

DIFFERENCES IN THE FORAGING BEHAVIOR OF INDIVIDUAL GRAY-BREASTED JAY FLOCK MEMBERS

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Abstract. Among Gray-breasted Jays (*Aphelocoma ultramarina*) subordinates are less successful in certain foraging situations than dominants, the foraging preferences of young birds are not as defined as those of adults, and subadults change their foraging behavior after observing the feeding of other flock members. By averaging behavioral data without regard for variables such as age, status, or social context, information may be lost, and emerging patterns may not be representative of any individual in the study population.

Key Words: Individual variation; age-related differences; cooperative breeding; Corvidae; *Aphelocoma ultramarina*; cultural transmission of information.

In the past, emphasis on detecting patterns in biological systems has minimized appreciation of individual deviations in behavior. Models such as optimal foraging models often assume homogeneity in the foraging abilities of their subjects (Charnov 1976a, Pyke et al. 1977) and may be confounded by the presence of much individual variation; yet, this variation may be important in uncovering the mechanisms producing phenomena of larger scale (Sibly and Smith 1985, Hassell and May 1985), such as cooperative breeding.

I studied individual variation in foraging success and patterns related to differences in the age or dominance status of Gray-breasted Jays by using field observations and experimental manipulations of certain behavioral parameters. My objectives were to examine age, dominance status, and social context as sources of individual behavioral variation that must be considered when designing sampling programs for foraging studies.

Gray-breasted Jays are cooperative breeders that live in groups of 5 to 20 individuals (Gross 1949, Brown 1987). Birds up to three years old (subadults) can be distinguished by pale patches in their bills; by age three (adults) most birds have completely black bills (Pitelka 1961, Brown 1963). Jays at the Southwestern Research Station were color-banded by Jerram and Esther Brown and at Santa Catalina by J. B. Dunning and me. The experiment in the Chiricahua Mountains involved three flocks, including fourteen subordinates and ten dominants. Parts of this study done in Bear Canyon involved one flock with three dominants and seven subordinates; of the subordinates in this flock, three were subadults and four were adults.

The study was done at the Bear Canyon Recreation Area in the Santa Catalina Mountains near Tucson, AZ, and at the Southwestern Research Station of the American Museum of Nat-

ural History, in the Chiricahua Mountains, Cochise County, AZ.

METHODS

Dominance trials

Dominance status was determined by calculating the individual binomial probabilities of winning an aggressive dyadic encounter with a particular flock member at a localized food source (McKean 1988). An individual was categorized as the winner of a bout when it: (1) continued eating while a new arrival (the loser) waited at the food source; (2) displaced an individual already at the food source by displaying, pecking, or merely by approaching the feeding area; or (3) chased the loser away. The technique and most of the criteria were discussed by Barkan et al. (1986). The most dominant bird in a flock was the individual with a significant binomial probability of winning an encounter with all other birds in the flock; the second most dominant individual had a significant probability of winning a bout with every flock member except the most dominant; and so on. I designated at least the top third of the individuals of a flock as dominants or until the binomial probability of a bird's winning dropped below 0.025.

In several cases, I observed ≤ 5 encounters between particular individuals. In these cases I looked for evidence of avoidance behaviors by looking at (1) whether one waited in the trees adjacent to the feeding area, and (2) which individuals used the food source at the same time. When an individual waited for a specific bird to leave the feeder in more than two instances, it was counted as a loser (McKean 1988).

Feeder experiment

This experiment tested (1) the ability of subordinates and dominants to solve a novel foraging problem, and (2) compared the success of individuals when alone to that after observing another flock member at the feeder. To test for effects of learning on success, I divided the trials into early and late periods, with approximately the same numbers of observations in each.

The Santa Catalina experiments were carried out in nine trials of about three hr each between 9–22 October 1984. The Station flock was the subject of 10 trials of up to 2.5 hr each from 28 January to 23 February 1985.

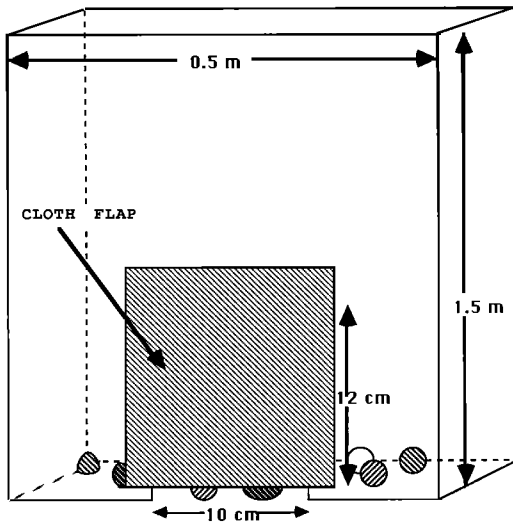


FIGURE 1. Diagram of feeder apparatus.

Trials ended when the flock left the area. I also performed 15 similar trials with the other two Chiricahua flocks. The trials were rotated between the periods of 06:30–09:00, 09:30–12:00, and 13:00–15:30 and tested for time of day (which had no significant effect).

I constructed two plexiglass feeders (Fig. 1), which I operated simultaneously to minimize competition between feeding individuals and other birds or squirrels. Peanuts and sunflower seeds, used as bait, were visible through the plexiglass sides of the feeder. In each feeder, rocks or cardboard slats were used to keep the peanuts near the door where the birds could reach them. The opening to the feeder was covered with a blue cloth flap, which was attached at the top of the opening so that the birds could lift it with their bill or feet and enter the feeder. This feeder was designed to be opened with a sweeping bill movement that the jays use in natural foraging.

I recorded approaches to the feeders, proximity of other individuals, and whether or not the individual was successful, i.e. in removing food. I calculated percent success for each individual (successful attempts/approaches), and I performed arcsine transformations to normalize percentages before executing an ANOVA.

Doughball color choice: color preferences

This experiment tested (1) color preferences of subadult versus older individuals, and (2) cultural transmission of feeding information, which I defined as the spread of information without direct experience with a phenomenon through observation of experienced others (Cavalli-Sforza and Feldman 1981; Fisher and Hinde 1949; Giraldeau 1984; Klopfer 1958, 1961).

I studied the jays' color preferences (25 March to 4 April 1984) for peanut butter doughballs (natural brown, red, and green). Each 1.5-cm-diameter ball was made of a mixture of peanut butter, flour, and egg. Vegetable food coloring was used to color the red and green balls. I placed 20 doughballs of each color on a neutral background on top of a table within the flock's home ter-

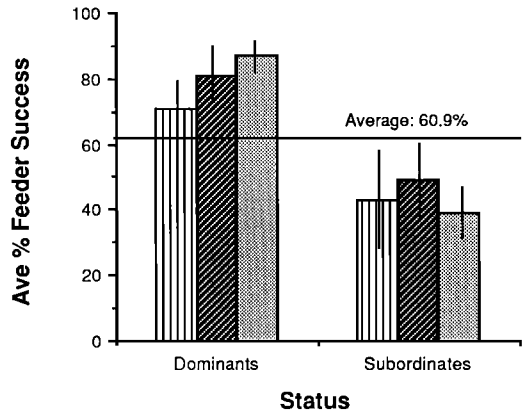


FIGURE 2. Mean percent feeder success for subordinates ($N = 18$) and dominants ($N = 13$) comparing doughball selections made alone (vertically striped bars) with those made after observing another subordinate (cross-hatched bars) or dominant (stippled bars) individual. Each individual made at least 10 attempts.

ritory, arranged so that access by birds was not biased. After approximately half of any particular color had been removed, I replenished the supply to 20 of each color.

I recorded the order of the birds' appearances, color of bait removed, and the identities of other birds present. I used arcsine transformations of all percentages to normalize the distribution (Sokal and Rohlf 1981), and compared colors chosen by each individual within an age-dominance class (dominants, older subordinates and younger subordinates) with those in the other classes using MANOVA (SAS 1985). I also compared color choices made alone with those made after observing another individual.

RESULTS

Dominants ($N = 10$) were significantly more successful than the subordinates ($N = 14$) (Fig. 2) (two-way ANOVA, $F = 8.978$, $df = 24, 48$, $P < 0.0001$), but success rates were not significantly different between birds that had or had not observed another bird (two-way ANOVA, $F = 1.044$, $df = 2, 48$, $P > 0.25$).

Brown was the preferred color overall, but less so by birds that had not observed others foraging (Fig. 3). When the selections of older birds made when alone were compared with those of subadults, they differed significantly (MANOVA, $F = 6.7$, $df = 1, 9$, $P < 0.03$). After observing others, the differences between the selections of birds in the two age classes were not significantly different (MANOVA, $F = 2.7$, $df = 1, 9$, $P > 0.14$).

When alone, older birds exhibited a preference for the brown doughballs and their selections were not significantly altered after watching the choices made by flock mates (paired t-test = 3.328, $df = 6$, $P > 0.1$). However, when young

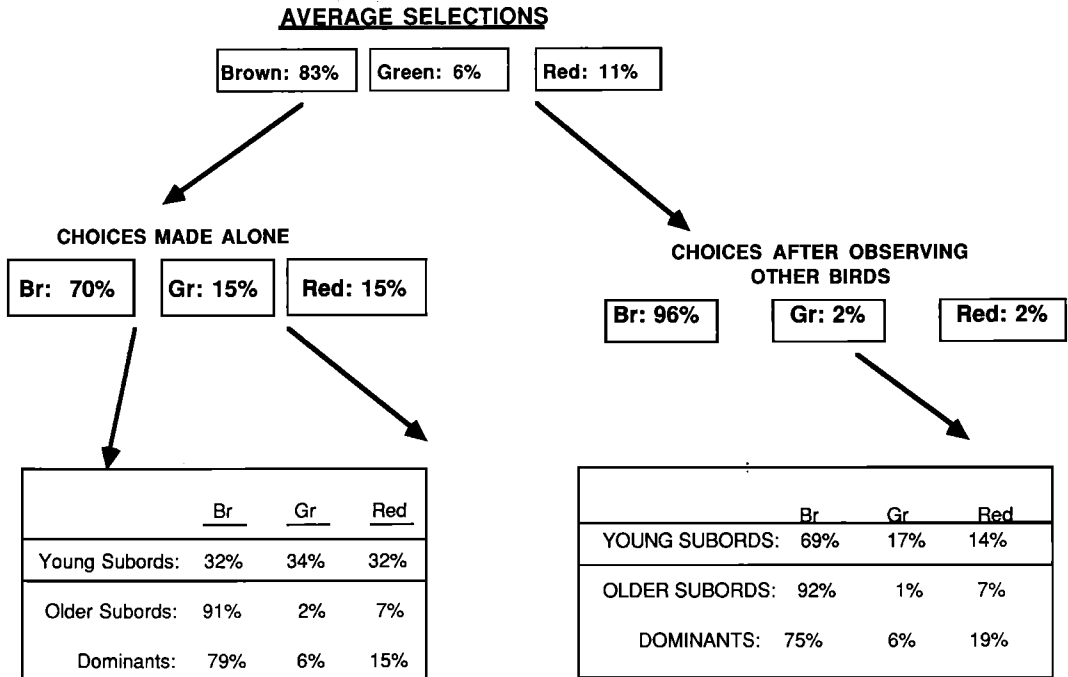


FIGURE 3. Mean percent color choice partitioned into three levels: (1) overall average percent of each color chosen, (2) choices made when feeding alone versus feeding after observing others, and (3) choices made when partitioned by status-age class. Sample sizes were three young subordinates, four older subordinates, and three older dominants, a minimum of 10 selections per individual.

individuals observed the choices of others their selections changed significantly, approximating those of the adult (paired t-test = -15.03, df = 2, P < 0.005) (Fig. 3). After observing another flock member, the young birds chose at least 25% more brown doughballs than when alone.

DISCUSSION

It is becoming increasingly apparent to students of behavior, including many in this symposium (e.g., Grubb and Woodrey), that selection affects individuals differently and is influenced by age, sex, dominance status and specific social context. In order to more accurately describe patterns of foraging (or other) behavior, it may be useful to categorize observations of individuals in a species by these criteria. In a population polymodal for a behavior, a model using averaged responses may not accurately describe the behavior of any individual in the population.

My research suggests that age, dominance rank, and social context contribute to the variability in the feeding behavior of individual Gray-breasted Jays. In this study, I observed that: (1) subordinates were less successful in certain foraging situations than dominants; (2) the foraging preferences of young birds, as defined by color

choice, were not as specific as those of adults; and (3) subadults changed their foraging behavior after observing the feeding of other flock members.

Reduced foraging efficiency in young animals is a well known phenomenon. In species in which foraging behavior is relatively complex (Orians 1969a, Blus and Keahey 1978, Morrison et al. 1978, MacLean 1986, Sasvari 1985, Goss-Custard and Durrell 1987), prolonged subadult periods may reflect the time necessary to acquire foraging and other skills, and depending upon individual abilities may affect reproductive success and other functions, at least short term. Researchers studying other corvid species (Lawton and Guindon 1981, Reese and Kadlec 1985, Hochachka and Boag 1987) have also found age-related differences in abilities, including some foraging skills, affecting reproductive timing and overall success. Even in species such as the Yellow-eyed Junco (*Junco phaeotus*), in which foraging behavior appears relatively simple, age-related variation in foraging efficiency may have profound effects on juvenile mortality patterns (Sullivan 1988).

The variation in feeding patterns, illustrated in this study by disparate selections of colored doughballs by jays of different ages, suggests the

ontogeny of a feeding behavior. Young individuals exhibited less defined preferences than older birds, suggesting that the older individuals had developed a foraging rule narrowing their initial color selections.

Cultural transmission of information may offer an efficient means of acquiring foraging information in a social context (Clark and Mangel 1984, Giraldeau 1984), with less skilled individuals benefiting by following experienced flock members and imitating their behavior (Lawton and Guindon 1981). In my study, the foraging behavior (doughball color choice) of young jays changed after they observed older birds. By averaging the color choices of individual birds without regard for social context, evidence of such interactions would have been blurred.

In this study, as in others (e.g., Ekman and Askenmo 1984, Baker et al. 1981), dominants had significantly more success than subordinates at acquiring food from the feeders, even when the subordinates approached the feeders alone. If the experimental results reflect natural pat-

terns, increased access to food may provide selective advantages to dominants and their offspring.

In order to accurately model behavior, variation resulting from differences in age and dominance classes must be considered, as these may be important in the understanding of behavioral mechanisms fundamental to community structure and demography. Particularly for social species, understanding of dispersal, territoriality, and patch choice, all of which are instrumental in producing large scale phenomena, may hinge upon predicting individual variation in behavior.

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