relations, and the formation of a dominance hierarchy does not necessarily lead to a reduction in aggression (e.g., Wolfe, 1966; Gartlan, 1968; Rowell, 1974; Marler, 1976; Potter, Wensch, and Johnston, 1976). Furthermore, a number of studies have indicated that there is often no correlation between different behaviors that are thought to be correlated with dominance. That is, social rankings based on different criteria frequently do not correlate well with one another (Gartlan, 1968; van Kreveld, 1970; Bernstein, 1970; Drew, 1973; Rowell, 1974; Syme, 1974; Lockwood, 1976; but also see Richards, 1974 and Clutton-Brock and Harvey, 1976 for alternative views). Suffice it to say, the concept of dominance still is in need of refinement.

Although global definitions of dominance are difficult to come by, it is a fact that in a wide variety of animal societies, individuals comprising a group can often be ranked on a dominance-subordinate scale and specific behavior patterns and physiological states can be associated with relative ranks among the individuals (e.g., priority of access to estrous females (see DeFries and McClearn, 1970; LeBoeuf, 1974; Hausfater, 1975; and Hanby, 1976 for discussions); the control of spatial relationships (McBride, 1964; Watson and Moss, 1970; Myers and Krebs, 1971, 1974; Bekoff, 1977a,b); activity (Dunbar and Crook, 1975); rate of ultrasound vocalization (Nyby, Dizinno, and Whitney, 1976) and electric organ discharge (Westby and Box, 1970; Bell, Myers, and Russell, 1974); altered maturation (Sohn, 1977); changes in heart rate and other physiological parameters (Candland, et al., 1969, 1970, 1973; Cherkovich and Tatoyan, 1973; Manague, Leshner, and Candland, 1975)). In this section, I shall briefly discuss one particular way in which dominance hierarchies can be "measured" with respect to their degree of linearity. Landau's (1951a,b, 1953, 1965; reviewed by Chase, 1974) method will be considered since it is applicable to studies of social dominance in a very general way. Since the

concept of dominance and all of its ramifications are still very much a part of modern day behavioral science, it is essential that more accurate descriptions be forthcoming.

### A. Types of Hierarchies

There are three major types of social hierarchies. The first is a despotism in which one individual dominates all other members of his or her social group, with no rank distinctions among the subordinates (Wilson, 1975). This has been observed in iguanid lizards living under conditions of unnaturally high densities (Carpenter, 1971, cited in Wilson, 1975). Most usually, hierarchies are referred to as being linear or non-linear. In the first case, an individual (usually called the alpha animal) dominates all other group members, another individual (beta) dominates all group members but alpha, and so on. In order for a linear hierarchy to exist, two conditions have to be fulfilled: (1) the dominance relations must be asymmetric, that is, for every paired interaction, one individual can be classified as being dominant and (2) dominance relations must be transitive (Figure 1 A,C; see Harary, Norman, and Cartwright, 1965, Chapter 11; and Moon, 1968, pp. 14ff), that is for any three animals if 1 dominates 2 and 2 dominates 3, then 1 also dominates 3. Non-linear hierarchies, on the other hand, are those in which there is at least one or more intransitive triads (Figure 1 B,D; Chase, 1974). Chase (person.

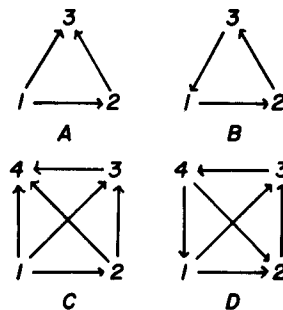


Fig. 1. Examples of linear (A,C) and non-linear (B,D) social hierarchies. The arrow means "dominant over". Note that in A and C, there are no intransitive triads. However, in D there is an intransitive triad among individuals 1, 3, and 4. That is, 1 dominates 3, 3 dominates 4, but 4 dominates 1. There is also an intransitive triad among individuals 2, 3, and 4 (adapted from van Kreveld, 1970).

comm.) further points out that there must be completeness (i.e., there must be a relationship between all pairs of animals).

In both linear and non-linear hierarchies, it is possible to have different types of "pecking" relationships (assertions of dominance) between pairs of individuals. If assertions of dominance go only in one direction, the term "peck-right" is frequently used as a shorthand description. This type of relationship can exist in both linear (pecking only goes "down" the hierarchy) and non-linear hierarchies (e.g., an intransitive triad). If, however, the situation is encountered in which two animals "peck" at one another in unequal amounts so that one can nonetheless be classified as being dominant, a "peck-dominance" relationship exists. Peck-dominance hierarchies can also be linear or non-linear (see Table 1).

#### B. The Application of Landau's Method

Landau developed a method by which the degree of linearity of a social hierarchy could be measured and standardized for intergroup comparisons. An index of linearity,  $h$ , is calculated using the following formula

$$h = \frac{12}{3-n} \sum_{a=1}^n \{v_a - (n-1)/2\}^2$$

where  $n$  = the number of animals in the group and  $v_a$  = the number of individuals that an individual dominates. The term  $12/(n^3-n)$  normalizes  $h$  so that values range from 0 to 1. When  $h = 1$ , the hierarchy under study is linear and the variance of  $v_a$  is at its maximum. When  $h = 0$ , each animal dominates an equal number of group members and  $v_a = 0$ . An  $h$  value of 0.9 or greater may be taken to mean that the hierarchy is "strong", that is, it is approaching linearity (Chase, 1974). Although Landau's method does not generate a statistic from which a level of significance ( $p$ -value) can be calculated to determine whether or not an observed hierarchy differs from that which would be expected by chance, other workers have developed a statistic (that generates a chi-square value) that is very similar to Landau's in form (David, 1959). However, the statistical measure of linearity only applies when group sizes are greater than 6. For the moment, at least, using  $h \geq 0.9$  as a "cut-off" for separating strong, nearly linear hierarchies, from non-linear hierarchies seems appropriate (see Chase, 1974).

Although Landau's method for assessing the degree of

linearity of a social hierarchy(ies) has been in the literature for approximately 25 years, it has been used only rarely (Chase, 1974; Lockwood, 1976). Chase (1974) has applied the technique to data collected on the formation and stability of pecking orders in birds, however, there do not appear to be any published reports for mammals. I would like to consider two examples in which the application of Landau's formula has been useful. The first set of data comes from ontogenetic studies on infant coyotes (*Canis latrans*) and Eastern coyotes (*C. l.* var; see section on Behavioral Taxonomy for the rationale behind separating these animals from one another). The second example stems from the work of Lockwood (1976) on pack structure in captive wolves (*C. lupus*).

#### C. Hierarchy Formation in Coyotes

Coyotes and Eastern coyotes engage in rank-related agonistic encounters during the 3rd to 5th weeks of life (Bekoff, 1974, 1977a, In Press<sub>a</sub>, Bekoff, Hill, and Mitton, 1975). Intense fights are extremely common and clear-cut dominant-subordinate relationships are established as a result of these early interactions. Data relevant to hierarchy formation are presented in Table 1. Full litters of animals were observed and patterns of interaction among all littermates were studied. In all three litters, a perfect linear hierarchy was established ( $h = 1$ ). Note that there is also a direct relationship between the size of the litters and the length of time that it took to attain linearity. For example, in coyote litter 2 ( $n = 4$ ), after only 3 days of fighting a linear dominance hierarchy was established. It should also be stressed that a linear hierarchy may remain linear in form even if some animals shift in rank. In coyote litter 1, for example, linearity was maintained from the second to the ninth month of life although there were some shifts in relative rank among the individuals during the first 90 days. From days 50-90,  $h = 1$ , with the exception of those days on which a reversal of dominance occurred, and "acceptance" of subordination required a series of agonistic encounters. For further details concerning the development of social relationships in canids, see Bekoff (1974, 1977a, In Press<sub>b</sub>). In particular, the necessity of my determining social rank for individual coyotes comprising a litter and overall hierarchical structure is amplified in Bekoff (In Press<sub>a</sub>).

#### D. Hierarchies in Wolf Packs

The only other mammalian species for which I could find

TABLE 1

*Hierarchy formation in infant canids analyzed using Landau's index (h). All of the hierarchies are examples of peck dominance hierarchies. One animal was assumed to be dominant over another individual if it "won" over 70% of the agonistic encounters in which there was a clear outcome. Among these young canids, it is not difficult to determine "winners" and "losers".*

	Days of Age	Number of Fights	h
Coyote litter 1* (n=6)	25-31	220	.77
	32-35	59	.88
	36-50	50	1.00
Coyote litter 2 (n=4)	23-25	40	1.00
	26-29	38	1.00
	30-35	36	1.00
Eastern Coyotes (n=5)	21-25	65	0
	26-29	178	.80
	30-35	137	1.00

\* Coyote litter 1 was mother-reared and the other two litters were hand-reared

data concerning a measurement of linearity for observed hierarchies is the wolf, *C. lupus* (Lockwood, 1976). The results of this study are presented in Table 2. The interesting aspect of this analysis, and the reason for its inclusion, is that Lockwood analyzed not only dominance hierarchies but also subordinate hierarchies as well. By looking at both sides of the coin in dominant-subordinate relationships, the importance of the subordinate individual to the formation and maintenance of social hierarchies is stressed (see further discussions of this idea by Rowell, 1966, 1974; Lockwood, 1976). Note that Lockwood found no "strong" dominance hierarchies and also that the subordinate hierarchy is stronger in one-half of the cases, and even is linear in one instance.

The above examples demonstrate that Landau's index of linearity is applicable and useful in the analysis of social relationships in groups of animals. Calculation of "h" is straightforward and the measure can be used in studies in which different groups are compared to one another. That is, a value of h is a standard that means the same thing for different groups. It simply is an indication of the degree of

TABLE 2

*The Linearity of Dominance and Subordinate Hierarchies in Captive Wolves (from Lockwood, 1976)*

Wolf Pack	$h_{\text{dominant}}$	$h_{\text{subordinate}}$
350-72 (n=5)	.10	.10
350-73 (n=4)	.30	1.00
350-74 (n=4)	.30	.30
OM-73 (n=4)	.50	.30
Big Pack (n=7)	.69	.43
Satan (n=5)	.20	.25
Release (n=5)	.20	.80
Mix-72 (n=6)	.65	.09
Mix-74 (n=6)	.17	.31
Jinx (n=6)	.54	.57

linearity of a social hierarchy. Lastly, Landau's formula can be used to analyze dominance relations that result from interactions between and among individuals comprising whole animal groups. This is important, since dominance hierarchies that are based on the results of experimentally controlled, paired, round-robin interactions frequently do not represent what actually is happening in the real world of social groups of animals (Chase, 1974).

## II. BEHAVIORAL TAXONOMY

Since the turn of the century, it has been recognized that behavioral characters can be used to assess and/or establish taxonomic relationships. This idea was laid out clearly in the work of Whitman and Heinroth and extended by Lorenz and his students. Implied in this belief are the notions that behavior, like any other character, evolves, and accordingly, that the "structure" of behavior has a traceable phylogeny. Precisely tracing the phylogenetic history of a behavioral phenotype is difficult or impossible since behavior does not fossilize. However, the use of extant organisms has provided some interesting and important data concerning the use of behavior in the assessment of taxonomic affinities (for review see Lorenz, 1941; Marler, 1957; Mayr, 1958; Cullen, 1959;

Atz, 1970; Eibl-Eibesfeldt, 1975).

There have been a considerable number of studies in which a wide variety of behavioral characters have been used to analyze taxonomic relationships (Table 3). Behavioral taxonomies have given support to taxonomic schemes based on non-behavioral characters or have been useful in clarifying discrepancies. Nonetheless, among the wide variety of studies that have been conducted, extremely few have had a strong quantitative base. I would like to consider a few examples that exemplify different approaches to the problem(s).

#### A. "Yes"- "No" Approaches

Earliest studies of behavioral taxonomy used the yes-no approach. If an animal performed a certain behavior pattern, a "yes" was recorded and conversely, if the same pattern was not observed for a given species, then it received a "no". The first major attempt to apply this checklist method to a group of closely related animals was performed by Lorenz (1941; translated in 1971). Lorenz studied 17 species and three genera of ducks and geese, Family Anatidae. The results of his work are summarized in his now classic diagram (Figure 2) in which the different species are linked together by shared characters. Lorenz's "anatidogram" (G. Barlow, pers. comm.) is useful in that evolutionary relationships are clearly pictured and the relationship between behavioral as well as non-behavioral characters is presented.

Another application of the yes-no method is presented by Dewsbury (1972). Dewsbury studied the copulatory patterns of male mammals and asked a series of yes-no questions for four major aspects of male reproductive behavior (Figure 3). Different species could then be classified into one of 16 patterns. Using this approach, Dewsbury (see his Table 1) found that closely related animals tended to fall within the same pattern, and taxonomic affinities were detected.

Although yes-no questions are useful in studying taxonomic relationships among animal groups, more rigorous quantitative procedures are available for behavioral taxonomic endeavors, particularly when the differences between or among groups are quantitative and not simply qualitative. These techniques are reviewed in Sneath and Sokal (1973) and have, to date, been used almost exclusively to assess taxonomic relationships using non-behavioral characters. The application of many of these procedures is entirely appropriate for behavioral studies.



TABLE 3

*Some Studies in Which Behavioral Characters  
Were Used in the Analysis of Taxonomic Relationships*

Authorities	Animal Group (and Criterion(a))
Heinroth (1910); Whitman (1919)	Drinking by pigeons
Petrunkévitch (1926)	Spiders: analyses of "instincts"
Lorenz (1941, 1958)	Anatidae (ducks and geese); general behavior patterns
Delacour and Mayr (1945)	Anatidae
Spieth (1952)	<u>Drosophila</u> courtship
Barber (1953)	Fireflies of the genus <u>Photuris</u> ; flash characteristics
Schmidt (1955)	Termite nests
Stokes (1955)	Gall midges; host plant choices
Andrew (1956a)	Passerine birds; flight intention movements
Sibley (1957)	Various birds
Simmons (1957)	Head-scratching by birds
Tinbergen (1959, 1960)	Gull displays
Dilger (1960, 1962)	African parrots of genus <u>Agapornis</u>
Johnsgard (1961)	Anatidae
Kaston (1964)	Spider webs
McKinney (1965)	Anatidae; comfort movements
van Tets (1965)	Pelican displays
Salthe (1967)	Salamandridae courtship
Littlejohn and Oldham (1968)	<u>Rana pipiens</u> mating calls
Lomax (1968); Lomax with Berkowitz (1972)	Human song and dance patterns
Struhsaker (1970)	<u>Cercopithecus</u> monkeys; vocalizations
Echelle, Echelle, and Fitch (1971)	Anolis; aggressive displays
Brown and Brown (1972)	<u>Rana pipiens</u> vocalizations
Cattell, Bolz, and Korth (1973)	Domestic dogs
Rovner (1973)	Wolf spiders; copulatory patterns
Berg (1974)	Strombid gastropods; feeding, locomotion, righting, predator escape
Michener (1974)	Bee sociality
Bekoff, Hill, and Mitton (1975)	Canids; patterns of social development
Dixon, Scruton, and Herbert (1975)	Talapoín monkeys (and other Old World Catarrhines); grooming invitations, facial expressions
Dunford and Davis (1975)	Chipmunk vocalizations
Heymer (1975)	Dragonflies
Vierke (1975)	Fish (Belontiidae); reproductive and parental behavior