Group foraging by a stream minnow: shoals or aggregations?

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Abstract. The importance of social attraction in the formation of foraging groups was examined for a stream-dwelling cyprinid, the rosyside dace, Clinostomus funduloides. Dace arrivals and departures at natural foraging sites were monitored and tested for (1) tendency of dace to travel in groups, and (2) dependency of arrival and departure rates on group size. Dace usually entered and departed foraging sites independently of each other. Group size usually affected neither arrival rate nor departure probability. Thus, attraction among dace appeared weak; foraging groups most often resulted from dace aggregating in preferred foraging sites. The strongest evidence of social attraction was during autumn, when dace departure probability often decreased with increasing group size, possibly in response to increased threat of predation by a seasonally occurring predator. Dace also rarely avoided conspecifics, except when an aggressive individual defended a foraging site. Otherwise, there was little evidence of exploitative competition among dace for drifting prey or of foraging benefits in groups, because group size usually did not affect individual feeding rates. These results suggest that the benefits of group foraging demonstrated under laboratory conditions in other studies may not always apply to field conditions.

Many animals forage in groups, and social foraging may provide a variety of benefits to group members, including higher or lower variable foraging rates and lower risks of predation (Pulliam & Caraco 1984; Pitcher 1986). The frequent and widespread occurrence of group foraging by stream fishes (Reimers 1968; Seghers 1974; Mendelson 1975) suggests that individual fish benefit from feeding in groups, and that groups form as a result of social attraction among individuals. In support of this hypothesis, several laboratory studies have demonstrated potential benefits of group foraging for freshwater fish (as discussed below). Field studies, however, have focused on habitat use and species segregation within mixed-species groups (Mendelson 1975; Gorman 1988), rather than on mechanisms promoting group foraging. Consequently, we have little information on the extent to which group foraging by stream fish in situ is a social behaviour. We attempted to quantify the importance of social attraction (i.e. attraction among individuals) on group foraging by a stream minnow under field conditions.

Recent studies suggest that freshwater fish may benefit from foraging in social groups (termed 'shoals', Pitcher 1983) through some of the same mechanisms demonstrated for flocking birds (Pulliam & Millikan 1982). For example, in laboratory tests in which food is hidden in discrete patches, individual fish can locate food more quickly when part of a group than when alone (Pitcher et al. 1982; Magnan & FitzGerald 1984; Street & Hart 1985). Shoaling also may decrease individual risk of predation through several mechanisms, including early predator detection, predator confusion, and evasive manoeuvres by the group (reviewed by Godin 1986 and Pitcher 1986). As a result of anti-predator advantages, shoaling fish may allocate more time to foraging and less to predator vigilance (field test: Seghers 1981; laboratory tests: Magurran & Pitcher 1983; Magurran et al. 1985; Morgan & Colgan 1987).

Although laboratory studies clearly demonstrate that stream fish may benefit from feeding in groups, these studies do not address the possible influence of habitat heterogeneity on group formation. Stream fish often occupy structurally diverse habitats composed of a heterogeneous mix of substrate types, current velocities and water depths. Numerous studies (e.g. Grossman & Freeman 1987 and references therein) have demonstrated that stream fish use the available habitat in a
Table I. Predicted patterns for regressions of arrival and departure rates ($Y$) as functions of group size ($X$)

<table>
<thead>
<tr>
<th>Mechanism of group formation (effect of group size on foraging rate)*</th>
<th>Arrival rate versus group size†</th>
<th>Departure rate versus group size†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aggregation (no benefits or costs of group foraging)</td>
<td>Open forager pool</td>
<td>Closed forager pool</td>
</tr>
<tr>
<td>Social attraction (benefits of group foraging exceed costs)</td>
<td>No relationship</td>
<td>Negative, linear</td>
</tr>
<tr>
<td>Aggregation (costs of group foraging exceed benefits)</td>
<td>$Y = a$</td>
<td>Positive, linear</td>
</tr>
<tr>
<td></td>
<td>$Y = a + bX$</td>
<td>$Y = a(N - X)$</td>
</tr>
<tr>
<td></td>
<td>$Y = a - bX$</td>
<td>$Y = a(X) - bX$</td>
</tr>
</tbody>
</table>

*For range of group sizes observed in the field.
†In arrival rate regressions $a$ represents site attractiveness, $b$ represents the effect of each group member on arrival rate (Caraco 1979a, 1980), and $N$ is the number of dace available to feed in a given site when the forager pool is closed. In departure rate regressions $a$ is the per capita probability of departure, and $b$ represents the effect of each group member on departure probability.

non-random manner. Consequently, suitable foraging habitat may be patchily distributed, and fish may aggregate in the best feeding sites even though they do not specifically benefit from group foraging. In fact, foragers may interfere with each other and continue to forage in groups as long as the benefits of feeding in a particular location outweigh the costs of competition (Pulliam & Caraco 1984). Thus, habitat heterogeneity may cause stream fish to aggregate (i.e. form groups through individuals independently selecting the same habitat: Williams 1964; Breder 1967; Caraco 1979a) in the absence of social attraction.

We investigated group foraging behaviour of a North American stream minnow, the rosy-side dace, \textit{Clinostomus funduloides}. Dace commonly forage alone and in groups in our study sites, where they are the most abundant water column fish present. Dace primarily forage on drifting invertebrate prey in deeper areas with low to moderate current velocity (Grossman & Freeman 1987), and habitat selection by dace appears to be an energy maximizing decision (Hill 1989). However, the effects of social attraction on habitat use by this minnow are unknown; groups of dace may represent aggregations in favourable habitat patches, or dace may choose sites on the basis of both habitat suitability and the presence of conspecifics. It also is possible that dace actually compete with conspecifics when aggregations form in suitable foraging sites.

To distinguish between social attraction and aggregation as mechanisms promoting group foraging, we observed dace in natural foraging sites and asked three questions:

1. Do dace move among foraging sites alone or in groups? A possible consequence of social attraction would be for dace to move among foraging sites in schools or pairs (Partridge 1980). In this case, dace should enter and depart at a given foraging site in groups. In contrast, if groups result from individuals aggregating in foraging sites, then individuals should primarily forage independently of conspecifics, and single dace should frequently arrive to and depart from a given foraging site.

2. Do arrival and departure rates at a foraging site, expressed as functions of group size, provide evidence of attraction (or avoidance) among foragers? If foraging groups result from social attraction, as opposed to aggregation, then this should be reflected in the relationship between arrival and/or departure rate and group size (Table I). We followed the approach used by Caraco (1979a, 1980) to model dynamics of bird flocks to derive alternative predictions of arrival rate relationships to group size. If dace groups are aggregations (and net foraging benefits are independent of group size) then the rate of dace arrivals to a particular site should be $a$, a constant value reflecting the attractiveness of the site. If dace are attracted to (or avoid) conspecifics, then the arrival rate to a site should be $a + bX$, etc.
where $X$ is group size and $b$ reflects the increase (or decrease) in site attractiveness for each fish added to the group. Avoidance among foragers would imply that groups are aggregations and that net foraging benefits decrease with group size. These equations assume there is an open pool of available foragers (Caraco 1979a, 1980). The number of dace available to feed at a particular site ($N$) may in fact be constant, so that arrival rates also depend on how many individuals are not already at the site (i.e. $N - X$, Table I; Caraco 1980).

Departure rate of dace from a foraging site should increase as a linear function of group size if there is neither attraction nor avoidance among dace foraging together at a site. If, however, there is an added effect of attraction or avoidance among dace, then the relationship of departure rate to group size should include either a negative or positive quadratic term (Table I).

Arrival or departure rates plotted across the full possible range of group size may actually be discontinuous or non-linear if, for example, foragers only benefit from group foraging, or only interfere with each other, after groups reach a threshold size. In the field, however, group sizes on the negative (less beneficial) side of a threshold should be rare unless habitat or foragers were limiting. Thus, regressions of arrival and departure rates versus group size at a particular site should reflect relationships among foragers for those particular conditions and the range of group sizes observed in the field.

(3) Do dace feeding or aggression rates vary as a function of group size? This was not a test for social attraction per se, but rather a question of whether we could identify costs or benefits of group foraging under field conditions. We did not witness any predatory attacks on foraging dace, and so we could not quantify group-size effects on predation risk. If foragers in groups devote less time to vigilance, however, this should result in a positive feeding rate–group size relationship. Conversely, a lack of relationship between feeding rate and group size would indicate that dace do not derive foraging benefits in groups. Finally, a negative group size effect on feeding rate would indicate a cost to group foraging because of increased exploitative competition. Similarly, if per capita aggression increases with group size, then greater interference among dace could be a cost of group foraging. Examining group-size effects on feeding and aggression rates also allowed us to test whether variation in dace arrival or departure dynamics in groups corresponded to variability in the net benefits of group foraging.

**METHODS**

**Study Site and Field Methods**

Our research site was located at the U. S. D. A. Forest Service, Coweeta Hydrologic Laboratory (Macon County, North Carolina), in the southern Appalachian Mountains. We worked in Coweeta Creek, a fifth-order stream, and one of its fourth-order tributaries, Ball Creek. Stream segments used in this study flow through relatively undisturbed, mixed-hardwood forest. Riparian vegetation is well developed and includes thick clumps of *Rhododendron maxima* and *Kalmia latifolia*. A more detailed description of the study site is provided by Grossman & Freeman (1987).

These mountain streams provide good habitat for observing water column fish, because interspersed riffles and pools create natural impediments to forager movement. Individual cyprinids normally forage within 10–15-m-long pools and may remain in particular pools for months (Hill & Grossman 1987). Also, heterogeneous current velocities and substrates (ranging from silt and sand to boulders) may subdivide suitable habitat for water column fish within pools. Thus, it is possible to observe foragers in patches of suitable habitat that are small and relatively discrete. We worked in four study pools, situated 40–190 m apart, that ranged from 9 to 16 m in length, with widths of 3–6 m. The particular observation site used in a given pool varied, depending on flow conditions and where groups of dace were foraging. We conducted observations from August through to November in 1988 and 1989, and during April and early May 1989. Because dace spawn during spring or early summer (Davis 1972), reproductive activity should not have affected our observations.

During each observation, we recorded activity in a $40 \times 40$ cm quadrat in an area where one or more dace were foraging. This quadrat size ensured that individual dace within the quadrat generally were no more than 5–7 body-lengths apart. Data from other investigators suggest that 5–10 body-lengths is the maximum distance between interacting fish (Seghers 1981; Pitcher et al. 1983; Helfman 1984).
Thus, dace within the quadrat probably were close enough together to interact. This quadrat size was too small, however, to contain large groups that formed in some habitats. Therefore, we placed quadrats in relatively discrete foraging locations; i.e. areas that individuals moved in and out of, but where fish usually did not feed in the immediately surrounding area. We used coloured markers placed on the stream bottom to delineate a quadrat at a selected foraging site.

We observed foraging activity by snorkelling; fish did not appear disturbed by a stationary observer. We used a tape-recorder (enclosed in a waterproof housing, with a waterproofed microphone attached to a snorkel) to record the numbers and species of fish present and fish movements in and out of the quadrat for periods of 25–40 min. During most observations we also recorded displacements or chases among foragers. A displacement involved one fish swimming laterally towards a target individual, which either shifted position or moved laterally back towards the aggressor. Chases involved an aggressor either swimming directly towards another fish, or approaching and pursuing a fish from behind. Finally, during most observations we also recorded displacements or chases among foragers. A displacement involved one fish swimming laterally towards a target individual, which either shifted position or moved laterally back towards the aggressor. Chases involved an aggressor either swimming directly towards another fish, or approaching and pursuing a fish from behind. During most observations we counted feeding strikes either by all individuals or by focal individuals. We counted all feeding strikes made by the foraging group if the group was small and feeding activity was relatively low. Otherwise, we haphazardly selected focal individuals from the group for 1–2-min observations, attempting to watch as many different individuals during sessions as possible. We could not usually see the particles that foragers captured from the drift, except when fish struck at debris which they subsequently spat out. During the 1989 observations, we tabulated rejected prey (typically strikes at debris) separately from other strikes.

Data Analysis

We transcribed tape-recorded data by tabulating activity (i.e. initial group size, arrivals, departures, aggressive acts, feeding strikes) occurring in the quadrat during successive 5-s intervals. To address our first question, whether dace moved among foraging sites in groups, we compared the frequencies of arrivals and departures by zero, one, two, three and four or more dace (in 5-s intervals) with expected frequencies generated from Poisson distributions (i.e. assuming independent movement). We used chi-squared goodness-of-fit tests (alpha = 0.025, to control type I error at 0.05 for two non-independent tests), and combined categories when necessary so that no expected frequencies were less than 1.

To test for either attraction or repulsion of dace to groups of conspecifics, we regressed average arrival and departure rates (per 5-s interval) on group size (= number of dace present at the beginning of a 5-s interval). Regressions were calculated separately for observations from different sites and dates. Arrivals and departures were approximately Poisson distributed; many 5-s intervals had no movement in or out of the quadrat, and variances among 5-s intervals were approximately equal to average rates. We therefore used weighted least-squares regression to correct for heteroscedasticity (Neter et al. 1989); weights were the inverses of arrival (or departure) rates predicted by unweighted least-squares regressions. We only included average rates in regressions for those group sizes with enough 5-s interval observations so that either (1) the standard error was 30% of the estimated rate or less, or (2) when the estimated rate was 0.2 or less, the standard error was 0.05 or less, assuming rates followed Poisson distributions. This procedure was necessary to avoid biasing regression analyses by including poorly estimated average rates (i.e. those for group sizes that were infrequently observed). The only exceptions were for four data sets in which the largest group size had frequent arrivals or departures and at least 1 min of observation; these group rates were included in analyses. We excluded from regression analyses those 5-s observations during which other water-column fishes were present in the foraging site, except (1) when heterospecifics were present for less than 2.5% or more than 90% of the total observation time, in which cases we pooled observations with and without heterospecifics for a given dace group size, and (2) when it was necessary to pool data to obtain sufficient sample sizes for analysis for one date when rainbow trout, Oncorhynchus mykiss, were present for 65% of the observation time.

To test whether dace arrivals (from a closed forager pool) or departures were dependent on group size, it was necessary to test fits of both linear and quadratic models (see Table I). Quadratic models of arrival rates were fit to deviation of group size from mean group size to reduce correlation between the independent variables (i.e. x and x², where x = group size; Neter et al. 1989). We regressed departure rates through the origin, and
independent variables were not transformed. Terms were retained in the models if partial F-tests were significant at the 0-1 probability level. We also used a 0-1 probability level to test overall regression significance. When both linear and quadratic models were significant, we judged the quadratic model to provide a better fit if the residuals showed less evidence of systematic variation than with the linear model.

We used weighted least-squares analysis to test for relationships between feeding and aggression rates and group size, analysing data for each observation set separately. Feeding rate data for focal dace were pooled to estimate (1) average per capita feeding rate, including rejected particles, and (2) the proportion of bites that resulted in rejected particles, for each observed group size. We estimated average feeding rates only for group sizes with at least 1 min of observation. Minimum sample size criteria for estimating aggression rates for a particular group size were the same as for estimating arrival and departure rates.

RESULTS

Did Dace Move to and from Observation Sites Independently, or in Groups?

Dace usually entered and departed observation sites independently of each other. Foragers did not enter or leave in groups more often than expected under the hypothesis of independent movement in 59% of the observation sets. However, groups of two or three fish entered sites significantly (P<0-025) more frequently than predicted from Poisson expectations in 25% (14 of 56) of the tested observation sets. Groups of two or three fish departed significantly more frequently than expected in 20% (11 of 55) of the tested observation sets. Single dace arrived or departed significantly more frequently than expected in one observation set each. Non-independence of arrivals during an observation was not significantly associated with non-independence of departures (G-test for independence, G = 0.4532, df = 1, P>0-1). This suggests that different motivational stimuli affected dace arrivals and departures.

Did Arrival and Departure Rates at a Foraging Site Depend on Group Size?

Arrival rates of dace to foraging sites were not related (P>0-1) to group size in 60% of all observations (N = 52 sets), indicating that the presence of conspecifics often did not attract or repulse approaching foragers (Table II). Probability levels associated with most of the non-significant regression tests exceeded 0-2 (Table II). Note also that although we used a 0-1 probability level for regression significance, actual type I error probabilities in these tests may have been as high as 0-2 because arrival and departure rate regressions were not independent. Thus, a failure to find a significant relationship was a conservative conclusion.

Arrival rates increased with group size, and thus provided evidence of attraction among dace, in only 12% of all observations. Arrival rates decreased with group size in the remaining 29% of the observation sets. Of the 52 observation sets with sufficient data for arrival rate regressions (Table II), 36 sets had a wide enough range of group sizes present for us to test the fit of quadratic models. Curvilinear regressions provided the best fits in five of the six data sets with positive functions and in two of the 15 data sets with negative relationships.

Regressions of arrival rates are difficult to interpret without knowing whether or not there were enough dace in the study areas to maintain arrival rates across the range of group sizes observed in foraging sites (i.e. whether the forager pool was

<table>
<thead>
<tr>
<th>Regression pattern</th>
<th>Number of observation sets (%)</th>
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<tbody>
<tr>
<td>Arrival rate versus dace number</td>
<td></td>
</tr>
<tr>
<td>Non-significant (i.e. arrivals independent of group size)</td>
<td>31 (60%)*</td>
</tr>
<tr>
<td>Negative (i.e. possible avoidance among foragers)</td>
<td>15 (29%)</td>
</tr>
<tr>
<td>Positive (i.e. attraction among foragers)</td>
<td>6 (12%)</td>
</tr>
<tr>
<td>Departure rate versus dace number</td>
<td></td>
</tr>
<tr>
<td>Linear (i.e. departures independent of group size)</td>
<td>24 (48%)</td>
</tr>
<tr>
<td>Positive quadratic (i.e. avoidance among foragers)</td>
<td>19 (38%)</td>
</tr>
<tr>
<td>Negative quadratic (i.e. attraction among foragers)</td>
<td>7 (14%)</td>
</tr>
</tbody>
</table>

*Ranges of probability levels associated with non-significant regressions were: P>0-1-0-2, N = 13 observation sets; P>0-2-0-4, N = 9 observation sets; P>0-4, N = 9 observation sets.
Figure 1. Monthly differences in departure rate–group size relationships. The number of observation sets best fit by linear (■), positive quadratic (□), and negative quadratic functions (●) are plotted for each month. Among month differences were significant (G-test for independence, G = 19.023, df = 8, P < 0.025).

open or closed). For example, negative relationships between arrival rate and group size (i.e. 29% of the sets), may be interpreted as avoidance among foragers only if an open pool of dace was available. Interpretation of departure rate–group size relationships is less ambiguous than that of arrival rates because the pool of foragers available to leave is the number of dace present in the quadrat.

Departure rate regressions suggested that the effect of group size on dace departure probability varied among observations, from no effect to either positive or negative effects. The only observation sets with non-significant regressions (P > 0.1, five of 55 observation sets) had data only for one and two dace present. Otherwise, departure rate always increased with dace number, and was best described by a linear function for 24 observation sets (Table II). Thus, for almost half of the observation sets there was no evidence that the probability of a particular dace leaving a site changed with the number of conspecifics present, suggesting that groups were aggregations in which group size did not affect net foraging benefits. The remaining observation sets were best described by quadratic regressions. Dace appeared to avoid larger aggregations during 19 observations (i.e. sets with positive quadratic coefficients). Conversely, there was evidence of attraction among foragers during seven observations, when dace were less likely to depart larger groups (i.e. sets with negative quadratic coefficients).

The relative frequencies of linear, positive quadratic and negative quadratic departure rate functions differed significantly among months (Fig. 1). Dace generally departed foraging sites independently of group size during spring (April and May) and autumn (October and November), whereas foragers avoided conspecifics in 72% of the observations made during August and September. In contrast, dace were attracted to larger groups in 43% of the November observations. This pattern was similar between years, except that we observed avoidance in October 1988 (when flows were reduced because of a drought from 1985 to 1988) but not in October 1989. This seasonal shift in behaviour did not correspond to any dramatic change in size distributions of foraging dace; most individuals averaged 5–7 cm total length during all observations.

In summary, analyses of arrival and departure rates suggest that groups most often were aggregations in which dace did not interact. However, there was evidence of avoidance among aggregating foragers on some dates (primarily during late summer), while there was evidence of attraction among dace in less than 15% of the observations (primarily during autumn).

Did Group Size Affect Dace Foraging or Aggression Rates?

Group size effects on foraging rates

Feeding rate generally was not linearly related to group size, indicating that dace usually did not compete with conspecifics or obtain foraging benefits in groups. Only six of 31 regressions of feeding
Table III. Summary of results of linear regression analyses testing for effects of group size (i.e. number of dace present in a foraging site) on feeding and aggression rates

<table>
<thead>
<tr>
<th>Regression analysis</th>
<th>Number of observation sets (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Per capita feeding rate versus</td>
<td></td>
</tr>
<tr>
<td>group size</td>
<td></td>
</tr>
<tr>
<td>Non-significant</td>
<td>25 (81%)*</td>
</tr>
<tr>
<td>Negative slope ($P &lt; 0.05$)</td>
<td>6 (19%)</td>
</tr>
<tr>
<td>% feeding strikes resulting in rejection vs. group size</td>
<td></td>
</tr>
<tr>
<td>Non-significant</td>
<td>9 (100%)†</td>
</tr>
<tr>
<td>Per capita aggression rate versus</td>
<td></td>
</tr>
<tr>
<td>group size</td>
<td></td>
</tr>
<tr>
<td>Non-significant</td>
<td>9 (100%)†</td>
</tr>
</tbody>
</table>

*Probability levels associated with non-significant regressions were: $P > 0.1$, $N = 7$ observation sets; $P > 0.2$, $N = 10$ observation sets; $P > 0.4$, $N = 8$ observation sets.
†Probability levels associated with non-significant regressions were: $P > 0.2$, $N = 3$ observation sets; $P > 0.4$, $N = 3$ observation sets.

Rate versus group size were significant (Table III); in all six, per capita strike rates were a decreasing function of group size. In addition, regressions of the proportion (arcsine transformed) of strikes that resulted in particle rejection versus group size for nine data sets all were non-significant (Table III). Thus, the general lack of relationship between feeding rate and group size was not caused by foragers in larger groups striking more frequently at inedible debris.

In five of the six cases where group size had a negative effect on feeding rate (Table III), dace were less likely to remain in larger aggregations (i.e. dace departure probability increased with group size). However, during 10 other observations in which departure probability increased with group size, per capita feeding rate was unrelated to the number of dace present. Thus, intraspecific exploitative competition could not account for most observations of dace avoiding larger groups.

**Group size effects on aggression among dace**

There was no evidence that the probability of being chased or involved in aggression changed predictably with the number of conspecifics present, and thus variation in this relationship did not correspond to whether or not dace were attracted to groups. Regressions of per capita aggression rate versus group size for nine observation sets all were non-significant (Table III). Aggression by dace was infrequent overall, averaging 0.016 chases and displacements per individual per 5-s interval ($N = 60$, $SD = 0.032$), or about one incident per dace every 5.2 min. During 13 of 60 observations, however, a single dace initiated all or nearly all aggressive acts. These aggressors tended to remain in the observation sites throughout observation periods, primarily leaving to chase out a conspecific, to meet a conspecific swimming toward the quadrat, or to intercept a drifting particle. On average, aggression rates were an order of magnitude higher when a single aggressor was present than when several dace initiated chases or displacements (means = 0.0581 versus 0.0057 incidents/5 s in sites with versus without a single aggressor; Wilcoxon test, $z = 5.13$, $P < 0.0001$). Nine of the 13 observations with a single aggressive dace were during August and September, and observation sets with aggressive dace were characterized by higher water temperatures than those without aggressors (means = 15.3°C versus 12.6°C, Wilcoxon test, $z = 2.25$, $P < 0.01$).

Although the average probability of being chased was unrelated to group size, the presence of a single aggressive dace apparently affected the relationship between departure probability and group size. In eight of the 13 observations with a single aggressive dace, departure probability increased with group size (i.e. there was a positive quadratic relationship between departure rate and dace number). Of the other five observations with a single aggressor, two had insufficient ranges of group sizes to regress departure rates, whereas in three, all from October or November, departure rate increased linearly with dace number. Dace were more likely to leave a site in groups of two or three when an aggressor was present: seven of the 12 data sets with non-independent departures were observations including a single aggressor ($G$-test for association, $G = 8.581$, $df = 1$, $P < 0.005$). Dace did not, however, enter sites in groups more frequently when a single aggressor was present ($G = 0.115$, $df = 1$, $P > 0.1$). This at least partly explains the lack of association between non-independence of arrivals and departures (described above).

In summary, the presence of a single aggressive dace could account for most observations of increased departure probability as a function of group size. However, we found no instances of
feeding benefits, or lower per capita aggression in larger groups.

**DISCUSSION**

Our results suggest that dace frequently foraged independently of each other and that groups most often resulted from fish aggregating in profitable foraging locations rather than from social attraction. Although there may have been a seasonal shift in this behaviour, dace arrival rate rarely increased as a function of group size, and departure rate most often was independent of group size. In addition, individuals usually did not enter or depart foraging sites in groups. Assuming dace forage so as to maximize individual fitness, our results suggest that dace did not obtain substantial benefits from foraging near conspecifics.

Group foraging has been shown to benefit freshwater fishes in laboratory studies. Why would these benefits not apply to minnows foraging in field conditions? Individuals may benefit from social foraging via two main mechanisms: (1) enhanced foraging success and (2) decreased risk of predation. Feeding data provided little evidence that foraging in groups benefits individual dace. Moreover, it is unlikely that local enhancement, through which group members benefit by sharing food discovered by others (Pulliam & Millikan 1982), generally is significant for drift feeding fishes. Local enhancement is effective when resources are patchily distributed, food in patches is shared by group members, and groups find or feed in patches more efficiently than solitary foragers (Pulliam & Millikan 1982). In laboratory tests, for example, shoaling minnows benefit because food patches are found more quickly by several searchers, and once discovered, food patches can be shared by group members (Pitcher et al. 1982; Magnan & FitzGerald 1984). Drift feeders use two identifiable resources: suitable feeding sites, and relatively large drifting invertebrates. Feeding sites may be patchily distributed but presumably are of known distribution to local foragers. Large drifting prey probably occur independently through time, assuming drifting invertebrates enter the current (and settle) independently. Thus, a dace usually would not benefit by joining a conspecific that has just taken a bite.

Group foraging could allow drift feeders to spend more time foraging because group members spend less time in predator vigilance. For example, in laboratory experiments, members of larger groups of cyprinids began foraging more quickly (Morgan & Colgan 1987), spent less time in cover or in evasive manoeuvres (Magurran & Pitcher 1983), and continued to feed longer in the presence of a model predator (Magurran et al. 1985; but see Rehnberg & Smith 1988 for contradictory results). Similarly, Hill (1989) found that rosided dace in an artificial stream would not forage unless at least four individuals were present in the stream together (in the absence of predators), suggesting that dace were less timid in larger groups. Our field data, however, provided no evidence of this effect; dace foraged alone (as well as in groups) during all monthly observations, and solitary foragers had the highest strike rates recorded.

Predation pressure on dace at Coweeta may be too low during much of the year for individuals to benefit appreciably from anti-predation functions of shoaling. The known piscivores at the study sites are northern watersnakes, *Nerodia sipedon*, belted kingfishers, *Megaceryle alcyon*, raccoons, *Procyon lotor*, and from late autumn through early spring, rockbass, *Ambloplites rupestris*. Watersnakes are uncommon, and we have only seen evidence of a single incident of fish predation by raccoons in 8 years of research at Coweeta Creek. Kingfishers were more common in 1988 and 1989 than in several years previous (personal observation). Group foraging may not offer much protection, however, against an aerial predator that attacks before it can be spotted by any group member (Goodey & Liley 1985; Pitcher 1986), a likely situation in streams with considerable surface turbulence.

The increased tendency during autumn for dace to remain in large groups may have been a response to a perceived increase in predation risk. For example, cyprinids threatened by a predator under experimental conditions form larger or more cohesive groups (Pitcher et al. 1983; Morgan 1988). Rockbass usually move upstream into the vicinity of the study areas in late autumn and leave by early spring (personal observation; Stouder 1990). We have no direct evidence, however, that rockbass actually pose a threat to cyprinids in the study sites (rockbass captured from these sites in previous years usually had empty stomachs; Stouder 1990).

**Competition and Aggression Among Dace**

The observation of increased departure probabilities with increasing group size during 19 observations indicated costs of foraging near conspecifics, especially during late summer. Negative
effects of group size on foraging rate, however, only were apparent during five of these observations. This was surprising given that drift rates of large prey (i.e. animals > 2 mm total length, the minimum-sized prey normally consumed by dace, Hill 1989; Stouder 1990) are low at Coweeta, averaging less than two prey per min in a 20 x 20 cm section of water column at dace foraging sites (Freeman 1990). Dace may not compete exploitatively in groups because foragers are unable to discriminate prey from inedible debris without striking (as is suggested by observations of dace striking large drifting debris and frequent rejections). In this case, opportunities for feeding strikes would often not be depleted even in large foraging groups.

Avoidance among foragers was most strongly associated with the presence of aggressive individuals, and it is interesting to consider what dace may gain through aggressive behaviour given that strike rate generally does not decline with increasing group size. We hypothesize that an aggressive (or solitary) individual may have greater access to large drifting prey. It is common for several foragers in a group to strike, in succession, at a large particle of drifting debris; aggressive individuals may often have the first opportunity to strike large prey. The potential importance of large prey is evidenced by energetic considerations. Standard metabolic requirements for a 6-cm dace (standard length; weight approximately 4 g) in autumn are approximately 911 J/day; assuming standard metabolic rate equals 0.7 mg O2/g/h (Facey & Grossman 1990), and 13.6 J/mg O2 (Elliott & Davison 1975). A dace would need to consume at least 43 mg of prey each day to meet resting metabolic costs (assuming 100% assimilation of invertebrates-averaging 21 J/mg dry weight), or greater than 800 individual 2-mm long prey (Smock 1980). Because insect mass increases exponentially with body size (Smock 1980), foraging dace may require captures of relatively large prey to meet their energetic requirements.

These calculations suggest that because of the low density of large drifting prey, dace at Coweeta may be limited by the time available for foraging. In this case, the increase in fitness produced by aggressive behaviour may depend on the energetic requirements of individuals. For example, aggression among flocking birds may increase with temperature because reduced energetic requirements allow more time for aggression (Caraco 1979b, 1980). Standard metabolic rates of dace acclimatized in the field actually were lowest in summer (15°C) and highest in autumn (10°C), possibly as a result of gonadal development in autumn (Facey & Grossman 1990). Dominance behaviour by dace may therefore have been more frequent during late summer because reduced energetic demands allowed more time for aggression than during autumn. Additionally, aggression by three individuals in late October and November 1989 did not result in increased departure probabilities from larger groups. Thus, aggression may become a less effective strategy (e.g. for defending access to large prey) if dace form larger groups during autumn in response to some other factor.

Conclusions

We conclude that dace foraged in groups most often as a result of individuals aggregating in profitable foraging locations rather than from attraction among individuals. Our observations are similar to those of house sparrows, *Passer domesticus*, feeding on patches of seed under conditions of low predation risk, in which arrivals were unrelated to flock size at a seed patch (Barnard 1980a, b). Per capita aggression among sparrows increased with flock size, increasing the probability of departure. Per capita aggression was unrelated to group size in dace; however, intense aggression by particular dace may have increased departure probabilities for targeted individuals. When aggression among dace was very low, departure probability often was unrelated to group size. Similarly, Krebs (1974) observed that herons foraging in flocks did not interfere with each other or directly benefit from the presence of conspecifics, and departure rates increased linearly with flock size.

Our results suggest that benefits of group foraging demonstrated for fish in laboratory conditions (Pitcher et al. 1982; Magurran & Pitcher 1983; Magurran et al. 1985; Street & Hart 1985; Morgan & Colgan 1987) may not always apply to groups foraging under field conditions. However, dace responses to groups of conspecifics varied considerably among our observations. This variation was only in part seasonal (e.g. attraction among dace was more evident during autumn), and a separate analysis failed to find any correspondence between departure rate–group size relationships and prey drift rate, water depth, or current velocity at the foraging sites (Freeman 1990). Variability in dace
behaviour may have represented stronger shoaling tendencies by a few individuals, similar to the variation observed by Helfman (1984) among individual yellow perch, *Perca flavescens*, and by Magurran (1986) among individual minnows, *Phoxinus phoxinus*, responding to a stalking predator. A possible source of variability among dace is seasonal and anti-predator behaviour may be more strongly developed (Seghers 1974; Magurran 1986, 1990). Additional field studies of cyprinid foraging behaviour, especially in habitat where piscivores are more common, could elucidate the conditions under which social attraction is important to these fishes and the extent to which dace behaviour in our study was a result of low predation pressure.

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