
Social Transmission of Acquired Behavior: A Discussion of Tradition and Social Learning in Vertebrates

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I. Introduction	77
II. Field and Associated Laboratory Studies	81
A. Spatial Utilization	82
B. Feeding and Predatory Behavior	84
C. Predator Avoidance	87
D. Bird Vocalizations	88
III. Learning and Conditioning Paradigms	88
IV. Problems of Terminology	92
V. Conclusions	95
References	97

I. INTRODUCTION

There are, broadly speaking, essentially three nonindependent means by which the behavior characteristic of a population may remain constant from one generation to the next. First, adaptive behavior in population members may be largely endogenously organized and genetically transmitted as propensities influencing ontogeny. Second, similar patterns of behavior in successive generations of a population may result from similar histories of individual transaction with the physical environment. And, third, long-term homogeneity of behavior may result from the transmission of patterns of behavior from individual to individual within a population as a consequence of social interaction (for a similar analysis, see Klopfer, 1961).

The assumption has often been made that in most species the adaptive behavior acquired independently by an individual as a result of its transactions with the physical environment is not readily transmitted either to others of its genera-

tion or to members of future generations. In this view, although the genetic material influencing the behavior of an individual which allowed it to acquire some pattern of behavior may be preserved and disseminated within a population via the mechanisms of Mendelian recombination and neo-Darwinian natural selection, the specific responses acquired by any individual are lost in every generation with the death of their acquirer. The logical extension of this position is that homogeneity in the behavior of members of a population must reflect either common genetic material or similar histories of individual organism-environment transaction in all population members, or both. The human species, and to a lesser extent the other primates, are treated as exceptional in their ability to disseminate throughout a population and project into future generations, individually acquired patterns of behavior.

There is, however, a large but scattered body of literature both on the observation of free-living groups of animals and the study of a few species under controlled laboratory conditions, suggesting that intraspecific interaction resulting in the transmission of acquired patterns of behavior from one individual to another within a population is a relatively common and important mode of adaptation in both primate and nonprimate vertebrate organisms.

The survival value of the ability of organisms to acquire patterns of behavior as a result of interaction with conspecifics, as well as from transactions with nonsocial aspects of the environment, are relatively straightforward. If laboratory learning paradigms are, in fact, accurate analogs of learning as it occurs in natural habitats, then the trial and error processes necessary for the acquisition of adaptive patterns of behavior must often be both energy-consuming and error-filled undertakings for the acquirer. A young animal, newly recruited to a population, must face particularly acute environmental challenges requiring rapid acquisition of behaviors necessary for survival within the particular area in which it achieves physiological independence. The need to locate areas suitable for survival and reproductive activities, to find and learn to ingest necessary dietary constituents, to learn to escape or avoid potential predators, and to behave appropriately with respect to conspecific individuals must place considerable demands on the young organism's capacities for behavior acquisition during a time when it is highly vulnerable to environmental stress and when errors in response can have serious consequences. Although the naive animal may have the capacity to acquire the learned adaptive behavior of more mature and experienced individuals by repeating their histories of transaction with the physical environment, it would clearly be advantageous to the young if they could in some way incorporate into their own behavioral repertoires the learned adaptive behavior of more experienced conspecifics through some process less cumbersome than *de novo* trial and error learning. Similarly, adult organisms living in unstable environments could benefit appreciably from the direct acquisition of conspecific patterns of behavior. In the absence of such acquisition, each individ-

ual would have to discover for itself the existence or novel distribution of important elements in the environment following any environmental change. Again, although each individual might have the capacity to learn its way about in a changed environment, direct acquisition of conspecific patterns of behavior could facilitate behavioral adaptation to changing circumstances.

Viewed in a broader context, the social transmission of acquired behavior may be seen as providing an alternative to the genetic transmission of behavioral propensities, allowing a population to maintain established patterns and to incorporate behavioral novelty into its repertoire rapidly (Mainardi, 1970, 1973). The most readily observable result of social transmission processes would be the existence of different modes of behavior within different geographic subpopulations of a species uncorrelated with gene or resource distribution.

Before reviewing examples of patterns of behavior apparently transmitted among conspecifics, it is important to define the range of phenomena to be considered. The task of definition requires that transmitted behaviors be distinguished from other observable changes in behavior resulting from interaction among conspecific individuals. The aim of the definition proposed here is to restrict consideration to instances in which organisms acquire specific patterns of behavior as a result of direct transaction with the environment and increase the probability of other species members exhibiting similar patterns of behavior as a result of interaction with them. Three criteria, discussed below, seem sufficient appropriately to limit examples to be considered.

First, our concern here will not be with cases in which social interaction is a necessary condition for the ontogeny of a pattern of behavior. Thus, excluded from consideration will be phenomena such as the development of normal species-specific sexual preference in the zebra finch (Immelman, 1972), the acquisition of species typical song in the white-crowned sparrow (Marler and Tamura, 1964), and the development of normal maternal behavior in rhesus monkeys (Harlow and Harlow, 1965), which are expressed in the behavioral phenotype of only those individuals experiencing crucial social interactions during development. Rather, we will consider only those instances in which social interaction is a sufficient condition for behavior acquisition and provides an alternative or optional route to direct transaction with the nonsocial environment in the development of behaviors in question.

The decision to limit discussion to cases in which social interaction is sufficient but not necessary for behavior development results from consideration of apparent differences in the functions of necessary and sufficient social interactions in the ontogeny of behavior. Organisms often require exposure to specific environmental conditions for the development of a given behavior pattern. If the environmental condition is a social one, as for example interaction with a parent, it is possible to confuse a social exposure necessary for normal development with a social transmission process. In the former case the result of

social interaction is normal development of a relatively invariant, species typical behavior. In the latter, idiosyncratic patterns acquired by the transmitter as a result of its history of transaction with the environment may be introduced into a population repertoire. The somewhat conservative approach adopted here is to assume that this qualitative difference in the function of social interactions necessary and sufficient for the development of behavior exists and to restrict discussion to those cases in which social transmission is facultative rather than obligate for behavior development.

Second, the change in behavior resulting from interaction among conspecifics should be in the direction of homogeneity rather than heterogeneity of behavior between interactants. This restriction serves to exclude from consideration social interactions, such as dominance hierarchy formation or territorial division of a species range, that produce changes in the behavior of interactants but in which the particular pattern of behavior of one organism is not acquired by another.

Third, I wish to consider only those cases in which the increased homogeneity of behavior extends temporally beyond the period of interaction between the recipient and the transmitter. Thus, the critical test for the successful transmission of behavior becomes the maintenance of the transmitted behavior in the recipient following the termination of interaction with the transmitter. This criterion is intended to exclude a variety of cases, such as mobbing of potential predators (Hinde, 1954) or simple following of one animal by another, in which the behavior of one individual releases similar behavior in others.

The statement of the preceding criteria is not to imply that behavioral phenomena that fail to meet them are of lesser importance than those that do. Rather, their purpose is to differentiate interactions functioning to disseminate patterns of acquired behavior through a population from those incapable of doing so (a similar approach with respect to the definition of "culture" is to be found in Menzel *et al.*, 1972).

The following sections review a variety of field and laboratory findings which have been or can be interpreted as demonstrating the social transmission of acquired behavior. The term *acquired behavior* is employed here broadly, to refer both to cases in which a novel motor pattern is acquired by an organism and to cases in which a typical response comes to be elicited by a novel stimulus. Thus, for example, the incorporation of a novel item into an organism's feeding repertoire will be treated as acquired behavior and, consequently, the spread among conspecifics of feeding on that item would be considered as a possible case of transmission of acquired behavior. The term *transmission of behavior* will be used to refer to any of a variety of processes by means of which the behavior of conspecifics is modified in the direction of homogeneity as a result of intra-specific interaction. In the following discussion of these processes, no implication of deliberate tuition of one organism by another is intended. No attempt

has been made to survey the literature exhaustively; rather, cases have been chosen to exemplify a number of mechanisms that are discussed in succeeding sections as possible bases for the transmission of behavior from one individual to another.

II. FIELD AND ASSOCIATED LABORATORY STUDIES

Criteria for the identification of socially transmitted behavior are difficult to specify in most field situations. Although the careful observer can often describe differences in the behavior of subpopulations of a species, simple observation is seldom sufficient for the identification of the processes leading to their establishment. The requisite analyses would often require laboratory study of events observed in the field, but in many cases both species and phenomena suitable for field observation are not particularly practical choices for laboratory research. Conversely, species chosen for laboratory investigation are often difficult subjects for field study. As a result, the controlled analyses necessary to interpret field data fully are often not available and the importance of phenomena studied in the laboratory for the life of organisms in their natural environment frequently remains undetermined. The existing literature on the transmission of acquired behavior clearly reflects these differences between the phenomena of laboratory and field investigations, and the synthesis attempted here has necessitated a certain amount of extrapolation from the available data.

The discussion has been organized around available field studies for two reasons. First, it is necessary to consider the frequency and importance of phenomena suggestive of behavioral transmission in natural settings. In terms of the approach adopted here, if possible instances of social transmission are infrequent, if social transmission does not play an important role under natural circumstances, it would be an entirely academic exercise to discuss it at any length. I do not personally view this as a serious problem. It is, for example, difficult to find an extended study of the life history of any mammalian or avian population which does not include the description of one or more behavioral phenomena amenable to consideration within the framework under discussion. Second, instances of transmission of acquired behavior in natural settings provide a necessary basis for evaluation of the importance of theoretical statements and empirical findings derived from laboratory investigations of social learning phenomena.

For the purpose of organization, the data have been categorized in terms of the roles of behavior patterns discussed in the life of the organism. Where laboratory investigations relevant to the field data are available, they have been referred to in the appropriate context.

A. SPATIAL UTILIZATION

In many vertebrate species the territories or home ranges of subpopulations or the specialized use of certain areas within subpopulation ranges remain relatively fixed over many generations, resulting in what might be described as "traditional" boundaries psychologically restricting the movement and activity of individuals. Although the factors responsible for selection of habitation sites have been explored in only a few species, there are several investigations indicating that the preferences of some vertebrates for particular habitation sites are modifiable by experience (Klopfer, 1969; Klopfer and Hailman, 1965; Wecker, 1963). The existence in many species of consistent subpopulation differences in habitation site selection suggests that interaction with conspecifics may be an important determinant of the selection of an area for occupation. As will become apparent in the following literature review, the transmission of preferences for locations in which to carry out life's activities may occur in any one of a variety of ways. Although the processes involved in the social transmission of patterns of spatial utilization have not in most cases been analyzed in sufficient detail to permit their precise description, it might prove useful to categorize them in a general way to facilitate organization of the material presented below, even though it is not always possible on the basis of present knowledge to specify into which category a given example may fall.

In the simplest instances, a parturient female can affect the choice by her young of a home range or habitat simply as a result of depositing or rearing them at one site rather than another. The social interaction responsible for selection of a specific site for habitation in the young is, in these cases, very limited, and the long-term consequences for the young of parental reproductive site selection depend on the young developing some attachment to the area in which they find themselves early in life. For example, numerous studies indicate that each of the many subpopulations of Pacific salmon return generation after generation to different streams to reproduce. The data available are consistent with the view that the young salmon become imprinted on chemical cues unique to the particular stream in which their mother spawned and in which they spend their first year (Hasler, 1966). Thorpe (1945) has proposed the term *habitat imprinting* to describe the well-documented tendency of some species of migratory bird with widely distributed nesting grounds to return to the area in which they were reared to engage in their own reproductive activity (Snyder, 1948). Similarly, there is evidence that sea turtles (Ehrenfeld, 1974) and many species of bat and frog show a strong tendency to migrate back to their place of birth for purposes of reproduction (Wynne-Edwards, 1962, p. 453).

In slightly more complex situations, one organism may alter the environment in such a way as to channel the behavior of others with respect to it. This might be considered a more complex type of transmission in that the environmental change to which the recipient responds is often a more active or specialized

product of the behavior of the transmitter than simple site selection and, in fact, subsumes the simpler case. For example, Atlantic salmon, which show consistent differences in spawning stream selection, like those of their Pacific relatives, are believed to respond to chemical cues deposited in breeding streams by fellow subpopulation members (Nordeng, 1971; Solomon, 1973). The size and position of prairie dog coterie territories remain essentially unchanged through complete population turnovers as a result of both the social organization of coterie and the effects of relatively stable burrow systems on territorial organization (King, 1955, p. 60). Similarly, Calhoun (1962, p. 142) has presented evidence that wild rats (*Rattus norvegicus*) born to low-status clans, living in suboptimal portions of the environment, remain in the area of their birth, and become low-status adults themselves. The scented runs created by adult rat clan members define clan territorial boundaries and are rapidly learned by new recruits to a clan (Telle, 1966, pp. 35-36). Traditional usage of restricted areas within subpopulation home ranges for specific purposes over many years have also been described and appear to result from alterations made in the environment by one individual that modify the behavior of others. Red deer, for example, use the same trails and wallows (Darling, 1937), whereas cliff swallows (Hochbaum, 1955) nest in the same locations for many generations.

Yet more complex cases, in which some form of direct interaction between the transmitter and receiver are essential to the transmission process, can be subdivided into two types. In the first, general orienting or following responses on the part of receivers to conspecific transmitters introduce the receivers to selected aspects of the environment to which they then respond directly. In the second, receivers respond directly to transmitter responses to environmental features and only later come to attach those responses to the environmental features to which the transmitter responded initially. Both these types of transmission seem more complex than those previously discussed in that they require direct interaction between transmitter and receiver; because of the richness of such interactions, they are particularly difficult to analyze satisfactorily. Possible examples of the first type of direct interaction resulting in the social transmission of patterns of spatial utilization are not uncommon. For example, Geist (1971, pp. 88, 176) reports that the widely scattered home ranges of individual mountain sheep are socially transmitted, the traditions passing from lead adults to the juveniles that follow them throughout maturation. Similarly, female red deer pass on their home range traditions to their female offspring (Schloeth and Burckhardt, 1961). Further, the inherited directional tendencies of young birds during migration are readily modifiable by the example of older birds of their species; whether this intergenerational influence during migration has long-term effects on breeding and wintering ground selection is not yet known (Matthews, 1968, p. 12). Emlen (1938) has reported that the location and boundaries of wintering grounds of crows may remain unchanged for as long as 50

years, although the precise causes of this stability are not apparent. I have found no instance in which it seems reasonable to assume that the second type of direct interaction described above plays a role in the social transmission of acquired patterns of spatial utilization. However, instances of the occurrence of this type of social transmission are to be found in the discussions of feeding and predatory behavior and of predator avoidance, presented below.

The preceding examples in which some aspect of spatial utilization appears to be determined at least in part by interaction among conspecific individuals indicate that long-term subpopulation differences in behavior may result from a variety of different mechanisms. Deposition of offspring into an environment, alteration of an environment, and the tendency of young actively to follow adults, may each serve in different species as the basis for the transmission and perseverance of subpopulation differences in spatial utilization. This multiplicity of processes responsible for the transmission of acquired behavior, although not discussed explicitly below, is common to all the examples to be considered.

B. FEEDING AND PREDATORY BEHAVIOR

The use of social transmission processes for the propagation of feeding and related behaviors appears to be quite common in vertebrates. A particularly well-documented case concerns a variety of novel eating and drinking patterns acquired by troops of Japanese macaques and apparently transmitted from individual to individual as a result of social interaction among troop members. Examples of feeding-associated behaviors transmitted in this way range from sweet potato washing and wheat "placer-mining" (Kawai, 1965) to troop utilization of novel food resources. Descriptions of the spread of washing behavior within a troop suggest that it is transmitted as the result of one individual observing the behavior of another, as are the learned feeding patterns of juveniles to adults. The acquisition of a troop's patterns of food utilization by juveniles seems to result from the young's habit of ingesting scraps dropped by their mothers (Kawamura, 1959). Similar observations by Carpenter (1934, p. 74) of the feeding interaction of Howler monkey mothers and their young and by Hall (1962) of the feeding of young chacma baboons support the suggestion that adult primates can readily introduce their young to the foods they are eating as a result of the tendency of the young to ingest scraps, although corroborating studies under controlled conditions to determine the effects of ingestion of food samples in infancy on later food preferences are lacking (Hall, 1963).¹ However, observations by Kuo (1967, p. 66) indicate that early feeding experience can have a profound effect on later food preferences in a variety of nonprimate vertebrates (cats, dogs, and myna birds) and support the contention of Kawamura

¹For a thorough discussion of social transmission in primates see Menzel, E. W., Jr. 1973. "Precultural Primate Behavior." Karger, Basel.

that ingestion by infants of food samples obtained from feeding adults may affect later dietary preferences (see also Rabinowitch, 1969).

Similar reports of young nonprimate organisms ingesting food samples acquired from their parents are common, and such parent-offspring interactions sometimes appear to introduce juveniles to substances they might otherwise not ingest. For example, young meerkats failed to recognize a novel food, bananas, as edible and only began to eat it when their mother, who was already familiar with bananas, did so (Ewer, 1963). Similarly, Burmese jungle fowl chicks are reluctant to ingest mealworms when they first encounter them unless the mealworms are presented by a mother hen making the "food-call" (Hogan, 1966, p. 275, and personal communication). Information concerning edible foods available in the environment could easily be transferred from mother to young as a result of such parent-offspring interactions (see also Wortis, 1969).

Cases of the social determination of feeding patterns resulting from somewhat different sorts of interaction have also been reported in rodents. Von Steiniger (1950), in discussing the "local traditions" of colonies of wild rats, observed that if zinc phosphide is used in rat control in one area over an extended period of time, despite initial success, later acceptance of the poison remains low; the offspring of the survivors continue to refuse to accept the poison bait. In a series of laboratory investigations of this apparent traditional poison-avoidance behavior (Galef and Clark, 1971, 1972; Galef and Henderson, 1972; Galef and Sherry, 1973), two complementary mechanisms have been described, either of which can result in rat pups preferentially ingesting the diet that the adults of their colony are eating and rejecting diets that these adults have learned to avoid. First, gustatory cues reflecting the flavor of a lactating female's diet are incorporated into her milk, and ingestion of the female's milk is sufficient to allow pups to recognize their mother's diet and to cause them to ingest that diet preferentially during weaning. Second, rat pups, when seeking their first meals of solid food, have a strong tendency to approach adult rats at a distance from the nest site and to take their first meal of solid food in the immediate vicinity of a feeding adult. In situations in which food sources are spatially separate from one another, this tendency to eat in the vicinity of adults results in pups ingesting the same diet as the adults of their colony are eating. Pups soon become familiar with the flavor of the diet that they and the adults are eating and thereafter show great hesitancy in ingesting unfamiliar foods.

A more complex feeding habit believed to be socially transmitted by Norway rats has been described by Gandolfi and Parisi (1972, 1973) who have found marked differences in the exploitation of bivalve mollusks as a food source by rat clans living on the banks of the Po River. Some clans feed extensively on bivalves, which they collect by diving to the river bottom, while other clans do not prey on the mollusks despite their ready availability in the river adjacent to clan territories. There is, in addition, considerable evidence that the specific mode of opening the shells of these prey differ from colony to colony and is also

socially transmitted. Techniques of opening mussel shells are also believed to be transmitted by parent oyster catchers to their young (Norton-Griffiths, 1967, p. 423).

The observation that members of various species of tit in restricted areas of England, Scotland, Wales, and Ireland have developed the habit of opening the tops of milk bottles to secure milk as food is suggestive of behavioral transmission of some sort. Available data on the spread of the milk bottle-opening behavior is sufficient to support the conclusion that the behavior was initiated by a number of individual birds independently learning about this food source but that the majority of birds engaging in it had "learned it in some way from others" (Fisher and Hinde, 1949; Hinde and Fisher, 1951, 1972). Turner's (1964) observations on the tendency of chicks to peck at objects pecked at by a mechanical "hen" suggest a possible means by which such behavior could be transmitted from one individual to another.

The preceding examples have involved the ingestion of relatively passive food objects. Predatory species have an additional problem in that food acquisition requires the capture of the intended food object prior to its ingestion. A number of investigations suggest the possibility that patterns of predation as well as ingestive behaviors are socially transmitted.

Von Steiniger (1950), for example, has reported that wild rat populations on the island of Norderoog regularly stalk, kill, and eat sparrows, whereas those in other areas of Germany are not observed to do so. Kruuk (1972, p. 119) has collected data indicating that different hyena clans living in the Ngorongoro crater have different prey preferences which are not explicable in terms of the relative abundance of the prey in question (wildebeest and zebra) in their territories. The mechanisms responsible for these differences in prey selection have not been determined.

In reviewing related evidence concerning the prey selection patterns of raptorial birds, Cushing (1944) favors the contention that differences between the prey preferences of raptor species are maintained more through the interactions of parents with offspring than through heritable factors. In the absence of parental or human guidance, young raptors are very slow to take live prey. For purposes of falconry, even a wild-caught adult must be taught to take the particular types of live prey for which it will be used in hunting if these are not already in the animal's diet, and it must be retrained to any new type of prey one wishes to add to its hunting repertoire. Although the evidence hardly justifies so strong a conclusion as Cushing reaches, it does suggest the probable importance of parental influence in the prey selection of raptor young.

Observations by Ewer (1963, p. 592), Schaller (1967, p. 272), Kruuk and Turner (1967), Liers (1951), and Leyhausen (1956) on the ways in which mammalian predators (meerkat, tiger, cheetah, otter, and domestic cat) introduce their young to the killing and eating of prey species suggest that parent-young

interactions may be important in the establishment of species typical predatory behavior. However, neither the extent to which the prey selection of young is determined by the selection of prey species introduced to them by adults nor the long term effects of parent-offspring interaction on the development of species typical predatory patterns have been determined. Kuo (1930, 1938) has demonstrated that kittens reared with females that killed rodents in the presence of their young, began killing rodents at a significantly earlier age and more frequently than kittens reared alone or with a small rodent. It is unfortunate that no comparison was made between kittens reared with killing and nonkilling mothers, but the data are suggestive. Van Lawick-Goodall (1968, 1970) has indicated that the use by chimpanzees of twigs and sticks in capturing termites is transmitted between generations by observational learning, although the observations she has reported are not sufficient to support this contention.

C. PREDATOR AVOIDANCE

The tendency of organisms to avoid potential predators while remaining undisturbed by the approach of harmless individuals is well documented. In most cases these differences in response are presumed to result either from instinctive responses to stimulus aspects of potential predators or from responses acquired by the individual as a result of its previous experience with similar stimulus configurations. There are, however, a few scattered reports of instances in which responses to novel stimuli appear to be learned as a result of interaction with conspecifics in the presence of those stimuli. Jackdaw fledglings, for example, learn to recognize enemies from the adults of their flock (Lorenz, 1952, p. 145). Upon the appearance of a predator, experienced individuals emit a "rattle" call that the young associate with the stimulus configuration eliciting the call in adults and which they thereafter avoid. Young gazelle, zebra, and wildebeest are believed to transmit to their young information concerning the flight distance to be maintained with respect to various predators (Hediger, 1964; Schaller, 1972, p. 389). Hochbaum (1955) reports, similarly, that loss of flight behavior from man in wild ducks arriving in a wild fowl refuge is transmitted from one bird to another and from flock to flock. All four of these reports are anecdotal and lack corroborating data, but investigation of these and similar phenomena under controlled conditions could prove interesting. In a laboratory study of the dissemination among captive chimpanzees of the habit of playing with novel objects; Menzel *et al.* (1972) have provided compelling evidence of the social transmission of two patterns of play behavior involving the approach to and manipulation of normally avoided novel objects.

Menzel (1966, p. 134) has also described a particularly intriguing observation of apparent intentional transmission of avoidance behavior in free-living Japanese macaques (see also Menzel, 1973, p. 200). On "more than six occasions,"

adult females were observed to pull their offspring away from a novel object that the females themselves were avoiding. No mention is made of the long-term effects of this interaction on the behavior of the young. However, in a laboratory analog, Stephenson (1967) trained adult male and female rhesus monkeys to avoid manipulating an object and then placed individual naive animals in a cage with a trained individual of the same age and sex and the object in question. In one case, a trained male actually pulled his naive partner away from the previously punished manipulandum during their period of interaction, whereas the other two trained males exhibited what were described as "threat facial expressions while in a fear posture" when a naive animal approached the manipulandum. When placed alone in the cage with the novel object, naive males that had been paired with trained males showed greatly reduced manipulation of the training object in comparison with controls. Unfortunately, training and testing were not carried out using a discrimination procedure so the nature of the transmitted information cannot be determined, but the data are of considerable interest.

D. BIRD VOCALIZATIONS

As mentioned in the Introduction, cases in which the occurrence of species typical song in adulthood require exposure to conspecific song during the fledgling period lie outside the range of phenomena to be considered here, because the transmitter is incapable of acquiring the relevant pattern of behavior in the absence of interaction with conspecifics. However, one aspect of the ontogeny of bird song may exemplify the social transmission of an acquired behavior in the sense in which the term has been employed here. A number of species of song bird show regular differences in the song pattern produced by members of geographically distinct breeding populations. The detailed structure of the song varies little among animals resident in one area but is consistently different between geographic populations (Armstrong, 1965). In one species, the white-crowned sparrow, laboratory analysis of the ontogeny of these dialects indicates that they, like the typical song, are acquired by juveniles during the first 100 days of life as a result of experiencing the song of older males that sing in the same dialect (Marler and Tamura, 1964). It is possible that the specific dialect within an area is a modification in song pattern introduced by an individual who acquired it in some way and transmitted it to his progeny. If this admittedly speculative account of dialect origins is correct, then song dialect traditions would be transmitted acquired patterns of behavior.

III. LEARNING AND CONDITIONING PARADIGMS

As the preceding discussion indicates, observers of animals in their natural

habitats have reported a wide variety of behaviors in a number of vertebrate species which may be interpreted as traditional in nature, that is, as resulting from the transmission of acquired behavior from individual to individual. In most instances this interpretation has not been established by adequate experimentation in either laboratory or field settings.

It has been proposed (Lehrman, 1970) that one task of the student of animal behavior is to seek an understanding of the sources of the behavior of organisms in their ontogeny and phylogeny. In pursuit of this goal many studies have been performed to determine the role of hereditary factors and individual experience in the development of adult behavioral phenotypes. There are, however, relatively few laboratory studies concerned with the role of behavioral transmission in the development of behavior. Ethologists have often implicitly assumed that such transmission is possible, and the frequently employed Kasper-Hauser or isolation-rearing design has served in part to control for behavior acquired through conspecific interaction. However, with some exceptions, little direct laboratory investigation of behavior acquisition through social interaction has been undertaken by ethologically oriented researchers. Most laboratory studies of transmission of behavior has been carried out within the experimental psychological framework.

The approach of experimental psychologists to the problem of behavior transmission has generally been to seek to extend the Skinnerian and Pavlovian paradigms to incorporate cases in which conspecific behavior serves as a discriminative stimulus for some learned response or as an unconditioned stimulus for some reflexive behavior and, thereby, to explain apparent "imitative" behavior in laboratory settings. The studies of learning by "imitation" undertaken by Thorndike (1911) played a fundamental role in the development of North American psychology and determined the approach to the study of social learning phenomena subsequently pursued. It is, therefore, worth considering the conclusions he reached from investigations of what would now be labeled observational learning.

During the latter part of the nineteenth century, students of animal behavior, Romanes (1882), in particular, believed that animals could readily learn to perform complex tasks by imitating the observed behavior of others. Supporting data were entirely anecdotal. Thorndike undertook a careful examination of the possibility that animals (cats, chickens, dogs, monkeys) could learn by "the formation of associations by imitation" (Thorndike, 1911, p. 81). As is well known, the general results were entirely negative; neither cats, dogs, monkeys, nor chicks proved capable of learning arbitrary tasks as a result of observing trained conspecifics perform these tasks. Thorndike reached the conclusion that "learning to do an act from seeing it done" did not play an important role in the development of behavior. Apparently imitative behavior was seen as identical in its process of acquisition to other types of learned performance, as depending

on the interaction of instinct, the law of effect, and the law of exercise. Experimental psychologists have generally adopted Thorndike's approach to behavioral transmission, treating it as a special case of trial and error learning, although more recent studies of observational learning in cats (Adler, 1955; Chesler, 1969; John *et al.*, 1968; Herbert and Harsh, 1944) and monkeys (Darby and Riopelle, 1959; Warden *et al.*, 1940; Warden and Jackson, 1935; but see Hall, 1963) suggest that there are situations in which observational learning may occur.

For the purpose of this discussion we will briefly describe only the work of Miller and Dollard, of Skinner, and of Church to indicate the approach of experimental psychologists working on problems of social learning within the Thorndikian tradition.² In their classic text, "Social Learning and Imitation," Miller and Dollard (1941) restrict their discussion of animal social learning to what they call "matched dependent behavior." In matched dependent behavior the behavior of one organism (the leader) serves as a cue or discriminative stimulus for a second organism (the imitator), indicating the behavior in which the imitator must engage in order to receive reinforcement. In their basic experiment, Miller and Dollard trained groups of rats either to make the same choice as their leader at the junction of a T-maze or to make the opposite choice from him in order to receive food reinforcement. It was found that, after approximately 40 reinforced trials, animals in the appropriate groups learned either to follow or not to follow. In successive experiments it was shown that animals trained with an albino leader in a T-maze for food reinforcement continued to behave appropriately without further training when the leader was changed from albino to black or the motivational state from hunger to thirst. Thus, a learned following response could generalize from one situation to another. Skinner (1953) in his analysis of imitative behavior, similarly indicates that one pigeon can be trained to imitate the behavior of another, but only if specific discriminative reinforcement has occurred. Thus, if one reinforces a pigeon if, and only if, it engages in the same behavior as another pigeon, the behavior of the first pigeon will come to resemble the behavior of the second.

The mechanism proposed by Miller and Dollard and by Skinner is certainly sufficient to produce a certain uniformity in the behavior of contemporaneous members of a group of animals, and it is possible that some behavioral phenomena observed in field situations reflect differential schedules of reinforcement experienced by individuals when they behaved similarly to or differently from conspecific individuals. The fundamental problem with the "matched dependent" model in terms of the definition of social transmission processes proposed here is that it will not suffice as a mechanism for the maintenance of transmitted behavior beyond the period of interaction. Because the behavior of the leader

²For a more complete review see Davis, J. M. 1973. Imitation: A review and critique. In "Perspectives in Ethology" (P. P. G. Bateson and P. H. Klopfer, eds.), pp. 43-72. Plenum, New York.

is the discriminative stimulus for the occurrence of similar behavior in followers, once the leader departs those aspects of the behavior of the followers dependent on the presence of the leader are lost. For the behavior pattern initiated by the leader to become part of the behavioral repertoire of the follower in the absence of the leader, it is necessary for it to be controlled by stimuli that are not dependent on the behavior of the leader.

The most direct examination of the possibility of such a transfer of stimulus control of behavior from a leader organism to some other stimuli in the environment is that of Church (1957). In one experiment, Church trained rats to follow leaders to the left and right arms of a T-maze. After 150 such trials an incidental cue was added such that the leader always entered the arm of the T-maze marked by a light. After 100 such following trials with the incidental cue present, the experimental subjects were tested for a series of 8 trials in the absence of a leader but with the incidental cue available. They showed a marked preference for the lighted arm. As Church (1968, p. 143) has indicated, the principles of incidental learning provide a viable mechanism by which certain behavior patterns may be transmitted among conspecifics and maintained after the departure of the original instigator. For example, the observation by Galef and Clark (1971) that young rats initially approach adults at a food site, eat in their vicinity, become familiar with the flavor of the diet eaten by adults, and develop a long-lasting preference for it, can be understood as an incidental learning process.

Whereas Miller and Dollard, Skinner, and Church considered imitative learning in animals as a special case of discriminative operant conditioning, Humphrey (1921) discussed imitative behavior as a type of Pavlovian conditioning and cited a number of observations in support of this position. For example, Breed had observed that pigeons, placed in a cage where they could observe others pecking food, pecked the floor of their cages although no food was available to them. According to a Pavlovian conditioning interpretation, the pigeons had in the past pecked the substrate (the unconditioned response) in the presence of food (the unconditioned stimulus). Ground pecking had frequently occurred while other pigeons were pecking the ground (the conditioned stimulus) and, as a result of these repeated pairings of the conditioned and unconditioned stimuli, the sight of other pigeons ground pecking was now sufficient to elicit ground pecking in the subjects. This observation may, however, be more parsimoniously explained within the ethological model by assuming that, in the pigeon, ground pecking by one individual serves to release ground pecking in conspecifics. Little experimental investigation has been undertaken to determine the role of conditioning processes in such situations.

An alternative Pavlovian model for the transmission of behavior between conspecifics has been developed by personality theorists for the study of selected aspects of interpersonal behavior (Berger, 1962). It would seem to have consider-

able potential as a basis for the transmission of acquired behavioral responses in animals though it has little empirical support to date. In this model the behavior of one organism is treated as an unconditioned stimulus, the unconditioned response being a similar behavior elicited in the observer, and the conditioned stimulus the stimulus to which the original organism has learned to respond. The possibility of such conditioning depends on the existence in any given instance of an appropriate "contagious" or "infectious" behavior (Armstrong, 1965) in which the performance of a more-or-less instinctive or reflexive pattern of behavior by one individual acts as a releaser for the same behavior in a conspecific (Thorpe, 1956, p. 133). Repeated observations by one organism (the observer) of the response of others (the models) to some stimulus, those responses eliciting similar behavior in the observer, could lead to a conditioned response on the part of the observer to the stimulus eliciting the response in the models. The possibility exists that not only overt behavior but also emotional states may be transmitted in this way (Berger, 1962; Bandura and Rosenthal, 1966). For example, a restrained rat that has observed a conspecific receiving shocks in association with presentation of a red light will subsequently accelerate its own shock avoidance responding in the presence of a red light (Riess, 1972; see also Stephenson, 1967; Menzel, 1973, p. 209). It is possible that such Pavlovian conditioning of contagious behavior is responsible for socially transmitted avoidance behavior or learned approaches to frightening stimuli.

As this brief review indicates, behavior may be transmitted from individual to individual as a result of processes formally similar to those at work in the usual cases of discriminative operant and of Pavlovian conditioning. Unfortunately, the extent to which such modes of behavioral transmission play a role in the development of the behavior of animals in their natural habitats remains undetermined. The relatively large number of trials required in the laboratory to establish the phenomena described above might seem to reduce the probability of their playing a role in field settings. It must be remembered, however, that the freedom of organisms to interact continuously in the wild may result in large numbers of interactions in a relatively brief period of time. Thus, the fixed trial procedures used to control interaction in the laboratory might disguise the rapidity with which social learning could occur under less controlled circumstances.

IV. PROBLEMS OF TERMINOLOGY

A third body of literature relevant to the topic of behavioral transmission is a very broad one involving attempts to categorize the ways in which organisms may influence one another's behavior. The psychological literature, in particular, is rich in terminology seeking to delineate various aspects of the ways in which

the behavior of one organism can influence the behavior of another. Some investigators prefer purely descriptive terms even though these can obscure differences in the mechanisms underlying surface similarities in behavioral interaction (allelomimetic behavior, social facilitation). Others utilize terminology reflecting hypothesized underlying mechanisms mediating observed behavioral interaction (coaction, local enhancement, matched dependent behavior, copying), and there are those who employ operationally defined categories (following, observational learning). Unfortunately, some terms (mimesis, contagious behavior, and social facilitation) have been used to refer to very different phenomena by different authors. As Oldfield-Box (1970) has noted, one of the major impediments to systematic investigation in this area stems from the confusion in terminology and the replacement of analysis of instances of social learning by a rather arbitrary labeling of inadequately explored phenomena.

The problems with attempts at classifying the possible social processes resulting in the transmission of acquired behavior are probably not purely semantic in origin. The difficulties inherent in attempting to categorize a wide range of complex interactions within a limited conceptual framework become apparent when one begins to explore the wealth of interactions that could result in a modification of the behavior of one organism toward homogeneity with that of another. To give a partial indication of this complexity (ignoring, for the moment, alternative mechanisms mediating similar observed effects on behavior) it is sufficient to outline some of the possible alterations in behavior of an individual organism A as a result of its exposure to a conspecific organism B in some environment E. For purposes of simplicity in this discussion, it will be assumed that the observer is already familiar with both A and B's behavior in E prior to A's experiencing B in E, although other procedures than using A as his own control are possible and, in many situations, preferable in the study of social interactions.

After experiencing B in E, (1) A may exhibit a motor pattern not previously in his repertoire while in E. (2) A may exhibit a change in the temporal or spatial distribution of his previous responses in E or in the stimuli eliciting or controlling his behavior in E. (3) Alterations in A's behavior in E may or may not outlast the period of interaction of A and B in E.

There are not only a variety of types of alterations in A's behavior possible in response to experiencing B, but also a variety of possible interactions between A and B in E.

1. Organism A may not encounter E until B has already departed from E. Interaction in this case would depend on durable alterations in E resulting from B's presence in E.

2. Organism A may observe some aspect of B's activities in E without actually co-occupying E with B.

3. Organisms A and B may be simultaneously present in E and free to interact

fully. This interaction between A and B in E may take many forms: A may approach or avoid B, follow B or flee from it, behave amicably, aggressively, submissively, sexually, or any of a variety of other ways toward it.

In attempting to reduce the large number of possible combinations and permutations of interactions and changes in behavior to a workable number of categories, important differences in both their causes and effects become obscured. Thus, to label a change in behavior as resulting from coaction [the presence of others leading to enhancement of dominant and well-developed responses (Zajonc, 1965, 1969)] leads to the strange situation of placing in the same category the observation that each of a pair of ants will dig faster than either alone (Chen, 1937; disputed by Sudd, 1972) and the observation that 2 human cyclists ride faster than one alone, although the mechanisms mediating these effects are in all probability quite disparate.

Again, wild rat pups approach adults, eat in their vicinity, learn incidental cues concerning the diet they eat, and show continued avoidance of alternative diets as a consequence of their neophobia. Juvenile mountain sheep follow adults and, thus, learn their way about their scattered home ranges. The social interaction responsible for the transmission of behavior is similar in the two cases, depending on a tendency of young to remain in the proximity of conspecifics, yet there seems to be little gain in categorizing the two behaviors as examples of socially facilitated or allelomimetic behavior. Such labeling of the interaction adds nothing to our understanding of the mechanisms or interactions responsible for the occurrence of the behavior of interest. The necessary precursors to useful classification are the precise description of the effects of social interaction, the determination of the necessary and sufficient conditions for the occurrence of observed changes in behavior, and an analysis of the mechanisms mediating those changes. At this early stage of our knowledge it seems premature to impose arbitrary structures on the inadequately analyzed observations available.

The test of a classificatory scheme lies in its heuristic value, and little seems to have been gained from the categorizations proposed to date. In fact, experimental social psychologists interested in animal interactions tend to be satisfied with an analysis of a behavioral social interaction that ends rather than begins with the discovery that the organisms in question show changes in behavior as a result of the interaction. If the result of such interaction is to produce increased homogeneity in the behavior of interactants, the use of such terms as "imitation" or "social facilitation" to describe that interaction seems to reduce the perceived need for an analysis of the mechanisms mediating the observed alteration in behavior or for a determination of the necessary and sufficient conditions for its occurrence.

It is possible that the discussion of behavioral phenomena resulting from social

interaction in terms of their functions or effects (Tinbergen, 1963) rather than their poorly understood causes or underlying mechanisms would prove useful. The focusing of attention on the results of an interaction might point to the need for analyses, in terms of observable events, of the processes by which those results were achieved and might help to avoid the errors of explanation by denotation that, as Oldfield-Box (1970) has pointed out, hinder progress in the area.

V. CONCLUSIONS

The preceding review of the literature, although in no way comprehensive, is intended to give a broad overview of the current state of knowledge of the means by which organisms are able to transmit acquired behavior. It is clear that much work is to be done before a complete picture of the processes involved is reached. Numerous instances of apparent behavioral transmission reported by field observers must be examined under controlled conditions to permit analysis of the mechanisms by which transmission proceeds, and an effort must be made to ascertain the adequacy of laboratory-derived models of behavioral transmission to explain the behavior of organisms in their natural environment.

There are at least two central questions. First, what is it that is being transmitted and, second, what are the mechanisms by which transmission is achieved? Although it is probably premature to attempt to answer these questions in the light of current knowledge, two general principles seem to emerge from consideration of the data described here. First, with respect to the nature of transmitted material, there would appear to be relatively few cases (bird song dialect, "placer-mining" of wheat) in which actual motor patterns are communicated from one individual to another. In almost every case, the motor patterns involved seem to develop independently of social interaction. Acquired stimulus control of behavior rather than acquired motor patterns themselves are the usual messages passing between individuals. Jackdaws, for example, do not learn to flee nor Japanese macaques to eat as a result of social interaction. Knowledge of the appropriate context within which to engage in these activities is acquired as a result of experience with conspecifics.

Second, if the preceding analysis of the message content is sound, then the mechanisms by which social transmission of behavior proceed should be ones that enable stimulus control of behavior to pass from one individual to another. This does, in fact, seem to be the case. In all but a few instances transmission of behavior appears to result in large part from the introduction by one organism of another into a stimulus situation to which the second organism is predisposed,

either as a result of previous experience or of instinctive tendencies, to respond in such a way as to acquire the behavior of the first organism (Ewer, 1969). In many cases, especially those involving transmission of behavior from parent to offspring, the social component of the interaction may be almost trivial, involving nothing more than giving birth to offspring in one locale rather than another. The continuity of reproductive behavior in one location from generation to generation, for example, depends on a tendency in the young to return to their place of birth to reproduce. Similarly the tendency of young to remain in close proximity to conspecific adults, may result in their acquiring adult feeding habits, home ranges, predatory patterns, or responses to potentially dangerous stimuli; but the particular response acquired depends on the reaction of the follower to the stimulus events to which the leader introduces him. This may be the case whether the "remaining close" response or the response to the stimulus situation is, for want of better terms, conceived as "instinctive" or "learned." Even in those cases in which the social interaction between initiator and acquirer seems more directly evolved for purposes of transmission of behavior, as is the case, for example, in the feeding behavior of maternal meerkats (Ewer, 1963, p. 592), otters (Liers, 1951), or mother hens (Hogan, 1966), the acquisition of the adult feeding patterns by the young depends on the tendency of the young to respond appropriately to the stimuli presented to them by their parents. The observed behavioral transmission, thus, results from a combination of social interactions and a predisposition to respond in a particular way to the stimuli encountered as a result of these social interactions. Maintenance of the transmitted behavior may depend either on the reinforcement contingent on engaging in the pattern of behavior in question or a predisposition to behave in certain ways toward some class of stimuli once they are experienced.

The conceptual dichotomy between the inheritance and individual acquisition of behavior embodied in the nature-nurture controversy of the 1950s has tended to obscure the existence of developmental processes involving the interaction of genetic and environmental effects in determining the behavior of individuals. Perhaps, as a consequence, the empirical analysis of the social transmission of behavior resulting from such interactions has been largely ignored by contemporary students of behavior. It is hoped that this intrinsically interesting aspect of the ontogeny of behavior will receive greater attention in the future.

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References

- Adler, H. E. 1955. Some factors of observational learning in cats. *J. Genet. Psychol.* 86, 159-177.
- Armstrong, E. A. 1965. "Bird, Display and Behavior." Dover, New York.
- Bandura, A., and Rosenthal, T. L. 1966. Vicarious classical conditioning as a function of arousal level. *J. Pers. Social Psychol.* 3, 54-62.
- Berger, S. M. 1962. Conditioning through vicarious instigation. *Psychol. Rev.* 69, 450-466.
- Calhoun, J. B. 1962. "The Ecology and Sociology of the Norway Rat." U.S. Dep. Health, Educ. Welfare, Bethesda, Maryland.
- Carpenter, C. R. 1934. A field study of the behavior and social relations of howling monkeys. *Comp. Psychol. Monogr.* 10, No. 2, Serial No. 43.
- Chen, S. C. 1937. Social modification of the activity of ants in nest-building. *Physiol. Zool.* 10, 420-436.
- Chesler, P. 1969. Maternal influence in learning by observation in kittens. *Science* 166, 901-903.
- Church, R. M. 1957. Transmission of learned behavior between rats. *J. Abnorm. Social Psychol.* 34, 163-165.
- Church, R. M. 1968. Applications of behavior theory to social psychology: Imitation and competition. In "Social Facilitation and Imitative Behavior." (E. C. Simmel, R. A. Hoppe, and G. D. Milton, eds.), pp. 135-167. Allyn & Bacon, Boston, Massachusetts.
- Cushing, J. E., Jr. 1944. The relation of nonheritable food habits to evolution. *Condor* 46, 265-271.
- Darby, C. C., and Riopelle, A. J. 1959. Observation learning in the rhesus monkey. *J. Comp. Physiol. Psychol.* 52, 94-98.
- Darling, F. F. 1937. "A Herd of Red Deer." Oxford Univ. Press, London and New York.
- Ehrenfeld, D. W. 1974. Conserving the edible sea turtle: Can mariculture help? *Amer. Sci.* 62, 23-31.
- Emlen, J. T., Jr. 1938. Midwinter distribution of the American Crow in New York State. *Ecology* 19, 264-275.
- Ewer, R. F. 1963. The behaviour of the Meerkat, *Suricata suricatta* (Schreber). *Z. Tierpsychol.* 20, 570-607.
- Ewer, R. F. 1969. The "instinct to teach." *Nature (London)* 222, 698.
- Fisher, J., and Hinde, R. A. 1949. The opening of milk bottles by birds. *Brit. Birds* 42, 347-357.
- Galef, B. G., Jr., and Clark, M. M. 1971. Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups. *J. Comp. Physiol. Psychol.* 75, 341-357.
- Galef, B. G., Jr., and Clark, M. M. 1972. Mother's milk and adult presence: Two factors determining initial dietary selection by weanling rats. *J. Comp. Physiol. Psychol.* 38, 220-225.
- Galef, B. G., Jr., and Henderson, P. W. 1972. Mother's milk: A determinant of the feeding preferences of weaning rat pups. *J. Comp. Physiol. Psychol.* 78, 213-219.
- Galef, B. G., Jr., and Sherry, D. F. 1973. Mother's milk: A medium for the transmission of cues reflecting the flavor of mother's diet. *J. Comp. Physiol. Psychol.* 83, 374-378.
- Gandolfi, G., and Parisi, V. 1972. Predazione su *Unio pictorum* L. da parte del ratto, *Rattus norvegicus* (Berkenhout). *Acta Natur.* 8, 1-27.
- Gandolfi, G., and Parisi, V. 1973. Ethological aspects of predation by rats, *Rattus norvegicus* (Berkenhout), on bivalves *Unio pictorum*, L. and *Cerastoderma lamarcki* (Reeve). *Boll. Zool.* 40, 69-74.
- Geist, V. 1971. "Mountain Sheep." Univ. of Chicago Press, Chicago, Illinois.

- Hall, K. R. L. 1962. Numerical data, maintenance activities and locomotion of the wild chacma baboon, *Papio ursinus*. *Proc. Zool. Soc. London* **139**, 181-220.
- Hall, K. R. L. 1963. Observational learning in monkeys and apes. *Brit. J. Psychol.* **54**, 201-226.
- Harlow, H. F., and Harlow, M. K. 1965. The affectional systems. In "Behavior of Non-human Primates" (A. M. Schrier, H. F. Harlow, and F. Stollnitz, eds.), Vol. 2, pp. 287-334. Academic Press, New York.
- Hasler, A. D. 1966. "Underwater Guideposts." Univ. of Wisconsin Press, Madison.
- Hediger, H. 1964. "Wild Animals in Captivity." Dover, New York.
- Herbert, M. J., and Harsh, C. M. 1944. Observational learning by cats. *J. Comp. Psychol.* **37**, 81-95.
- Hinde, R. A. 1954. Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*). I. The nature of the response, and an examination of its course. *Proc. Roy. Soc., Ser. B*, **142**, 306-331.
- Hinde, R. A., and Fisher, J. 1951. Further observations on the opening of milk bottles by birds. *Brit. Birds* **44**, 392-396.
- Hinde, R. A., and Fisher, J. 1972. Some comments on the republication of two papers on the opening of milk bottles by birds. In "Function and Evolution of Behavior" (P. H. Klopfer and J. P. Hailman, eds.), pp. 377-378. Addison-Wesley, Reading, Massachusetts.
- Hochbaum, H. A. 1955. "Travels and Traditions of Waterfowl." Univ. of Minnesota Press, Minneapolis.
- Hogan, J. A. 1966. An experimental study of conflict and fear: An analysis of behavior of young chicks toward a mealworm. Part II. The behavior of chicks which eat the meal worm. *Behaviour* **27**, 273-289.
- Humphrey, G. 1921. Imitation and the conditioned reflex. *Pedagog. Seminary J. Genet. Psychol.* **28**, 1-21.
- Immelman, K. 1972. Sexual and other long-term aspects of imprinting in birds and other species. In "Advances in the Study of Behavior" (D. S. Lehrman, R. A. Hinde, and E. Shaw, eds.), Vol. 4, pp. 147-169. Academic Press, New York.
- John, E. R., Chesler, P., Bartlett, F., and Victor, I. 1968. Observation learning in cats. *Science* **159**, 1489-1491.
- Kawai, M. 1965. Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Inlet. *Primates* **6**, 1-30.
- Kawamura, S. 1959. The process of sub-culture propagation among Japanese macaques. *Primates* **2**, 43-60.
- King, J. 1955. Social behavior, social organization and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. *Contrib. Lab. Vertebr. Biol., Univ. Mich.* No. 67.
- Klopfer, P. H. 1961. Observational learning in birds: The establishment of behavioral modes. *Behaviour* **17**, 71-80.
- Klopfer, P. H. 1969. "Habitats and Territories." Basic Books, New York.
- Klopfer, P. H., and Hailman, J. P. 1965. Habitat selection in birds. In "Advances in the Study of Behavior" (D. S. Lehrman, R. A. Hinde, and E. Shaw, eds.), Vol. 1, pp. 279-303. Academic Press, New York.
- Kruuk, H. 1972. "The Spotted Hyena." Univ. of Chicago Press, Chicago, Illinois.
- Kruuk, H., and Turner, M. 1967. Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. *Mammalia* **31**, 1-27.
- Kuo, Z. Y. 1930. The genesis of the cat's response to the rat. *J. Comp. Psychol.* **11**, 1-35.

- Kuo, Z. Y. 1938. Further study on the behavior of the cat toward the rat. *J. Comp. Psychol.* **25**, 1-8.
- Kuo, Z. Y. 1967. "The Dynamics of Behavior Development." Random House, New York.
- Lehrman, D. S. 1970. Semantic and conceptual issues in the nature-nurture problem. In "Development and Evolution of Behavior" (L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt, eds.), pp. 17-52. Freeman, San Francisco, California.
- Leyhausen, P. 1956. Verhaltensstordien an Katzen. *Z. Tierpsychol.* No. 2.
- Liers, E. E. 1951. Notes on the River Otter (*Lutra canadensis*). *J. Mammal.* **32**, 1-9.
- Lorenz, K. 1952. "King Solomon's Ring." Crowell, New York.
- Mainardi, D. 1970. La trasmissione culturale. *Boll. Zool.* **37**, 449-456.
- Mainardi, D. 1973. Biological basis of cultural evolution. *Atti Accad. Naz. Lincei, Cl. Sci. Fis., Mat. Natur., Rend.* **182**, 175-188.
- Marler, P., and Tamura, M. 1964. Culturally transmitted patterns of vocal behavior in sparrows. *Science* **146**, 1483-1486.
- Matthews, G. V. T. 1968. "Bird Navigation," 2nd Ed. Cambridge Univ. Press, London and New York.
- Menzel, E. W., Jr. 1966. Responses to objects in free-ranging Japanese monkeys. *Behaviour* **26**, 130-150.
- Menzel, E. W., Jr. 1973. Leadership and communication in young chimpanzees. In "Pre-cultural Primate Behavior" (E. W. Menzel, Jr., ed.), pp. 192-225. Karger, Basel.
- Menzel, E. W., Jr., Davenport, R. K., and Rodgers, C. M. 1972. Protocultural aspects of chimpanzees' responsiveness to novel objects. *Folia Primatol.* **17**, 161-170.
- Miller, N. E., and Dollard, J. 1941. "Social Learning and Imitation." Yale Univ. Press, New Haven, Connecticut.
- Nordeng, H. 1971. Is the local orientation of anadronous fishes determined by pheromones? *Nature (London)* **233**, 411-413.
- Norton-Griffiths, M. 1967. Some ecological aspects of the feeding behaviour of the Oystercatcher *Haematopus ostralogus* on the edible mussel *Mytilus edulis*. *Ibis* **109**, 412-424.
- Oldfield-Box, H. 1970. Comments on two preliminary studies of "observational" learning in the rat. *J. Genet. Psychol.* **116**, 45-51.
- Rabinowitch, V. 1969. The role of experience in the development and retention of seed preferences in Zebra finches. *Behaviour* **33**, 222-236.
- Riess, D. 1972. Vicarious conditioned acceleration: Successful observational learning of an aversive Pavlovian stimulus contingency. *J. Exp. Anal. Behav.* **18**, 181-186.
- Romanes, G. J. 1882. "Animal Intelligence." Kegan, Paul, Trench, London.
- Schaller, G. B. 1967. "The Deer and the Tiger." Univ. of Chicago Press, Chicago, Illinois.
- Schaller, G. B. 1972. "The Serengeti Lion." Univ. of Chicago Press, Chicago, Illinois.
- Schloeth, R., and Burckhardt, D. 1961. Die Wanderungen des Rotwildes *Cervus elaphus* L. im Gebiet des Schweizerischen National-parkes. *Rev. Suisse Zool.* **68**, 146-155.
- Skinner, B. F. 1953. "Science and Human Behavior." Macmillan, New York.
- Smith, N. G. 1968. The advantages of being parasitized. *Nature (London)* **219**, 690-694.
- Snyder, L. L. 1948. Tradition in Bird Life. *Can. Field Natur.* **62**, 75-77.
- Solomon, D. J. 1973. Evidence for pheromone influenced homing by migrating Atlantic salmon, *Salmo salar* (L.). *Nature (London)* **244**, 231-232.
- Stephenson, G. R. 1967. Cultural acquisition of a specific learned response among rhesus monkeys. In "Progress in Primatology" (D. Starek, R. Schneider, and H. J. Kuhn, eds.), pp. 279-288. Fischer, Stuttgart.
- Sudd, J. H. 1972. The absence of social enhancement of digging in pairs of ants (*Formica lemani* Bondroit). *Anim. Behav.* **20**, 813-819.

- Telle, H. J. 1966. Beitrag zur Kenntnis der Verhaltensweise von Ratten, vergleichend dargestellt bei *Rattus norvegicus* und *Rattus rattus*. *Z. Angew. Zool.* 53, 129-196. (Eng. transl. *Nat. Res. Council. Can., Tech. Transl.* No. 1608.)
- Thorndike, E. L. 1911. "Animal Intelligence." Hafner, Darien, Connecticut.
- Thorpe, W. H. 1945. The evolutionary significance of habitat selection. *Anim. Ecol.* 14, 67-70.
- Thorpe, W. H. 1956. "Learning and Instinct in Animals," 2nd Ed. Methuen, London.
- Tinbergen, N. 1963. On aims and methods of ethology. *Z. Tierpsychol.* 20, 410-429.
- Turner, E. R. A. 1964. Social feeding in birds. *Behaviour* 24, 1-46.
- van Lawick-Godall, J. 1968. The behaviour of free-living Chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.* 1(3), 161-311.
- van Lawick-Goodall, J. 1970. Tool-using in primates and other vertebrates. In "Advances in the Study of Behavior" (D. S. Lehrman, R. A. Hinde, and E. Shaw, eds.), Vol. 3, pp. 195-249. Academic Press, New York.
- von Steiniger, F. 1950. Beiträge zur soziologie und sonstigen Biologie der Wanderratte. *Z. Tierpsychol.* 7, 356-379.
- Warden, C. J., and Jackson, T. A. 1935. Imitative behavior in the Rhesus monkey. *J. Genet. Psychol.* 46, 103-125
- Warden, C. J., Fjeld, H. A., and Koch, A. M. 1940. Imitative behaviour in Cebus and Rhesus monkeys. *J. Genet. Psychol.* 56, 311-322.
- Wecker, S. C. 1963. The role of early experience in habitat selection by the Prairie Deer Mouse, *Peromyscus maniculatus bairdi*. *Ecol. Monogr.* 33, 307-325.
- Wortis, R. P. 1969. The transition from dependent to independent feeding in the young ring dove. *Anim. Behav. Monogr.* 2, 1-54.
- Wynne-Edwards, V. C. 1962. "Animal Dispersion in Relation to Social Behaviour." Hafner, New York.
- Zajonc, R. B. 1965. Social facilitation. *Science* 149, 269-274.
- Zajonc, R. B. 1969. "Animal Social Psychology." Wiley, New York.