

Examination of the functional morphology and behavior of these species supports this argument. The bluegill possesses long, fine gill rakers which retain small prey, whereas the pumpkinseed has very short, widely spaced gill rakers that are less effective in retaining small prey but do not foul when sifting organisms from sediments. The bluegill exhibits a greater tendency to school, while the pumpkinseed is more solitary and aggressive; in general, these adaptations are associated, respectively, with open water planktivores and benthic feeding fishes. Thus these two species opt for quite different habitat or prey types when competitive pressure lowers the utility of the vegetation foraging mode. We have evidence that the advantage of the green sunfish in the vegetation stems both from a greater foraging efficiency in this habitat and interference with the foraging of conspecifics. Whether the habitat ordering or segregation is hierarchical or not is not known because experiments with combinations of two species have not yet been performed.

These fish exhibit considerable phenotypic niche flexibility, a trait generally associated with those species inhabiting marginal environments and therefore frequent colonizers (10). We believe that the adaptive significance of plasticity in sunfishes is related to the seasonal patterns in resource availability. The food habits of fish in temperate lakes often converge during the spring flush in food levels; however, as resources decline through the summer and fall, these food habits diverge (11). The ability to shift to foraging patterns that maximize yield during periods of superabundant resources would be of obvious benefit. The increased segregation with decline in resources tends to support the foraging model invoked earlier.

We have demonstrated niche shifts related to the presence of congeneric sunfishes, an indication of the importance of competition in structuring this community. Furthermore, these niche shifts reveal the extent and potential significance of phenotypic niche flexibility. Species such as these, which possess considerable ecological flexibility, hold much promise for experimental study of mechanisms potentially important to the organization of communities.

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5. This observation is based on extensive underwater transect data in several Michigan lakes; manuscript in preparation.
6. Since habitat utilization appeared to be fairly discrete, only 900 individuals were stocked when a species was alone so as not to alter intraspecific competition within a habitat type. The number of fish stocked was chosen on the basis of previous experience so that resource limitation would be evident but would still permit a measurable growth response.
7. Fish exhibit indeterminate or plastic growth, and factors bearing on fitness are generally positively related to size, that is, fecundity [T. Bagenal, in *The Biological Basis of Freshwater Fish Production* (Ed. by J. R. Brett, Academic Press, New York, 1971), p. 105].

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Abstract. *Panhandling was used to study sharing of resources. Male panhandlers were more successful in spring than in autumn. Female panhandlers were more successful than males in autumn. Panhandlers were generally successful only when submissively approaching individuals who were eating. Families and male-female pairs were resistant to panhandling. The results are discussed in terms of reciprocal altruism and kinship selection.*

Food sharing among nonhuman primates has been observed only in chimpanzees (*Pan troglodytes*) (1). Baboons (*Papio anubis*) sometimes tolerate the stealing of food (2). Submissive behaviors and begging gestures are essential displays. Food sharing between related chimpanzees, such as between mother and offspring or between siblings (3), and the portioning of captured prey among the hunters and other familiar conspecifics indicate that there are "rules-of-the-game" as well. These rules may be influenced by kinship selection (4) and reciprocal altruism (5). The evolution of sharing food with relatives could be mediated by kinship selection, with the sharing increasing the fitness of individuals with common genes. Sharing food with individuals who are not relatives but who could benefit the giver or his relatives could be an example of reciprocal al-

truism. Although the sharing of food and other resources is an established practice among humans (6), the important behaviors, contexts, and rules have not been studied in detail until now.

Panhandling is a social situation where a supposedly needy individual requests or begs for money from a potentially helpful stranger. Observations of several panhandlers indicated that sex, eye contact, postural stance, dress, weather, and the amount of money specifically requested may be important in successful panhandling. For our experiment we used several college students as panhandlers. The experiment was designed to answer four questions: (i) What combinations of individuals share with strangers, (ii) what characteristics of the panhandler facilitate sharing, (iii) what environmental aspects influence the process, and (iv) what per-

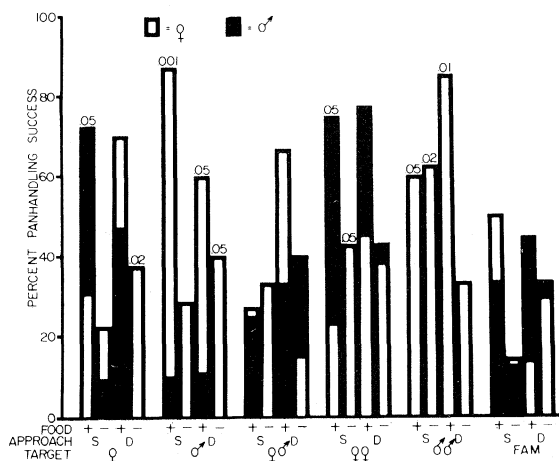


Fig. 1. Comparative success of female and male "panhandlers" individually approaching an approximately equal number of target groupings of (i) one or two females or males, (ii) a female and male together, (iii) a family with at least one child. Significant differences between male and female panhandlers, in terms of probabilities, are shown above the respective bars. Panhandlers approached either submissively (*S*) or dominantly (*D*) a target consuming food (+) or not (-); *FAM*, family.

Table 1. Analysis of variables affecting the success of "panhandlers" requesting 10 cents. Target groupings were one female or two, one male or two, and one female and one male together. A total of 79 targets were approached. The overall proportion of success was .53. Percentages are given to the nearest whole number.

Variables	N	Percent success	χ^2	P
Target group				
(a) ♂ + ♂♂	27	22	(a,b) 22.60	<.001
(b) ♀ + ♀♀	25	88	(a,c) 5.08	<.05
(c) ♀♂	27	52	(b,c) 7.96	<.01
Food				
With	43	70		
Without	36	36	8.95	<.005
Approach				
Dominant	51	59		
Submissive	28	49	1.12	*
Dress				
Shabby	38	50		
Nice	41	58	0.58	*
Weather				
Sunny	46	54		
Overcast	33	55	0.00	*

*Not significant.

centage of people share when kinship selection is not applicable and reciprocity unlikely? Two studies were conducted.

In the pilot study two male student "panhandlers" approached 79 different target groupings (a single male, a single female, two males, two females, or a male and a female together) and requested 10 cents without explanation. The dress and the approach of the panhandlers were as follows. The submissive posture consisted of a bent head, stooped shoulders, avoidance of eye contact, and a right hand extended in a begging gesture. The dominant approach consisted of an upright stance, an erect head, eye contact, and no begging gesture. Panhandlers were dressed either nicely or shabbily. Target individuals both eating and not eating were approached in public places on sunny and overcast days during spring.

Male panhandlers were far more successful approaching a single female or a pair of females than a male and female together (Table 1); they were particularly unsuccessful when approaching a single male or two males together. The panhandlers were also more successful when approaching target individuals who were eating than those who were not. The overall success rate was 53 percent.

A more comprehensive second study extended the initial findings and compared the success rate of male and female panhandlers. It was conducted in autumn, and the panhandlers wore casual clothing, neither nice nor shabby. Two female and two male students (the males had been in the pilot study) approached separately, in either a dominant or submissive posture, a

total of 218 and 229 target groupings, respectively. A family grouping (one adult female, one adult male, and at least one child) was added to the original target groups. The panhandlers again asked for 10 cents without explanation; they approached 141 male and 174 female target individuals, and 132 male-female pairs, who were eating ($N = 216$) or not eating ($N = 231$).

The main study replicated the findings of the pilot study (Table 2). Although females were more successful panhandlers than males, the same males in the pilot study were more successful (53 percent) than the females of the main study (41 percent). Two aspects of the main study may account for this result: (i) it was conducted in the fall rather than in the spring; and (ii) family target groupings, which rarely gave, were included in the design.

The more specific findings are shown in Fig. 1. Male panhandlers were comparatively successful only when submissively approaching females who were eating. Females were considerably more successful than male panhandlers, particularly when submissively approaching males who were eating, or when approaching in a dominant posture, a single female or a single male who was not eating. Targets of more than one individual, especially a family or a male and a female together, were resistant to panhandling.

The most potent variable, even though the panhandlers were requesting only a small amount of money, was whether the target individuals were eating. Moreover, in addition to giving 10 cents, target individuals who were eating often offered some of their food to the panhandler. The common practice among humans of trading resources may have its origin in primitive food sharing tendencies.

The results also suggest appropriate behaviors (submissive postures and begging gestures) and specific rules (for example, a female may approach a male but not a family) for achieving one's share of food. When food consumption was not in evidence, a dominant female panhandler was relatively successful when approaching another single female (but not two females together) or one or two males. The dominant-submissive implications of the former and the potential sexual connotations of the latter are interesting. Also, since the same male panhandlers were more successful in spring, regardless of the weather, than in autumn, there may be a seasonal influence as well.

A target grouping of at least two individuals was sufficient to reduce the dominant advantage. This result is consistent with findings that groups are generally less willing to come to someone's assistance

Table 2. Analysis of variables affecting the success rate of female and male "panhandlers" singly approaching in either a dominant or submissive posture, target individuals who were either eating or not eating. A total of 447 targets were approached. The overall successes were 34 percent.

Variables	N	Percent success	χ^2	P
Approach				
Dominant	218	38.1		
Submissive	229	30.1	3.139	*
Food				
With	216	45.8		
Without	231	22.9	26.061	.001
Panhandler's sex				
Female	239	41.0		
Male	208	26.0	11.214	.001

*Not significant.

than single individuals (7). Whereas sharing among individuals of a family is common, and has been documented for hunter-gathers (8), the family unit per se may be a natural barrier to more general food distribution. The economics of modern society may overcome (through reciprocal altruism) a tendency to share only among relatives (favored by kinship selection). However, kinship selection may be the more basic rule, as evidenced here by the reluctance of families to share resources with strangers, with whom reciprocal altruism is unlikely. The occurrence of reciprocal altruism may require some familiarity among the parties concerned, since, in the pilot study, a nicely dressed male panhandler (indicative of the potential to reciprocate) was no more successful than a shabbily dressed male panhandler when either was a stranger to the target individuals.

The fact that one-third to over one-half of the people approached by the panhandlers did share, suggests that sharing is important for human survival. To the extent that a begging individual could appear to be a relative, or at least a member of one's immediate group, the probability of that individual's acquiring a handout would undoubtedly increase. As with chimpanzees, knowing the rules and displaying the appropriate behaviors in the proper context should be adaptive.

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Pigeons Can Learn Identity or Difference, or Both

Carter and Eckerman (1) found that one can predict a pigeon's ability to learn a symbolic matching or simple matching task from its ability to make simple simultaneous and successive discriminations. On the basis of these data they concluded that in both symbolic matching and simple matching, pigeons learn simple if-then relations. For instance, in the case of simple matching, if the sample is red then a response to red will be reinforced with food; in the case of symbolic matching, if the sample is red then a response to a vertical bar will be reinforced with food. They concluded that "the ease with which both matching and symbolic matching are learned is independent of the similarity between sample and comparison stimuli." While their analysis is ingenious, their conclusion that "identity . . . plays no role for pigeons" is overstated.

First, one must be particularly cautious about maintaining that a difference between two treatments does not exist, particularly when conditions are not optimal to observe such a difference. A more direct method for determining if matching and symbolic matching were learned at different rates would be with four equally discriminable colors, with responses to the same color reinforced in the simple matching task and those to a specified other color reinforced in the symbolic matching task. If colors alone were used, then it would not be necessary to differentially scale the abscissa for the different stimulus classes (colors or shapes).

Second, the learning measure used by Carter and Eckerman may avoid the problem of stimulus novelty, but transfer to new stimuli following matching training may provide a more sensitive measure of identity learning.

Our data from pigeons indicate that the identity relation can be learned. Pigeons were trained to either match a sample shape (matching) or mismatch a sample shape (oddy). They were then shown new stimuli that differed from one another only in color, and were trained to either match or mismatch colors. For half the pigeons the second task was of the same type as the training task, matching or oddity (nonshifted groups). For the remaining birds the second task was different from the training task (shifted groups). If pigeons can learn the identity and difference rela-

tions, then the nonshifted groups should learn the second task faster than the shifted groups.

Eight domestic pigeons were maintained at 80 percent of their free-feeding weights. Each bird was placed in a cubicle containing an opening through which the bird could eat mixed grain when an externally mounted food tray was raised. Above the opening were three horizontally mounted response keys, each consisting of a 2.5 by 2.5 cm piece of translucent Plexiglas attached at the top edge to a microswitch. A miniature projector behind each response key projected onto the response key one of two shapes (a white circle or cross) on a black background, or one of two colored fields (red or green) (2). The birds were trained to eat from the food tray and were then shaped to peck the center key, which was alternately illuminated with the circle and the cross; pecks were followed by 3-second access to grain. Once the key-pecking response was well established the pigeons were divided into two groups. One was given matching training, the other oddity training. Each trial started with the projection of either the cross or the circle on the center key. Five pecks to the center key illuminated the side keys and a single peck to either side key terminated the trial and initiated a 5-second intertrial interval.

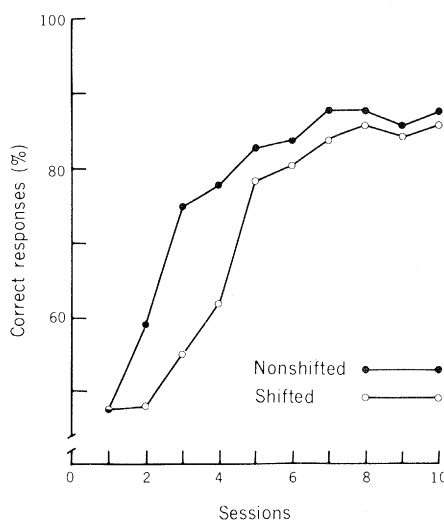


Fig. 1. Acquisition of the transfer task for nonshifted groups (trained first on shape matching, then on color matching, or first on shape oddity, then on color oddity) and shifted groups (trained first on shape oddity, then on color matching, or first on shape matching, then on color oddity).

The stimulus on one of the side keys was the same as the sample, while the stimulus on the other was different from the sample (the other shape). For pigeons given matching training, pecks to the side key that matched the sample were reinforced. For those given oddity training, pecks to the nonmatching side key were reinforced. Sample shape and the side on which the correct shape appeared were counterbalanced within each session. Each of the 40 training sessions consisted of 96 trials. All birds were then given ten transfer sessions consisting of matching or oddity training with the colors red and green. For each of the training groups (matching and oddity), half were tested on the same concept as during training (nonshifted), and half on the other concept (shifted). This design allowed for a sensitive measure of concept transfer since it could assess immediate transfer effects as well as differences in learning rates between the shifted and nonshifted groups.

The difference between matching and oddity performance on the first task was not significant (3) in analyses of either a learning-rate measure (number of sessions to 65 percent correct) ($F = 1.07$; d.f. = 1, 6) or a measure of the final level of performance (performance during the last five training days) ($F = 2.27$; d.f. = 1, 6). On session 40 mean overall performance was 91.8 percent correct.

The transfer data are presented in Fig. 1. A two-way analysis of variance on pooled data for the first four transfer sessions indicated that nonshifted birds performed significantly better than shifted birds ($F = 8.02$; d.f. = 1, 4). By session 4 nonshifted birds were near asymptotic performance. Oddity performance was somewhat better than matching although the difference did not reach statistical significance ($F = 5.49$; d.f. = 1, 4). The interaction was also not significant ($F = 1.46$; d.f. = 1, 4). A similar analysis for the learning-rate measure indicated that nonshifted birds learned significantly faster than shifted birds ($F = 10.00$; d.f. = 1, 4). Again, the matching-oddy difference and interaction were not significant (for both, $F < 1$). On transfer session 10 mean overall performance was 87.2 percent correct. Chance performance on the first transfer session by both groups, due perhaps to stimulus novelty, suggests the importance of using an extended transfer test.

The results indicate that pigeons tested under the proper conditions can show evidence of learning the relations same or different (or both) with a similar problem involving new stimuli. These results support and extend previous findings that pigeons can learn these relations, as evidenced by differential transfer to new stimuli along the training dimension (color) or to new