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Cultural transmission of learned behavior among male bobwhite quail (*Colinus virginianus*)

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Cultural transmission of utilization of a learned food source was demonstrated across five sequential cultural generations of male bobwhite quail. Inclusion of control procedures that allow estimation of the probable spontaneous occurrence of the behavior, which unfortunately are not included in many studies of cultural transmission phenomena, indicated that, although behavioral acquisition also occurred among female bobwhite quail, the acquisition could not be attributed to cultural transmission among the females.

A topic of theoretical and practical importance to all disciplines concerned with behavioral development is the nongenetic transmission of learned behavior among nonhuman conspecifics. This has sometimes been referred to as "cultural transmission" and has periodically been of considerable interest to various contributory disciplines such as comparative anthropology, ethology, behavioral ecology, behavior genetics, developmental psychology, and sociobiology (Klopfer & Hailman, 1972; Kroeber, 1963; Ricklets, 1973; Wilson, 1975). There has been a burgeoning of literature purporting to deal with the cultural transmission of a wide variety of behaviors within a wide range of species. However, a recent review (Passe, Note 1) concluded that although fascinating and suggestive, this literature is, with few exceptions, devoid of the experimental controls that would be sufficient to differentiate cultural transmission from independent individual acquisition wherein acquisition varied as a function of subject variables such as age and sex. The most notable exceptions in which experimental rigor is sufficient to demonstrate cultural transmission include the studies by Galef (1971, 1976; Galef & Clark, 1971; Galef & Heiber, 1976) concerned with the ontogeny of dietary preferences among rats (*Rattus norvegicus*) and investigations concerned with the acquisition of vocal behavior in various passerine bird species (cf. Marler, 1970; Nottebohm, 1972).

A problem central to the demonstration of cultural transmission is that knowledge of a baseline or "spontaneous" level of behavioral acquisition is essential for determining the extent to which changes in frequency of occurrence of any behavior might be the result of acquisition occurring independently for different individuals or be mediated by cultural processes. Sufficient control procedures have simply not been included in most research designs, and control data have not been reported or are not available for the fascinating anecdotal accounts given from field observations (Passe, 1978).

A primary purpose of the research presented here was to ascertain whether or not the propagation of a behavior via cultural transmission could be demonstrated across several behavioral generations using experimental procedures that provide baseline control data. The procedures employed allow an ascertainment of baseline levels of the behavior in question for all subjects for each behavioral generation. The species chosen (bobwhite quail, *Colinus virginianus*) is one in which individuals under natural conditions spend much of their time in apparently stable social groupings (Bent, 1963; Johnsgard, 1973) and might therefore be expected to display cultural phenomena.

METHOD

Subjects

Fifteen naive adult male and 14 naive adult female bobwhite quail (*Colinus virginianus*) served as subjects. They were incubator hatched and prior to the study were housed in mixed-sex lots of two to four individuals. The cages were 30.5 x 50.8 x 22.8 cm. During the study subjects were housed in groups of two or three. Food and water were continually available in the home cages.

Apparatus

The experimental space consisted of an indoor flight room measuring 2.9 x 1.8 x 3.7 m. It contained a small tree, a shelter in one corner, and a metal tray centered along one wall. A water container and covered food cup (6.5 cm diam, 1.2 cm deep) were placed on the tray approximately .5 m apart. The food

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cup contained commercially available gamebird chow (Purina) and was covered by an 11 x 13 cm piece of thin (onion skin) opaque paper secured in place by a rubber band. Wood shavings covered the floor and metal tray.

Procedure

The behavioral act monitored consisted of removing a tightly secured paper cover from a food cup. No requirement was placed on response topography. The paper cover was counted as removed if a hole had been pecked or scratched in it large enough to allow removal of the grain.

The food container was inspected once in the morning and once in the evening each day and counted as open or intact. At each inspection the paper cover was replaced, regardless of the presence or absence of holes in it.

The procedure consisted of four phases: The first phase extended from Day 0 to Day 3.5. It was a pretreatment baseline observation period, during which the social unit, always same-sex and usually a dyad, was placed in the flight room and observed for spontaneous removal of the paper covering the food cup. For one behavioral generation, a triad was introduced. This was done as a control procedure to determine if the presence of three subjects was sufficient to occasion opening of the cup. It was not.

In Phase 2, a single conspecific, either trained or naive to the experimental setting, was introduced and remained for 2 days. An initial single male and female were trained by the experimenter to open the food cup. These were then introduced to the first male and female generations, respectively. All later introduced trained birds were obtained from previous behavioral generations and had not been trained by the experimenter.

For one group of males and one group of females, a naive conspecific was introduced as a control procedure to determine if the mere addition of a third animal to the group might occasion opening of the cup. It did not. On those occasions, after 2 days, the naive bird was removed and a trained conspecific introduced for 2 more days.

Phase 3 was a 2-day period during which the original social unit was again tested for removal of the cover from the food cup.

During the final phase, each individual subject was tested alone in the flight room for food-cover removal. This phase lasted 2 days for each subject. Subjects were housed in their home cages while awaiting individual testing.

Following final individual testing, a next behavioral generation was initiated with the introduction of another naive group. Phases 1-4 were repeated sequentially until all groups were tested. The sequence of procedures was followed first for males and then for females. One additional dyad of males and one additional dyad of females was simply placed in the apparatus and tested for spontaneous cup openings for 4.5 and 3.5 days, respectively.

RESULTS AND DISCUSSION

The results can be very simply summarized. For males, of the six groups tested for spontaneous openings of the food cup, none opened it spontaneously. Of the five male groups tested for the transmission of learned behavior, all five demonstrated acquisition as a function of an introduced trained conspecific. Furthermore, each of the individual subjects across the five cultural generations demonstrated proficiency at opening the covered cup when subsequently tested individually. Thus for males no individual or group spontaneously acquired the behavior while acquisition was promulgated behaviorally across five sequential cultural generations.

The results for the female replication were less clear-cut. Of the six groups tested for spontaneous opening of the cup, three spontaneously opened the cup. Of the five of these groups subsequently tested for cultural transmission, two demonstrated an effect. The other three groups opened the cup spontaneously, that is, prior to the introduction of a trained conspecific. All of the female subjects that had been exposed to the opening of the cup demonstrated proficiency at cup opening when later tested individually.

In addition, two of the female groups displayed levels of aggressive interaction that resulted in the removal of a member of the group due to its moribund condition. Such a high level of vigorous aggression was not displayed in the male groups. Although general theoretical suggestions exist that predict higher levels of agonistic interactions among conspecific females than among conspecific males for birds generally (Whitney, 1976), aggression was not systematically quantified during this study.

With the number of social units included in the present study, the frequency of females vs. males opening the cup spontaneously was not significantly different (Fisher one-tailed exact probability test, $p = .12$).

In the absence of data from control groups, the results of the present experiments might be interpreted as indicating that cultural transmission of behavior was demonstrated by both male and female groups, since all males and all females opened the cup after introduction of a trained conspecific.

However, inclusion of the control data lacking from most studies in this area leads to quite another interpretation, since three of the six female groups opened the cup without prior exposure to a trained conspecific. Male groups clearly demonstrated cultural transmission across five generations, since none of six male groups spontaneously engaged in the behavior during the baseline control procedure.

It is clear that among males the promulgation of the behavior across groups was culturally maintained, since only a single individual introduced only to the first group was trained by the experimenter. All subsequent individuals and group-transfer individuals acquired the behavior from conspecifics. Thus it is apparent that among males the trained subjects in this experiment acted as behavioral programmers for subsequent individuals, resulting in a clear adjustment of the probability of a particular operant response in conspecifics.

Analogous cultural phenomena may be very widespread among animals under natural conditions and could contribute to local group and population differences in behavior. Unfortunately, the descriptive field studies that predominate in the cultural transmission literature are generally unable to clearly demonstrate the very phenomena they attempt to study.

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