Behavior Genetics, Vol. 6, No. 4, 1976

Issues in the Genetics of Social Behavior

John L. Fuller[1,3] and Martin E. Hahn[2]

Received 22 Aug. 1975

The genetics of social behavior presents special difficulties because the phenotype is the product of an interaction between two or more individuals. Social interactions are of two kinds: (1) cooperative, in which the probabilities of transmission of the genes of all participants are similarly affected by the outcome, and (2) agonistic, in which the probabilities for the participants are affected in opposite directions. The latter are of particular interest for evolutionary theory. Three major types of designs for measuring social behavior in genetic experiments are available: (1) homogeneous sets, (2) standard tester, and (3) tester panel representing a reference population. The advantages and limitations of each method are discussed. Important areas for future development include the relationship of genetic and experiential factors in early life to social status as an adult and the extension of the genetic analysis of social behavior to natural populations.

KEY WORDS: social behavior; genetic analysis; evolution; developmental genetics.

INTRODUCTION

Social behavior has not been overlooked by behavior geneticists. An extensive literature deals with the genetics of courtship and mating in *Drosophila* (Parsons, 1967; Manning, 1963; Ayala, 1972). Examples from vertebrates include Scott's research on fighting in mice (1966) and McGill's (1970) observations on sexual behavior in the same species. In domestic fowl,

Supported by Grant GB 24827 from the National Science Foundation and Grants MH 22005 and MH 13058 from the National Institute of Mental Health.

[1] State University of New York at Binghamton, Binghamton, New York.
[2] William Paterson College of New Jersey, Wayne, New Jersey.
[3] Reprint requests should be directed to Dr. John L. Fuller, Department of Psychology, State University of New York at Binghamton, Binghamton, New York 13901.

genetic factors have been shown to influence social status (Craig *et al.*, 1965) and male sexual behavior (Wood-Gush, 1958). Scott and Fuller (1965) emphasized social behavior in their behavior genetic analysis of the domestic dog.

However, if one compares the volume of such studies with the amount published on individual traits, emotionality, learning, activity, alcohol preference, audiogenic seizure susceptibility, and the like, it is clear that the genetics of social behavior has been relatively neglected. Why is this so? It is obvious that success in competitive encounters, and in cooperative ones as well, is of primary importance in assuring the transmission of an animal's genes to the next generation.

There are two major reasons for this relative neglect. In the first place, social behavior, by definition, involves the interaction of at least two individuals. The unit observed is a group and the outcome of the interaction cannot be attributed solely to either the genetic or the experiential history of any one of the participants. Yet geneticists must rely on a behavioral phenotype (psychophene) to give evidence for a particular genotype. Clearly the psychophene in a social encounter usually is more variable than one measured by a test procedure which is completely under the experimenter's control. Second, there are reasons to suspect that genetic contributions to variability of social behavior in natural populations are small. Christian (1970) lists many nongenetic factors which contribute to social status in rodents. Falconer (1960, p. 167) states that the heritabilities of traits closely related to Darwinian fitness tend to be low in comparison with those of apparently less evolutionary significance.

With increased interest among behavior geneticists in evolutionary problems, the situation is changing. There are calls to observe "species-specific" behavior (Thiessen, 1972) and to develop the field of "population behavior genetics" (Bruell, 1970; Selander and Yang, 1970). The purpose of this article is to indicate some of the methodological problems in social behavior genetics, to survey several commonly used designs, and to suggest new approaches. Because of limitations of space and personal experience, we shall concentrate on work with vertebrates. Our primary concern is with methods of phenotypic measurement in the laboratory and their genetic implications.

CLASSIFICATION OF SOCIAL BEHAVIORS

Social behavior is an interaction of two or more organisms, usually of the same species, involving a mutual exchange of stimuli which regulate the onset, continuation, and termination of a sequence of related behaviors. Experimenters in the genetics of social behavior have generally manipulated

the genotypic composition of groups and related these to a group phenotype. Social behaviors have been divided into several categories (Scott, 1958). Those of most interest to geneticists are agonistic, sexual, caregiving, care-soliciting, and allelomimetic behaviors. Although many social interactions actually have characteristics of more than a single category, the scheme is useful for describing the varieties of behavior observed.

The genetic consequences of social transactions are of two kinds. Sexual, caretaking, and care-soliciting contacts, if successful, increase or, if nonsuccessful, decrease the probability of transmission of the genes of all participants. In contrast, agonistic transactions, if carried to a decision, alter the transmission of genes by either excluding some participants from mating or limiting their choice of mates.

It appears that these two forms of social behavior have evolved in parallel. Birds, mammals, and among insects the Hymenoptera are preeminent in care of young and also in dominance hierarchies, territoriality, and other manifestations of agonistic interactions. Although superficially paradoxical, the association may be a necessary one. The biological mission of a species is survival of its gene pool, and cooperative social transactions favor this end. It is also desirable to have population density kept within limits set by the food supply, number of suitable nesting sites, and other specific needs. In most species, the proximate means of population control is not starvation, however, but behavioral responses which result in dispersal of excess individuals, reducing population density to fit the average long-term carrying capacity of the region (Christian, 1961; Wynne-Edwards, 1962).

Obviously genes favoring the success of cooperative social transactions will favor gene survival and population growth. If the probability of agonistic social transactions increases as optimal density is surpassed, the risk of exhausting resources is decreased. The negative feedback role of agonistic encounters need not be exerted alone through dispersal of low-ranking individuals; there may be effects on reproductive and caretaking functions—in our terms, a reduction in the effectiveness of cooperative social interactions (Calhoun, 1962). Eventually such feedback systems may have effects outside the local population. If one invokes the concept of group selection (Wynne-Edwards, 1962), it is clear that the benefits obtained by improved cooperative interactions within a group can be retained only at the cost of less efficiently reproducing neighboring groups. The scope of competition is simply shifted from interindividual to intergroup. Perhaps because of the central role of agonistic behavior, with its implications of exclusion of some participants from the gene pool of later generations, its genetics has been somewhat more widely investigated than that of other forms of social interaction. Thus we are emphasizing the

behavior genetic analysis of agonistic behavior in this article, although we recognize the great importance of cooperative social interactions for the stability and prosperity of a population.

VARIABILITY IN SOCIAL BEHAVIOR

A large body of research (Scott, 1958; Marler and Hamilton, 1966) has demonstrated that sex, age, physiological status (often cyclic), and the external situation influence social behavior. If we are to detect genetic influences, it is clear that there must be extremely good control of other possible sources of variation. Rigorous controls by themselves, however, are not enough. Genetic influences on behavior may be obscured by the unstimulating conditions of ordinary laboratory rearing (Henderson, 1970). A good rule is to approximate the natural habitat and rearing procedures as closely as is consistent with the need for making environmental variables constant for the animals whose social behavior is to be compared (Willems, 1969).

The variability of greatest interest is that existing between individuals which are most likely to be coparticipants in agonistic interactions. Success in such encounters is determined by the ability of an individual relative to its near neighbors rather than to a population of individuals who will never be met in direct competition. Laboratory studies will be more relevant to evolutionary issues if the kinds of social groups set up artificially bear a reasonable resemblance genetically to groups which might form naturally. Inbred strains have great usefulness in genetic research, but comparisons of inbred lines will not by themselves provide the necessary information (Bruell, 1970).

QUANTIFICATION OF SOCIAL BEHAVIOR

Some of the problems inherent in measuring social behavior for genetic experiments can be illustrated by the determination of dominance hierarchies. Fundamentally we seek to place individuals of a group in rank order with the possibilities of ties at some levels. The probability of access to scarce resources and of leaving progeny is, in general, greater for those high in the dominance order. An ordinal scale based on ranks within groups small enough to permit a degree of stable organization is here more meaningful than interval or ratio scales (Stevens, 1951). Yet it has been common to observe agonistic behavior in pairs of the same genotype, obtain quantitative scores for amount or intensity of fighting, and rank the strains with respect to aggressiveness (Southwick and Clark, 1968). But can one actually predict the outcome of competition between a strain X and a strain Y male

mouse from the knowledge that strain X males fight each other for 10 min of a 30-min encounter and strain Y males fight for 20 min? The questions invoke the validity of *transformability* of numerical indices of social behavior to ordinal ranking of competitive encounters.

A related problem is that of *transitivity*. If it is possible to test every genotype represented in a group with every other genotype, the issue does not arise. But if we can determine only that A dominates B, and B dominates C, can we assume that A will dominate C? There is some empirical evidence on this point. In small flocks of chickens, linear orders predominate, but triangular relationships (nontransitive) were found in the lower ranks of large flocks (Allee, 1938). In litters of dogs, straight-line hierarchies were common in more aggressive breeds; ties among the lower ranks were frequent in more peaceful breeds (Scott and Fuller, 1965). The problem of transitivity assumes different forms depending on the nature of the test situation. If one is observing a stable dominance order achieved by a group which has been forced to share restricted territory for a time, it is often possible to determine dominance in all possible pairings within the group. But if one's interest is observation of the development of dominance in initial paired encounters there can be only one initial encounter for each individual. Here inbred strains are useful, since one can replicate genotypes and, in a sense, observe the same individual in two or more "initial" encounters.

Finally a laboratory test of agonistic behavior should be predictive of behavior in other situations. It should have the property of *generality*. Complete generality is probably impossible to attain. Many passerine birds defend their territories ably, but retreat when they intrude upon the territory of another conspecific (Hinde, 1956). A home-cage enhancement of dominance is clearly seen in mice (Uhrich, 1938). The problem of generality is especially pertinent when models, rather than other animals, are used to elicit responses which are normally restricted to social interactions.

Another aspect of generality is the consistency of genetic interpretations from different but similar experiments. McGill (1970) found in his studies of the genetics of male sex behavior in mice that the mode of inheritance for supposedly related measures of sex behavior showed no consistent pattern in the same crosses, and the mode of inheritance of the same traits varied unpredictably among different crosses. This is a serious problem and, unfortunately, no simple solution is in sight.

DESIGNS FOR GENETIC STUDIES OF SOCIAL BEHAVIOR

Three basic methods of measurement of the social phenotype have been used in the behavior genetic analysis of social interactions. These are

illustrated in Table I as though all measurements were made on pairs, but this is not a necessary restriction. Some designs involve combinations of the three methods, and there are important differences among some of the variants shown in the third column of Table I. The essential features of the three methods are as follows. (1) *Homogeneous sets:* individuals of the same genotype are observed in a social situation; comparisons are made between the various tested genotypes. (2) *Standard tester:* all the genotypes to be tested are matched with a standard genotype in a social situation; a model may be substituted for the tester animal to achieve greater stimulus control;

Table I. Designs for Genetic Studies of Social Behavior

Plan for pairs	Measurements obtained	Genetic considerations
1. Homogeneous sets A-A B-B C-C . . K-K	Comparisons of groups A . . . K on frequency, duration, latency, and intensity of encounters	The pairs must be genetically replicable: inbred strains or F_1 hybrids. Not useful for segregating populations
2. Standard tester A-S B-S C-S . . K-S	Comparisons of groups A . . . K on frequency, duration, latency, and intensity of encounters	Standard must be replicable: inbred strain, F_1 hybrid, or model. Tested individuals may come from segregating generations
3. Panel of testers A-W A-X . . A-Z B-W B-X . . B-Z . . . . K-W K-X . . . . K-Z	Comparisons of groups A . . . K as above. Ranking of A . . . K in the ordinal scale based on testers W . . . Z	Several possibilities: (a) extensive panel drawn from a heterogeneous reference population; (b) a set of replicable individuals from inbred strains in F_1 hybrids. The tester panel may be identical in composition with the groups to be tested, or different. The identity panel design is limited to testing inbreds and F_1 hybrids. Other panels are suitable for segregating generation testing

the tested genotypes are compared with respect to quantitative measures of their interactions with the standard. (3) *Panel of testers:* the genotypes to be tested are ranked with respect to a panel of testers chosen to be representative of a reference population; each tested genotype is assigned an ordinal ranking within the reference population; in agonistic encounters, this is expressed as the probability of achieving dominance in a paired encounter.

The Homogeneous Set Design

The homogeneous set design is illustrated by Southwick and Clark's (1968) survey of 14 inbred lines of mice which were compared on intensity of agonistic behavior in intrastrain pairings of males. In another example, groups of four male mice were placed in multiple connected cages by Hahn (1971). In groups drawn from an aggressive strain, stable dominance patterns developed, while no detectable organization appeared in a strain which did not show agonistic behavior. Similar experiments have been reported with selected, noninbred lines. Rigidity of dominance structure within litters of dogs was found to be correlated positively with amount of agonistic behavior observed (Pawlowski and Scott, 1956). The design has also been employed to demonstrate statistical interaction between genotypic and experiential conditions. A specific rearing condition was required to demonstrate differences in level of agonistic behavior in lines of mice selected for high and low brain weight (Hahn *et al.,* 1973).

The homogeneous set design can be modified for sexual or caretaking interactions by intrastrain pairing of males with females, or parent with young. It is possibly the most commonly used design for the behavior genetic analysis of social interaction in the laboratory.

Most studies utilizing this design have stopped with the demonstration of strain differences, although some have included consideration of the dependence of strain differences on the environment (Fuller and Clark, 1968). It is, however, compatible with genetic experiments involving F_1 hybrids between pure lines as in the popular diallel experiment, and we are currently using it in this manner. The method is inappropriate for measurements on a backcross or F_2 generation whose members are not genetically identical and cannot be assigned with certainty to homogeneous sets.

A practical advantage of the homogeneous set is the relative ease of securing subjects of the same genotype, age, and sex by using littermates, raised separately or apart, as sources of groups. Pairing of like subjects probably minimizes within-group variation, increasing the probability that genetic effects will be detected. Despite its convenience and wide usage, the homogeneous set design has serious limitations in addition to its inapplicability to genetically segregating populations. Contests between identical

genotypes must be extremely rare in nature, and when they do occur their outcome has no genetic significance since winner and loser have identical genes to transmit. Also, the ordinary experiment in which dominance is observed in homogeneous pairs affords no basis for relating success to known factors. However, genetically homogeneous sets with heterogeneous pretreatment could be effectively used in the study of developmental aspects of social interactions. These would be of the form $A^1\ A^2\ A^n,\ K^1\ K^2\ K^n$, where the superscripts identify individuals given specific physiological or experiential treatments. Another disadvantage of the method is that the behavior shown in a homogeneous set may not encompass all the responses which are potentially evocable. If one of a set of tested strains never fought unless attacked, it would receive a score of zero for agonistic behavior, yet the same strain might fight vigorously if attacked by a spontaneously aggressive animal. In summary, the method is useful, but its limitations must be recognized.

The Standard Tester

In the standard tester design, all tested animals are paired with the same standard stimulus. For example, we are currently testing the products of a 4×4 diallel cross of inbred strains of mice in a food competition situation. All subjects are paired with a representative of a standard genotype (in this case, one of the F_1 hybrids produced in the diallel). The design is also suitable for genetic experiments requiring measurements on segregating generations (McGill, 1970) or on naturally heterogeneous populations. The standard test partner can be of three types: a model employing some of the attributes of a "real" social partner, a standard genetically replicable animal, or a replicable animal altered physiologically, by experience or by circumstance.

Models have been used extensively to study social behavior, but little of this work has included a genetic manipulation. Tinbergen (1948) used models to isolate the releasing stimuli for territory defense in the stickleback; Harlow and Harlow (1966) determined the essential stimuli in a mother–infant relationship in rhesus monkeys. This method has not been used to assess genetic effects on behavior, but it is obvious that a stimulus which can be held constant when testing animals could be very important.

A model for elicitation of social behavior need not be a representation of the "real" social partner such as the terrycloth mother employed by the Harlows; the function of the model is to provide stimulation in any form which will elicit the behavior. Thus Lagerspetz and Raija (1965) used movements of a bottle brush to induce attack or flight behavior in male mice. Ulrich *et al.* (1965) have been similarly successful in eliciting aggression in

rats by footshock. A model may, however, produce deceptive results. Ulrich *et al.* observed that shocked male rats attack not only other male rats but also female rats, dolls, and dead rats moved about on a stick—behavior very unlike that obtained in natural circumstances. A requirement for the use of a model is closeness of fit between the behavior elicited by a model and that elicited by a "real" animal.

The replicated standard test animal is a natural stimulus which *a priori* would seem to be the ideal. McGill (1970) used this technique in his extensive studies of the genetics of sexual behavior in male mice. He studied such characteristics as latency to intromission, thrusts per intromission, and latency to ejaculation by pairing several inbred strains and their hybrids with females of a reference strain. Although the standard tester animal is a complete social partner and provides all necessary cues for the elicitation of a particular behavior, the standard's own behavior may be altered by stimuli from the tested animal, thus altering the data output from the pair. For example, in an agonistic study, a moderately aggressive standard animal may submit to a highly aggressive test partner while dominating a less aggressive one. A model, on the other hand, can provide stimulation which is independent of the tested animal's behavior, and thus all variability between tested groups can be attributed to the subjects themselves.

Another disadvantage of a replicated standard test animal is illustrated in a study of mouse sex behavior by Vale and Ray (1972). They discovered that an A/J strain male mouse would root under a C57BL/6J strain female when she was in lordosis rather than mounting her. This disoriented the female, which would often turn and attempt to mount the male as he approached, thus disrupting his pattern. The lack of synchronizing patterns between these particular partners led to a number of failures to mate—failures that did not occur when the strains were paired *inter se.* If the behavior under study is a complex one involving close meshing of reciprocal behaviors by partners and the experimenter is interested in obtaining the entire stereotyped behavior pattern of a particular strain, the homogeneous set design seems ideal. On the other hand, if the experimenter is interested in observing all possible variants in a certain pattern (e.g., female sexual behavior) that a strain may exhibit, then a partner of another strain would be appropriate.

A third type of standard test animal is a replicated tester altered in some fashion to restrict its behavioral capacity. Scott (1966) wished to study the effects of a series of defeats on a mouse's behavior. In order to administer his treatment, he needed male fighters which would consistently defeat their partners. He trained his winners, in part, with a "dangled" mouse—a mouse held by the tail slightly above the test area floor. The "dangled" mouse was a standard tester with the stimulus qualities of a real

mouse, but it could not reciprocate with fighting behavior. The trained fighters also became standard testers, since they subsequently won all encounters with inexperienced subjects. Because of their consistency, they were free from the difficulty incurred by testers whose behavior would be a function of the differential response of various partners. Another variation on the altered tester derives from the findings of Ropartz (1968). He discovered that anosmia in a male mouse (via olfactory bulbectomy) produces a mouse that fights only in response to attack, never spontaneously. This type of altered tester to our knowledge has yet to be used in a genetic study and caution should be employed in its use since little is known about the effects of the ablation on behaviors other than fighting. In summary, of the three types of standard testers, we feel that the altered replicated tester has the most research potential for the genetics of social behavior since the tester provides all the cues of a real organism while retaining the property of repeatability from one test to the next.

The Panel of Testers

An example of the panel of testers technique is McBride's (1958) use of a panel from a large flock of fowl to determine the social ranking of individual birds. Each subject to be tested was paired individually with each member of a test panel and the outcome was recorded as a win, draw, or loss. An interval of at least 3 hr between encounters was necessary in order to eliminate interference between tests. A similar method of evaluation has been successfully used to select lines with high and low social status in the domestic fowl (Craig *et al.*, 1965). Ratings based on a panel of five testers had a correlation coefficient of 0.76 with ratings from a panel of 20 testers. The realized heritabilities of social dominance scores in these experiments varied between 0.163 and 0.278. After five generations of selection, there was little decline in within-line variance or in heritability, indicating that genetic heterogeneity for this characteristic was still present.

Another type of tester panel is obtained by using the array of strains to be compared as its own reference population. We call this an *identity panel.* The procedure is sometimes referred to as a "round robin." Ginsburg and Allee (1942) paired male mice of strains C57BL, C3H, and BALB/c in this fashion and ranked them in the above order with respect to probability of achieving dominance. A small-scale study using similar pairings compared dominance in two situations, priority in reaching a narrow runway to escape shock and attaining top position in a confining tube, and yielded similar though not identical rankings for these three strains (Doner *et al.*, 1952).

A variant of tester panel design was used by DeFries and McClearn (1970) to study the relationship between social dominance as measured by

absence of tail wounds and the ability to sire young. Triads of males from six different inbred strains were placed in large cages with three BALB/c females homozygous for two recessive coat color alleles, *b* and *c*. The composition of the male triads was restricted by the requirement that the paternity of any offspring could be determined by its coat color. Sixty-one litters were obtained, of which 56 (92%) were sired by the dominant male. Because of the limited availability of subjects and the limitations of assignment noted above, only three of the six strains could be reliably ranked. Strains A and BALB/c tended most often to be dominant; DBA/2 was most frequently subordinate. A control experiment using another strain of females yielded similar ranking. It is not clear, however, whether the failure of low-status males to mate was primarily due to exclusion by their companions or to reduced acceptance by the tester females.

The panel method of evaluating social status has, to our knowledge, been used only to test for differences between inbred or selected lines. It is also suitable for other types of genetic experiments, although evaluation of individuals from segregating generations requires multiple encounters of a tested individual with panel members. It is easy to conceive of an identity panel being superimposed on a genetic diallel. In its complete form, a diallel of k strains will generate k^2 cells in the genetic matrix and k^4 cells in the identity panel matrix. When $k = 4$, $k^4 = 256$; the necessary within-cell replications would produce an expensive and unwieldly experiment. Simplification is possible, however, without loss of information essential for a genetic analysis. Each row of the diallel matrix can be an identity test panel. All individuals in such a panel share common maternal genetic, prenatal, and postnatal background. Significant differences between the cells in the row are attributable to the paternal genetic contribution.

If k lines are crossed, there are $k!/2(k\text{-}2)!$ paired combinations for each of k rows; a 4×4 diallel produces 16 genotypes, four identity panels with six types of pairing in each, 24 in all (Table II). It is convenient, if social

Table II. Plan for Evaluating Social Dominance from a Genetic Diallel[a]

		Sires			
		A	*B*	*C*	*D*
Dams	*A*	$\underline{AA^b}$	$\underline{AB^b}$	$\underline{AC}$	$\underline{AD}$
	B	$\underline{BA^b}$	$\underline{BB^b}$	$\underline{BC}$	$\underline{BD}$
	C	$\underline{CA}$	$\underline{CB}$	$\underline{CC}$	$\underline{CD}$
	D	$\underline{DA}$	$\underline{DB}$	$\underline{DC}$	$\underline{DD}$

[a] Individuals from cells with a common underline comprise a set for dominance determinations.

[b] Cells for determining dominance and reciprocal relationships of *A* and *B*.

status is the behavior of interest, to score dominance as 1, subordination as 0, and no decision as 0.5. For each complete set of pairings, the row score will total 6; the maximum possible genotypic score will be 3 and the minimum 0. A significant row × column interaction is evidence for maternal effects on the expression of paternal genes. *Genetic dominance* and reciprocal cross differences cannot be determined with this design alone since each parental line is scored against a different panel and the same holds for the reciprocal F_1s. If estimates of such effects are desired, additional identity panels can be constituted, for example, *AA, AB, BA,* and *BB.* Six such sets can be made from the 4 × 4 diallel of Table II, and six types of encounters are possible in each, 36 in all. In each set, two of the six types of encounters are common to the row panels and need not be repeated. These encounters directly match parental strains and their F_1 hybrids; dominance and reciprocal effects are readily detected. The use of both types of panels in a 4 × 4 diallel would generate 48 types of pairing, a substantial number but a marked reduction from the 256 types called for by a complete design.

DEVELOPMENTAL SOCIAL PSYCHOGENETICS

Genetic studies of social behavior are not limited to manipulation of genotypes and measurement in adults. There is great interest in early indicators of adult variations in social behavior and social organization. Cairns (1976) has proposed that, for some social behaviors, ontogeny determines phylogeny since behavioral adaptation in the young contributes to the reproductive success of the adult. That is, variation in social behaviors produced in young organisms by differential development patterns provides variation which can be acted on by natural selection. Research problems in this area center about the degree to which genes contribute to variations in individual status and group structure.

Group social structure is based on individual behavior, but it is possible to characterize groups in terms of patterns of relationships. For example, Pawlowski and Scott (1956) reported that the time course of dominance hierarchies and their eventual form differed sharply among four breeds of dogs. Actually the development of a dominance hierarchy in a litter of pups is an example of an identity tester panel, although there is usually no scientist available to take records.

Behavior genetic analysis requires, however, control and identification of the genotypes of the interacting young animals. For this purpose, homogeneous groups of young (e.g., litters of mice) could be drawn from an inbred or selected strain. Differences of individual status within such groups are due to environmental factors. An experimenter might also analyze these

factors by selected treatments such as hormone manipulation, special handling, or some other variable of interest and follow the effects into adult life. For example, Lagerspetz and Seija (1967) observed the maturation of aggressive behavior in young mice that were progeny of lines selected for aggressiveness. Various environmental manipulations, e.g., pain or food deprivation, altered the rate at which "adultlike" aggression was expressed by young mice. By observing homogeneous groups of animals of different genetic composition, and holding environmental factors as constant as is feasible, it is possible to test for generality of such effects, and to determine the genetic contribution to group social structure as distinct from individual status.

Also possible are developmental studies of natural or synthesized genetically heterogeneous groups, but space does not permit extensive description of possible designs. Perhaps the most useful ones involve fostering young animals of diverse known genotypes upon the same mother. Such studies could demonstrate the effects of genetic variability on adult social behavior, and they would permit direct observation of behavioral antecedents of the differentiated social structure characteristic of many adult groups.

SOCIAL ORGANIZATION DEDUCED FROM GENETICS

Our discussion to this point has centered on experiments in which the genetic nature of a group is specified and social behavior and organization are observed directly. In natural populations where direct observation of behavior may be impossible, some deductions regarding social organization can be based on genetic findings. The rationale of such investigations is that the frequency of allelic combinations in a panmictic population is predictable by the Hardy–Weinberg law. If there are excessive numbers of matings with near relatives, there will be more homozygotes and fewer heterozygotes than panmixia would produce. Furthermore, a population broken up into smaller interbreeding subgroups (demes) will tend to show large localized deviations in allelic frequencies within a relatively small area.

Two examples of such studies illustrate their potential. Klein and Bailey (1971) captured wild *Mus musculus* males from several farms separated by 2 km or more. These were bred to females of an inbred line. Skin transplants were then made between (1) offspring of the same sire, (2) offspring of sires from the same farm, and (3) offspring of sires from different farms. The last were rejected rapidly; types (1) and (2) were successful or rejected slowly. The result indicated very little gene flow between adjacent farms.

Even more extreme is the finding in the same species of genetic evi-

dence for deme structure within a single large barn (Selander and Yang, 1970). The distances between demes were so small that some kind of behavioral barriers to extrademe matings must exist. Neither of these findings demonstrates that the genes which serve as indicators for deme structure have any functional relationship to the mating barriers. In fact, there is no evidence that any genes have a role in maintaining demes in the house mouse, except as they specify the kinds of social learning which are possible in this species.

FUTURE DEVELOPMENTS

The title of this article, "Issues in the Genetics of Social Behavior," implies the existence of problem areas where additional research is needed. We see four major areas which are particularly important. The first is the investigation of the ways in which heredity affects the vulnerability of animals to crowding, isolation, and other factors which have been shown to impair social organization (Fuller and Clark, 1968). The importance of genetics will probably vary among species and the nature of the stressful condition. Second, and related to the first objective, is the retrograde analysis of variations in social behavior patterns in relation to their genetic determinants. This is the area we have called developmental social psychogenetics. The basic principles of these two areas can be established through laboratory experimentation with available genetically controlled strains.

A third area for investigation is the behavior genetic analysis of social behavior in natural populations. Bruell (1970) has called for a "population behavior genetics," but separating genetic and environmental sources of variation in free-living animals is almost impossible. Field observation alone will not suffice, and combinations of field and laboratory techniques will be required.

Finally, these three approaches may be applied to man. Currently the emphasis in human behavior genetics is on individual traits. Insofar as social behavior is considered, it is viewed as a component of personality. We have argued here that genotypes have effects on social structure as distinct from their effects on individual behavior and see no logical reason that this is not true of man as well as mice and fowl. Despite the importance of this extension, the difficulties are immense and the most promising areas for the immediate future involve better-designed and -executed studies with experimental and wild animals. Theoretical models must be tested by experiment.

REFERENCES

Allee, W. C. (1938). *The Social Life of Animals,* Norton, New York.

Ayala, F. J. (1972). Frequency-dependent mating advantage in *Drosophila. Behav. Genet.* **2**:85–92.

Bruell, J. H. (1970). Behavioral population genetics and wild *Mus musculus.* In Lindzey, G., and Thiessen, D. D. (eds.), *Contributions to Behavior-Genetic Analysis: The Mouse as a Prototype,* Appleton-Century-Crofts, New York, pp. 261–291.

Cairns, R. B. (1976). The ontogeny and phylogeny of social interactions. In Hahn, M. E., and Simmel, E. C. (eds.), *Communicative Behavior and Evolution,* Academic Press, New York, pp. 115–139.

Calhoun, J. B. (1962). A "behavioral sink." In Bliss, E. L. (ed.), *Roots of Behavior,* Harper, New York, pp. 295–315.

Christian, J. J. (1961). Phenomena associated with population density. *Proc. Natl. Acad. Sci.* **47**:428–449.

Christian, J. J. (1970). Social subordination, population density, and mammalian evolution. *Science* **168**:84–90.

Craig, J. V., Ortman, L. L., and Guhl, A. M. (1965). Genetic selection for social dominance ability in chickens. *Anim. Behav.* **13**:114–131.

DeFries, J. C., and McClearn, G. E. (1970). Social dominance and Darwinian fitness in the laboratory mouse. *Am. Naturalist* **104**:408–411.

Doner, R. D., Inman, C., and Davis, R. T. (1952). Competitive behavior between inbred strains of mice. *Proc. S. Dakota Acad. Sci.* **31**:172–176.

Falconer, D. S. (1960). *Quantitative Genetics,* Ronald Press, New York.

Fuller, J. L., and Clark, L. D. (1968). Genotype and behavioral vulnerability to isolation in dogs. *J. Comp. Physiol. Psychol.* **66**:151–156.

Ginsburg, B. E., and Allee, W. C. (1942). Some effects of conditioning on social dominance and subordination in inbred strains of mice. *Physiol. Zool.* **15**:485–506.

Hahn, M. E. (1971). Social relationships and their development in two strains of *Mus musculus. Diss. Abst. Int.* **32**:**(1-B)**:585.

Hahn, M. E., Haber, S. B., and Fuller, J. L. (1973). Differential agonistic behavior in three lines of mice selected for brain weight. *Physiol. Behav.* **10**:759–762.

Harlow, H. F., and Harlow, M. K. (1966). Learning to love. *Am. Scientist* **54**:244–272.

Henderson, N. D. (1970). Genetic influences on the behavior of mice can be obscured by laboratory rearing. *J. Comp. Physiol. Psychol.* **72**:505–511.

Hinde, R. A. (1956). The biological significance of the territories of birds. *Ibis* **98**:340–369.

Lagerspetz, K., and Raija, M. (1965). Simulation experiments on stimuli eliciting aggressive behavior in mice. *Reports of the Psychology Institute, University of Turku,* No. 13.

Lagerspetz, K., and Seija, T. (1967). Maturation of aggressive behavior in young mice. *Reports from the Institute of Psychology, University of Turku,* No. 28.

Manning, A. (1963). Selection of mating speed in *Drosophila melanogaster* based on behaviour of one sex. *Anim. Behav.* **11**:116–120.

Marler, P. H., and Hamilton, W. J. (1966). *Mechanisms of Animal Behavior,* Wiley, New York.

McBride, G. (1958). The measurement of aggressiveness in the domestic hen. *Anim. Behav.* **6**:87–91.

McGill, T. E. (1970). Genetic analysis of male sexual behavior. In Lindzey, G., and Thiessen, D. D. (eds.), *Contributions to Behavior-Genetic Analysis: The Mouse as a Prototype,* Appleton-Century-Crofts, New York, pp. 57–88.

Parsons, P. A. (1967). *The Genetic Analysis of Behaviour,* Methuen, London.

Pawlowski, A. A., and Scott, J. P. (1956). Heredity differences in the development of dominance in litters of puppies. *J. Comp. Physiol. Psychol.* **49**:353–358.

Ropartz, P. (1968). The relation between olfactory stimulation and aggressive behaviour in mice. *Anim. Behav.* **16**:97–100.

Scott, J. P. (1958). *Animal Behavior,* University of Chicago Press, Chicago.
Scott, J. P. (1966). Agonistic behavior of mice and rats: A review. *Am. Zoologist* **6**:683–701.
Scott, J. P., and Fuller, J. L. (1965). *Genetics and the Social Behavior of the Dog,* University of Chicago Press, Chicago.
Selander, R. K., and Yang, S. Y. (1970). Biochemical genetics and behavior in wild house mouse populations. In Lindzey, G., and Thiessen, D. D. (eds.), *Contributions to Behavior-Genetic Analysis: The Mouse as a Prototype,* Appleton-Century-Crofts, New York, pp. 293–334.
Southwick, C. H., and Clark, L. H. (1968). Interstrain differences in aggressive behavior and exploratory activity of inbred mice. *Commun. Behav. Biol.* **A(i)**:49–59.
Stevens, S. S. (1951). Mathematics, measurement and psychophysics. In Stevens, S. S. (ed.), *Handbook of Experimental Psychology,* Wiley, New York, pp. 1–49.
Thiessen, D. D. (1972). A move toward species-specific analyses in behavior genetics. *Behav. Genet.* **2**:115–126.
Tinbergen, N. (1948). Social releasers and the experimental method required for their study. *Wilson Bull.* **60**:6–52.
Uhrich, J. (1938). The social hierarchy in albino mice. *J Comp. Physiol. Psychol.* **25**:373–413.
Ulrich, R. E., Hutchinson, R. R., and Azrin, N. H. (1965). Pain elicited aggression. *Psychol. Rec.* **15**:111–126.
Vale, J. R., and Ray, D. (1972). A diallel analysis of male mouse sex behavior. *Behav. Genet.* **2**:199–209.
Willems, E. P. (1969). Planning a rationale for naturalistic research. In Willems, E. P., and Rausch, H. L. (eds.), *Naturalistic Viewpoints in Psychological Research,* Holt, Rinehart and Winston, New York, pp. 44–71.
Wood-Gush, D. M. G. (1958). Genetic and experimental factors affecting the libido of cockerels. *Proc. Roy. Soc. Edinburgh* **27**:6–7.
Wynne-Edwards, V. C. (1962). *Animal Dispersion in Relation to Social Behavior,* Hafner, New York.