

---

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

---

BENNETT G. GALEF, JR.

DEPARTMENT OF PSYCHOLOGY  
MCMASTER UNIVERSITY  
HAMILTON, ONTARIO, CANADA

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 intraspecific 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).<sup>1</sup> 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

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

