

GROUP FORAGING: THE SKILL POOL EFFECT AND FREQUENCY-DEPENDENT LEARNING

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Submitted February 14, 1983; Accepted January 11, 1984

The many hypotheses put forward to explain the evolutionary significance of group foraging generally suggest either feeding efficiency or antipredatory advantages (Bertram 1978). A hypothesis specific to mixed-species foraging groups proposes that such groups increase the diversity of food items available to each individual member, thereby increasing the average feeding rate of individuals within a group (Krebs 1973). Foraging differences among species may be substantial. Joining mixed-species foraging groups could be a way for an individual to increase its chances of profiting from the foraging specializations of other individuals through the discovery of unfamiliar foraging sites (Krebs 1973) or food types. To test this hypothesis, Rubenstein et al. (1977) collected field data for mixed-species flocks of tropical seed-eating finches which showed that individuals did increase their diet breadth by joining flocks. Similar results have been found for mixed-species flocks of tropical, insectivorous birds (Buskirk 1972 cited in Rubenstein et al. 1977; Powell 1974). In this paper I argue that the functional advantages favoring the evolution of mixed-species foraging aggregations can also apply to single-species groups. I present evidence suggesting the widespread occurrence of intraspecific individual foraging specializations. For species which acquire new types of food or foraging sites by individual learning, this advantage may be particularly common because the dynamics of the group itself will favor the development of individual foraging specializations.

THE SKILL POOL EFFECT

It is often the case, when food occurs in rich clumps and animals forage in groups, that the food discoveries of a few lead to the feeding of many. This is because a feeding animal can seldom fail to advertise the presence of the food it is eating and consequently attracts the attention of others, a phenomenon labeled "local enhancement" and described in various flock-feeding birds (Fisher and Hinde 1949; Hinde and Fisher 1951; Rand 1954; Lockie 1956; Thorpe 1956; Kear 1962; Newton 1967; Lack 1968; Murton 1971*b*; Krebs et al. 1972; Krebs 1973;

Rubenstein et al. 1977; Wiens and Johnston 1977; Brockmann and Barnard 1979; Barnard and Sibly 1981; Waite 1981). The witness to a discovery may be influenced in several ways. By observation it may learn the foraging technique of the discoverer (Dawson and Foss 1965; Sasvári 1979) or the food choices of the discoverer (Klopfer 1959; Newton 1967; Murton 1971*a*, 1971*b*; Krebs 1973; Partridge 1976; Lawton and Guindon 1981). If the prey are large and few, the animal may try to "steal" the discovery (kleptoparasitism, Brockmann and Barnard 1979). If the prey are small and numerous, such that they can neither be defended nor stolen easily, several individuals may exploit the same food source simultaneously (Rand 1954; Newton 1967). I will discuss the latter case.

Individuals within foraging groups may have different repertoires of foraging behaviors, each specializing on a subset of a population's diet range (Tinbergen 1960; Van Valen 1965; Curio 1976). If individuals can join the food discoveries of others, then the searching efficiency of an individual foraging on subset A will profit individuals foraging on subset B and vice versa. I call this the *skill pool effect*. It is the result of different foraging specialists each having the option of joining discoveries. The result of the skill pool is twofold. First, an individual can partake of an increased diversity of food (which translates to quantity) when it is in a group. Second, each individual may increase its searching efficiency by concentrating its searching efforts on a limited range of food items (Partridge 1976). This contrasts with situations in which animals copy the behavior of others in which case the effect of the group on diet breadth is achieved by the, often only temporary, addition of new foraging modes.

INTRASPECIFIC INDIVIDUAL FORAGING DIFFERENCES

As a rule, individuals of one species do not all occupy the same range of the food spectrum, but rather, differ from each other by preferring certain prey items over others (Curio 1976). There is evidence for considerable intraspecific foraging specialization in insects (Heinrich 1979); fish (Bryan and Larkin 1972); birds (Vince 1956; Tinbergen 1960; Selander 1966; Storer 1966; Newton 1967; Norton-Griffiths 1967; Brown 1969; Goodwin and Hess 1969; Jackson 1970; Murton 1971*a*; Smith and Dawkins 1971; Williamson 1971; Davis 1975; Partridge 1976; Grant 1981); small mammals (Partridge 1981); and social carnivores (Kruuk 1972; Schaller 1972). There is also evidence, especially for vertebrates, that learning is a major component in the development of foraging behavior (Klopfer 1958, 1959, 1961; Hinde 1959; Tinbergen 1960; Dawson and Foss 1965; Norton-Griffiths 1967; Alcock 1971; Smith and Dawkins 1971; Bryan and Larkin 1972; Schaller 1972; Partridge 1976, 1981; Stallcup and Woolfenden 1978; Heinrich 1979; Sasvári 1979). In many cases, learning acts to magnify the effects of small individual differences into pronounced individual foraging differences (Hinde 1959; Dawkins 1971; Bryan and Larkin 1972). In other cases, chance events during an individual's experience may result in considerable individual variation (Vince 1956; Hinde 1959; Klopfer 1959; Tinbergen 1960; Coppinger 1969; Rabinowitch 1969; Partridge 1981). Differences in learning propensity for particular tasks lead to dramatic changes in individual performances when even minute changes are made

to the task to be learned (Vince 1956; Bovet et al. 1969). These differences could be reduced by observational learning, but I suggest instead that the group may provide conditions which generate frequency-dependent effects favoring the expression and maintenance of such differences.

FREQUENCY-DEPENDENT LEARNING

Operant conditioning may be described as an increase in the probability that a behavior will be repeated when, in the past, it has been temporally correlated with a positive reinforcer (Manning 1967). Through operant conditioning, those individuals that first discover a food source will have a higher probability of discovering a similar source again. Individuals that join a discovery, on the other hand, will have an increased probability of doing so again. The probability that an animal will either learn to discover or join a food source is dependent on the frequency and performance of discoverers already in the group. There are three possible sources of frequency dependence: (1) the more an individual joins, the less time it has to search and discover; (2) as the rate of discoveries increases, the joining opportunities also increase; (3) reinforcement for joining may reduce the potential for forming other behavioral associations simultaneously (Dickinson 1980).

The number of discoverers of a given food type which develop in a group may also be a function of the amount of food provided by the food source. If, for example, one food source, discovered by a single individual, provides enough food to feed the whole group to satiation, then the chances that the joiners learn to discover that food type are diminished. If, on the other hand, the discovery of one food type produces little food to joiners (maybe none), the joiners will spend more time searching, increasing their chances of making other, possibly novel, food discoveries. At some point, the number of discoverers of a given food type in the group would be such that individuals who have not yet learned to discover only have minute probabilities of doing so. If one looked at discovering and joining as strategies then, at this point, the individual would do better by attempting to join this food type rather than attempting to discover it. Because it is frequency dependent and because it would ultimately lead to the attribution of discovering and joining strategies, this process is analogous to a mixed evolutionarily stable strategy (ESS) reached by frequency-dependent selection (Maynard Smith 1974). The idea that learning processes may lead to situations analogous to an ESS has already been suggested by Dawkins (1980) and Harley (1981). Both authors emphasize that animals that develop strategies by learning would cope more rapidly with changing environmental conditions than those that have genetically determined strategies regulated by frequency-dependent selection.

Individual differences in learning potential of the type reported by Bovet et al. (1969) would act to increase the likelihood of individual foraging specializations. Individuals could become discoverers for food types corresponding to their learning tendencies. Such individual differences may unbalance the frequency-dependent learning effects and possibly lead to relatively stable situations even if discoverers and joiners had unequal payoffs. In any case, frequency-dependent learning would lead to food-specific role attribution within groups. Individuals

would discover some food types and join for others: a situation analogous to “producing” and “scrounging” observed for flocks of house sparrows (Barnard and Sibly 1981). Barnard and Sibly suggested that a mixed ESS could account for the distribution of roles because each bird kept its role even when conditions made the alternative behavior much more rewarding. When interactions over all prey types and food-discovery problems are recorded, discovering and joining roles may be reversed for different situations, creating a skill pool.

Frequency-dependent learning may be involved in two important components of foraging: search and capture. When searching for prey, animals often form search images by learning (Tinbergen 1960; Croze 1970; Dawkins 1971). If animals are foraging in a group for rich, yet cryptic, clumps of prey which require some special behavior in order to be made available (peeling of bark, turning of a leaf, etc.) and joining is possible, learning a search image could be frequency dependent. Some individuals would form search images by successively encountering and discovering the clumps, while the joiners might not because they would have arrived after the clump had been discovered. This is likely given the variability in learning performances following small changes in the task to be learned (Vince 1956; Bovet et al. 1969) and the sensitivity of search image formation to frequency of encounter (Tinbergen 1960; Croze 1970; Murton 1971a).

When prey can escape, predators must capture them. There is strong evidence that, in many vertebrates at least, this component of a forager’s behavior often relies on trial-and-error learning (Curio 1976). If the captured prey is large, providing food for those who have not captured it, then only some individuals should develop specialized capture behaviors. This is consistent with Estes and Goddard’s (1967) claim that in packs of wild dogs it is often the same individual that selects and chases the quarry.

High levels of aggression will make the skill pool inoperative. Aggression during foraging (reported for great tits in the lab [Krebs et al. 1972] and juncos both in the lab [Baker et al. 1981] and in the field [Czikeli 1983]) may reduce the benefit which these individuals could obtain through the skill pool. Joining, however, has been reported in many species of birds (Rand 1954; Newton 1967) and carnivores (Kruuk 1972; Schaller 1972).

PREDICTIONS

Several ecological and behavioral predictions follow from the skill pool effect. (1) The diversity of the realized diet (the food which enters the digestive tract) of individuals foraging in groups should be greater than the realized diets of similar individuals foraging singly in similar habitats. (2) An individual will use fewer prey-capture techniques when it forages in a group than when it forages alone. (3) Generalist-opportunistic species—those that eat a great variety of food types and readily include novel food items in their diets—should show a higher incidence of group feeding than specialist-conservative species. (4) Species that frequently invade new habitats either through migration or colonization should show a higher incidence of gregarious foraging. (5) Species confronted regularly with highly fluctuating food diversity should show a higher incidence of gregarious foraging.

(6) Gregarious foragers should reach a higher biomass than solitary foragers because they can exploit a greater diversity of foods more efficiently. (7) The diversity of food capturing and searching behaviors observed over a whole population of gregarious foragers should be greater than the range observed for a similar population of solitary foragers.

Insufficient information is presently available to test these predictions. Interest in individual variation within species is recent, and most studies report either average diets or average behavioral repertoires. Comparison of diets inside and outside groups is common for mixed-species foraging flocks and social carnivores. The effects of mixed-species flocking on diet breadth are ambiguous. Joining a flock may either increase (Buskirk 1972 cited in Rubenstein et al. 1977; Rubenstein et al. 1977; Powell 1974), decrease (Morse 1970, 1974; Austin and Smith 1972), or have no effect on diet breadth (Caldwell 1981). Social carnivores obtain different prey when foraging in groups (Estes and Goddard 1967; Kruuk 1972; Schaller 1972; Caraco and Wolf 1975), but this appears to result from active cooperation in capture of large prey rather than the skill pool effect.

CONCLUSIONS

If intraspecific foraging differences and joining the discoveries of others commonly occur together, then the skill pool effect may be a general benefit of group foraging. The skill pool does not exclude the operation of other benefits. The skill pool hypothesis does make several predictions which could not be made by other group foraging hypotheses. Predictions of the skill pool hypotheses could be tested by giving more attention to individual variations in diet and foraging mode (including joining the discoveries of others), in relation to the presence or absence of foraging groups.

Some hypotheses concerning the value of gregarious foraging state that social learning is the major mechanism generating the foraging benefits (Krebs et al. 1972; Krebs 1973; Thompson and Vertinsky 1975). If learning in a group is frequency dependent, it will lead to increased foraging specializations, a result which is the opposite of what we expect from social learning. It is not known whether animals faced with the possibility of learning by observation and by experience simultaneously will do either, neither, or both. Hence, the defendability of food sources will have important consequences for theories which involve cultural transmission in animals (Wyles et al. 1983).

SUMMARY

It is hypothesized that mixed-species foraging aggregations provide each individual with a wider range of food items as a result of social learning and the diversity of foraging specializations among species (Krebs 1973). I hypothesize that the skill pool effect should provide similar benefits to single-species foraging groups without social learning. The skill pool occurs when different foraging specialists join the discoveries of others. While providing an increased range of food items, it permits increased individual foraging efficiency through specializa-

tion. When individual learning is important in the development of foraging behaviors, it should generate frequency-dependent effects which promote individual specializations favoring the occurrence of skill pools. From the skill pool effect several ecological and behavioral predictions are generated that require more attention to comparisons of individual diets and behaviors inside and outside foraging groups.

ACKNOWLEDGMENTS

I thank Louis Lefebvre, Don Kramer, Rob Peters, Graham Bell, Gilbert Cabana, and Darren Gillis for suggestions concerning earlier drafts of this manuscript. During this research financial support came from an F.C.A.C. scholarship.

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