Maximizing foraging success: the roles of group size, predation risk, competition, and ontogeny

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Abstract. Grouping is an evolutionary strategy that allows individuals to optimize foraging success in habitats of varying quality and when under the risk of predation, but group foraging can lead to competition between group members. The effects of group size, habitat, predation, and competition on foraging success also can change as animals grow. Our study explored how these concurrent factors influenced the foraging success of group members at two different life stages. In a wild population of coho salmon (Oncorhynchus kisutch), we first tested four hypotheses concerning the effects of group size on foraging success. We then analyzed our field observations with structural equation modeling to test causal relationships between group size, habitat, predation risk, competition, and the foraging success of individuals during two periods of development. We found support for the hypothesis that the relationship between group size and foraging success was parabolic during both study periods, revealing an optimal range of group sizes that maximized individual foraging success, which was conserved as fish aged. Predation risk had a positive effect on group size, particularly for older fish, and distance to cover and water depth were indicators of risk for both age groups. As group size increased, so did competition, but only for young fish; competition only had a weak positive effect on foraging success for older fish. Our results reveal that the relative direct effects of predation risk and competition on foraging success were weak compared with the direct effect of group size. Our study provides new insights and theoretical implications for understanding how selective forces—that is, group size, predation risk, competition, habitat, and ontogeny—act concurrently to affect foraging success in wild populations.

Key words: feeding; fish; foraging theory; grazing; group living; habitat quality; optimal foraging; patch choice; salmon; shoaling; structural equation modeling.

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INTRODUCTION

Understanding animal foraging is a central theme in ecology and evolution because foraging is directly related to an animal’s fitness (Waite and Field 2007). As such, ecologists have developed multiple theories and hypotheses to understand how animals maximize or optimize foraging success (MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977, Mangel and Clark 1986, Stephens et al. 2007). To maximize foraging success, animals must deal with multiple selective forces at the same time. For instance, predation, competition, habitat quality, and variable resource distributions concurrently affect foraging success, and the effects of these selective forces may altogether change with ontogeny (Werner and Hall 1988). Many animals exhibit strategies to maximize foraging success when dealing with multiple selective forces (Werner and Hall 1988, Grol et al. 2014, Matich and Heithaus 2015), one of which is to associate or to
group with conspecifics (Krause and Ruxton 2002).

The costs and benefits of grouping are dynamic (Clark and Mangel 1984, Chase et al. 2002, Krause and Ruxton 2002, Olson et al. 2015). Among the benefits of grouping behavior are minimizing energy expenditure in the search for food (Pitcher et al. 1982), reducing predation risk in high-risk habitats (Lima and Dill 1990, Wrona and Dixon 1991, Cresswell 1994, Lima et al. 1999, Cresswell and Quinn 2011, Creel et al. 2014), and enabling predators to capture large prey that would otherwise be difficult to secure by any one individual (Creel and Creel 1995, Courchamp and Macdonald 2001). Costs to individuals in groups may include lower reproductive and developmental rates (Borries et al. 2008), reduced food availability (Vijayan et al. 2012), and more intense competition between conspecifics leading to a reduction in per capita consumption (Moody and Ruxton 1996, Beauchamp 1998).

The costs and benefits associated with grouping are likely to be mediated by several environmental and biological factors. For example, habitat can reduce the risk of predation by providing refugia from predators (Bugert et al. 1991, Ruiz et al. 1993, Sih 1997, Beauchamp 2007), which in turn can increase time spent foraging (DeCesare et al. 2014). The size of a group and within-refuge competition can also influence the foraging success of individuals (Orrock et al. 2013, Creel et al. 2014). Moreover, foraging-related costs and benefits in grouping animals are likely to change with ontogeny (Werner and Hall 1988). With growth, individuals may experience reduced predation risk from gape-limited predators (Urban 2007), changes in the strength of intra-specific competition (Werner and Anholt 1993, Cameron et al. 2007), and shifts in habitat use (Copp 1992, Olson 1996, Match and Heithaus 2015). Such ontogenetic changes regarding the effects of predation and competition, along with shifts in habitat use, may dramatically alter the costs and benefits of grouping behavior, and the relationship between group size and foraging success. In some cases, the benefits of grouping in some species may disappear altogether with age.

Despite a great number of theoretical developments, we still lack a full understanding of the factors that regulate the foraging success of grouping animals in wild populations. Much of our knowledge of what drives the foraging success in grouping animals is based on experimental studies, which generally use a small number of individuals, and therefore may not reflect the natural spectrum of group sizes for a variety of species. This is not a criticism of such studies, but there is a paucity of confirmatory observational studies that capture natural variation in group size, foraging success, predation risk, and competition beyond a single life stage (Persson and Stenberg 2006). Such empirical information is essential to validate or refine foraging theories.

We conducted a field study with the goal of empirically assessing the connections between foraging success, predation risk, competition, and ontogeny, in a wild stream-dwelling population of coho salmon (Onchorhynchus kisutch) without in situ manipulations. From field observations, we first tested four general hypotheses from the literature concerning the effects of group size on foraging success under different selective pressures (Beauchamp 1998, 2014): (1) Individuals do not derive any foraging benefits associated with group size; (2) as group size increases, foraging success will also increase; (3) as group size increases, foraging success will decrease; and (4) foraging success will increase with group size until the costs of grouping outweigh the benefits (Fig. 1). Subsequently, we developed a structural equation model (SEM) to explore in a multivariate context how group size and foraging success were themselves affected by predation risk, competition, and developmental life stage. Based on multiple tenets of foraging theory (e.g., summarized in Stephens et al. 2007), we developed a meta-model to guide the relationships and hypotheses tested in the SEMs (Fig. 2).

**METHODS**

**Field site and study species**

We conducted this study in the Onion River, which is a clear-water tributary of Lake Superior located in Bayfield County, Wisconsin, USA (46°45’ N, 90°55’ W). We recorded juvenile coho salmon behavior during two time periods, from 22 May to 15 June (early summer, young fish) and 13 to 23 August in 2007 (late summer, older fish). The study reach was approximately 1 stream km and consisted of a diverse mix of habitat conditions. Coho salmon were chosen...
because they are abundant in the Onion River (Lonzarich et al. 2009) and because they are known to establish dominance hierarchies, display aggression, and form cohesive groups during their stream residency (Chapman 1962, Pitcher 1986, Nielsen 1992, Grand and Dill 1999). During this residency period, juvenile coho salmon establish feeding territories and primarily pluck small invertebrates from the drift and of the stream benthos (Chapman 1962, Dill et al. 1981). The length of time an individual will stay in a group is dependent on the strength of competition in groups, which when high can trigger emigration (Chapman 1962). We also chose this species because individuals grow rapidly (Fausch and White 1986, Ebersole et al. 2006), which allowed us to overlay an ontogenetic component in our examination of the way environmental factors affected foraging success and group size dynamics.

Field observations and measurements

The objectives of this study relied on our ability to identify a group of interacting individuals. We defined a cohesive interacting group of fish from an unstructured aggregation (Pitcher 1983, Nielsen 1992) as a cluster of individuals swimming together within four body lengths of each other (Pitcher 1983). To ensure observations were made on cohesive interacting groups, observers watched groups for at least two minutes before concluding whether the identified clusters were clearly an interacting group or an aggregation of floaters (Nielsen 1992).

For groups that were comprised of five or more individuals, five focal individuals from each were chosen from different positions along the upstream–downstream axis of the group. Each of these individuals was observed for 150 s. For groups containing between two and five individuals, we made 150-s observations on all group members. Foraging success, defined as the number of feeding events per minute, and aggressive interactions—our surrogate variable for competition—were recorded for each of the focal individuals. A feeding event was defined as a fish ingesting a food particle without egestion occurring. Fish were often observed ingesting drift material that was egested. This was assumed to be exploratory feeding behavior and was not included in the analysis because no caloric value would have been attained. Aggression was defined as nip and chase behaviors (sensu Hoar 1951, Chapman 1962).

After having completed our behavioral observations for a group, we measured all habitat variables from the center of the group’s location in the channel at the end of each day of observations. A heavy washer with flagging attached to it was placed in the center of each group to mark the location of microhabitat measurements. These measurements included surface velocity (m/s), distance to stream bank (cm), distance to nearest cover (cm), and depth (cm). Cover included undercut stream banks or woody debris fields. For a woody debris field to be considered cover, it had to contain woody debris with at least an 8 cm diameter. We treated predation risk as a theoretical construct that potentially varied with naturally occurring habitat features (analysis for theoretical construct described below). Multiple studies have shown that stream pools are habitats of high predation risk due to the presence of piscivores and other types of predators (Power et al. 1985, Schlosser 1991, Martel and Dill 1993, Magoullick 2004, Al-Chokhachy and Budy 2007). In our stream system, we
observed several predators in the stream pools including green herons (*Butorides virescens*), great blue herons (*Ardea herodias*), and belted kingfishers (*Megaceryle alcyon*), but the predominant predators were brown trout (*Salmo trutta*).

The majority (>90%) of behavioral observations were conducted via snorkeling with a team of two observers. One observer conducted underwater observations, and the other was stationed on the stream bank to record data reported by the underwater observer. The underwater observer estimated group size, feeding events per minute, and agonistic behavior perpetuated against and by the focal individual per minute. Upon entering the stream, the underwater observer would move upstream from the original entry point so as to reduce disturbance on potential focal groups and maintain water clarity. Observations were typically made within one meter of the focal individual. Accuracy was largely dependent on the ability of the observer to keep track of the focal individual. If the focal fish was lost, observations on that individual were aborted. We recorded observations for groups in <20 cm of water from the stream bank because it was difficult to observe them underwater.

Keeping track of individuals within a group to avoid conducting multiple observations on a single individual was important. Unique characteristics such as markings on the body, coloration patterns, fin structure, protrusion of fecal matter, and position made it possible to track individuals within a group. The flagging placed in the center of each group for microhabitat analyses limited the likelihood that we would conduct observations on any one group multiple times. Further, we started each day of observations in a separate reach of stream from the previous day observations.

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**Fig. 2.** Meta-model used to guide our examination of how predation risk, group size, and aggression affected the foraging success of juvenile coho salmon. Depth (cm), distance to stream bank (cm), current velocity (cm/s), and distance to nearest cover (cm) were indicators of predation risk, which was a composite variable (see Methods for details).
Data analyses

To examine the relationship between group size and foraging success, we averaged the foraging success of each focal individual within a group—that is, the average foraging success for a group served as the replicate. A second-order least-squares regression model best described how much variance in foraging success was explained by group size for the early and late summer time periods. An $\alpha$-level of 0.05 was used to evaluate statistical significance in the regression models. The early summer (normality $P = 0.087$, constant variance $P = 0.355$) and late summer (normality $P = 0.102$, constant variance $P = 0.973$) models did not violate parametric assumptions of the least-squares regression.

We used structural equation modeling to analyze how group size, habitat, and aggression affected the foraging success of coho salmon. We chose SEM because it provides a multivariate framework for investigating causal processes (Grace et al. 2012) and accounts for direct and indirect effects in the calculation of path coefficients (Grace and Bollen 2005, Grace 2006). Further, SEM allowed us to test multiple models of how abiotic and biotic variables might affect foraging success and evaluate alternatives before identifying the model that best fit the data.

Predation risk was not a directly observed variable in our SEMs; rather, it was a composite variable. Predation risk can be defined in multiple ways, and there can be many measured indicators of predation risk (e.g., density of predators, habitat type, density of conspecifics). In our study system, it was difficult to quantify the density and distribution of predators because the Onion River is a meandering, densely forested ecosystem. This made quantifying risk related to piscivorous bird predators unfeasible. Further, sampling piscivorous fish predators to quantify their density and distribution would have required us to use invasive netting and electrofishing techniques. Doing so may have triggered emigration from our study reach or caused cohesive coho salmon groups to disband. In stream ecosystems, deep pools are generally the highest risk habitats because they often contain large piscivorous fishes (Power et al. 1985, Schlosser 1987, 1991, Harvey 1991). In our study system, adult brown trout ($S. trutta$) were common in these pools. Piscivorous birds may also have high success rate foraging on coho salmon in stream pools, particularly if there is minimal cover in the form of large woody debris (Reinhardt and Healey 1997). Since stream pools are often deep, lower velocity habitats, we used the measured microhabitat variables of depth, water velocity, distance to cover, and distance to stream bank as indicators of predation risk, which was an unknown weights composite variable in the SEMs. Composite variables represent the collective effects of the indicator variables on the response variables, similar to a multiple regression predictor variable (Grace 2006, Grace and Bollen 2008). In our models, the response variables were group size, foraging success, and aggression (i.e., competition). For further discussion on the mechanics of using composite variables in SEMs, see Grace and Bollen (2008).

For group size in the SEMs, we had to account for the non-linearity between group size and foraging success. We use the composites for endogenous non-linearity procedure described by Grace and Bollen (2008) to accomplish this. However, rather than using the square of foraging success, we used predicted values of foraging success generated from the observed bivariate models between group size and foraging success.

There are multiple fit indices for SEM, and each can have their own biases; therefore, we used multiple fit indices to evaluate our final models. We evaluated model–data consistency for the SEMs with a chi-square test ($P > 0.05$ indicates good model fit) to determine whether the model significantly deviated from the data (Grace et al. 2010). We also report the goodness-of-fit index (GFI), for which values above 0.90 suggest a good model fit to the data (Hooper et al. 2008). For each SEM, we also report the root mean square error of approximation (RMSEA), which favors model parsimony. An RMSEA value below 0.08 indicates a good model fit (MacCallum et al. 1996). As another measure of model fit, we report the standardized root mean square residual (SRMR) where a value $<0.08$ is considered a good fit (Hu and Bentler 1999). Lastly, we report $P$-values and the associated path coefficients for each path in our illustration of the SEMs where $P < 0.10$. All other paths $\geq 0.10$ are indicated as “NS” for non-significant.
RESULTS

In the survey of our 1-km study reach, we encountered 230 groups, varying in size from 2 to 36 individuals (Fig. 3A). Most groups consisted of 3–17 individuals, but most fish were in groups of 12–17 individuals (Fig. 3B). Behavioral observations were made on a subset of all fish encountered. In the early summer, we quantified foraging and aggression from 433 fish in 92 groups. In late summer, we collected data on 267 fish from 55 groups. The greatest percentage of the focal individuals were in groups of intermediate size for both sampling periods (Fig. 4).

The relationship between group size and foraging success was parabolic and consistent with the expectations of the hypothesis represented graphically in Fig. 1D. In both early and late summer, the data were best fit by second-order polynomial regression models (Fig. 5). In early summer, maximal rates of foraging in groups of intermediate size were 2–4 times higher than rates for individuals in smaller and larger groups. For this season, group size explained 41% of the variance in foraging success (Fig. 5A). Although foraging success in late summer also peaked in groups of intermediate size, the relationship was not as strong as that uncovered from the early summer sampling period. Focal individuals foraging in groups of intermediate size during late summer had foraging rates as much as three times higher than individuals from the smallest groups; however, foraging rates declined only slightly for fish associated with larger groups. Overall, group size explained 24% of the variance in foraging success in late summer (Fig. 5B).

The SEM for early summer fish was a good fit to the data with a high GFI, low RMSEA and SRMR, and non-significant chi-square (Fig. 6A). Only water depth and distance to cover were retained in the best fit model as significant predictors of the predation risk composite variable. Predation risk had a positive effect on group size ($P = 0.031$); that is, larger groups were generally found in higher risk habitats. Aggression increased with group size ($P < 0.001$) and was inversely related to predation risk ($P = 0.003$). Together, group size and predation risk explained 24% of the variance in aggression. Foraging
success was positively associated with group size ($P < 0.001$) and predation risk ($P = 0.053$), and together, these two variables explained 46% of the variance in foraging success in early summer.

The SEM for late summer fish was also a good fit to the data with a high GFI, low RMSEA and SRMR, and non-significant chi-square (Fig. 6B). As for the model for early summer fish, only depth and distance to cover were retained in the best fit model as significant indicators of the composite variable of predation risk. However, for these late summer fish, predation risk was a much stronger predictor of group size patterns ($R^2 = 0.34$). Foraging groups were larger in habitats associated with higher predation risk—that is, deep water, farther from the cover ($P < 0.001$). But unlike for the early summer model, neither group size nor predation risk were associated with aggression in late summer. Group size was again the strongest predictor of foraging success for older fish ($P < 0.001$). Aggression was positively related to foraging success for late summer fish ($P = 0.044$). Together, group size and aggression explained 31% of the variance in foraging success for late summer fish.

**DISCUSSION**

In this study, we investigated how multiple selective forces affected foraging success during two early life stages in a wild population of juvenile coho salmon. Our first study objective was to characterize the association between group size and foraging success, testing different hypotheses regarding this relationship. We found support for the hypothesis that this relationship was parabolic; that is, foraging success increased to groups of intermediate size and then decreased steadily in groups of larger sizes. This pattern suggests the existence of an optimal range of group sizes in this population, where individual foraging success was maximized. Moreover, as the young salmon grew over the summer, the parabolic relationship between group size and foraging success, although still evident, became much less pronounced. This result suggests that although growth and development may reduce the role of group size as a direct or mediating factor on foraging success, groups that maximize foraging success are still conserved as ontogeny progresses.

Our findings regarding the relationship between group size and foraging success are consistent with the expectations of foraging theory. With respect to small- to medium-sized groups, higher rates of foraging with increasing group size could have been a consequence of reduced vigilance, which thereby enabled fish to devote more time to feeding. This is consistent with previous research in a variety of animal taxa (Roberts 1996, Fortin et al. 2004, Pays et al. 2012, Sorato et al. 2012, Vijayan et al. 2012, Olson et al. 2015). Larger group sizes (those with lower foraging returns), food scarcity, and competition (exploitative or interference) may have been
responsible for diminished foraging returns (Moody and Ruxton 1996, Bednekoff and Lima 2004, Vijayan et al. 2012). Although these explanations for the group size–foraging relationship are compelling because of their alignment with theoretical expectations, our causal multivariate analysis indicates some deviation from theoretical expectations.

Unexpectedly, predation risk did not have a strong direct effect on foraging success. Predation risk was, however, positively associated with group size during both sampling periods—larger groups formed in habitats of high risk. This relationship was stronger during late summer, perhaps indicating that as fish grew, they may have learned which habitats were more risk-prone. Thus, predation risk affected group size in a way consistent with theoretical predictions that there is reduced individual risk in larger groups (Cresswell and Quinn 2011, Sorato et al. 2012, Creel et al. 2014), but the direct effects of predation risk on foraging success were weak for early summer fish and non-significant for late summer fish. We suggest that group size may act as a mediating variable between predation risk and foraging success in wild populations. Our data indicate that predation risk primarily influenced the size of a group, which then directly affected foraging success. For young fish, the effect of risk on group size was weak, indicating

Fig. 6. Structural equation models representing the relationships between predation risk, group size, competition, and foraging success for young fish (early summer) and older fish (late summer). Solid arrows indicate positive effects, and dashed arrows indicate negative effects. NS = non-significant ($P > 0.10$) for the respective path coefficient.
that group size may have been the primary force driving foraging success at this age—this is also consistent with a stronger relationship between group size and foraging success in our bivariate analysis for young fish (Fig. 5A). As the fish aged, the positive relationship between predation risk and group size was much stronger. Our bivariate analysis also indicated a reduction in the explanatory power of group size on foraging success in late summer. Thus, it would appear that the role of group size in mediating the effects of predation risk on foraging success increases with ontogeny. We cannot know the manner in which group size mediates the effects of predation risk from our data, but we conclude that predation risk was a poor direct predictor of foraging success in this population.

Food availability or within-refuge competition may serve as explanations for why predation risk did not have a stronger effect on foraging success. It is possible that food scarcity significantly constrained foraging returns in low-risk habitats. Our study site contained an abundance of structural habitat (e.g., large woody debris). We expected access to such refuge would have increased foraging success through reduced risk, yielding a stronger negative relationship between reduced risk and foraging success. The weak positive relationship between risk and foraging success suggests that foraging returns were higher in high-risk habitats (i.e., stream pools) for young fish (Fig. 6A). However, habitat refuge from predators can have non-consumptive effects such as reduced prey activity, growth, and increased resource competition between conspecifics (Persson 1993, Orrock et al. 2013). We observed a negative relationship between predation risk and competition in the SEM for younger fish, indicating that in our study system, competition was highest in low-risk habitats (Fig. 6A).

Thus, at least for young fish, within-refuge competition for resources may have offset potential foraging gains resulting from reduced risk.

We acknowledge that the four habitat indicator variables may not have fully captured predation risk dynamics in this system. Nonetheless, stream pools were the deepest habitats and depth had the strongest relationship to grouping in the SEMs of the four variables that we assumed reflect predation risk. Because larger groups formed in stream pools, we believe that the greatest risk to predation of coho salmon was associated with these habitats. Moreover, stream pools are well known to harbor a high density and variety of predators (Power et al. 1985, Schlosser 1991) and predators may drive smaller fishes into shallow water habitats (Schlosser 1987, Harvey 1991). Thus, we believe our theoretical construct of predation risk was sufficient to capture a large degree of perceived risk in our study system.

Competition, as measured by agonistic interactions between conspecifics, was surprisingly a weak predictor of foraging success. Competition only affected the foraging success of older fish. For young fish, competition increased with group size and high-risk habitats yielded lower rates of competitive interactions, but we did not find any evidence of a direct effect of competition on foraging success. Nonetheless, the optimal foraging strategy is likely to change over time. For example, the optimal foraging strategy may shift from foraging individually to foraging in larger groups as the perceived risk of predation increases (Stenberg and Persson 2005), which is common in stream ecosystems (Cooper et al. 1997). In fact, Krause et al. (2000) found that the time a fish spends in a group is inversely related to the size of the group. These findings support the view that animals may continuously sample groups of varying sizes and, as a consequence, the groups may vary substantially in size over short periods of time. As such, the optimal foraging returns in groups of intermediate size may apply...
to a greater percentage of a population rather than for just those individuals observed within an optimal group size at a single time point.

**Conclusions**

Our results have several implications for understanding how foraging success in grouping animals is affected by multiple selective forces at different life stages. First, across a natural spectrum of group sizes, the relationship between group size and foraging success is parabolic rather than positively or inversely related. This relationship was conserved among age classes, but was less pronounced in older individuals. Second, group size appears to be the main driver of foraging success compared to predation risk and competition, at least in our study population. And third, there appears to be an endogenous awareness of the foraging returns associated with intermediate-size groups.

As with so many studies, our investigation generates more questions than answers. Perhaps most elusive in the current study are the mechanisms driving the parabolic relationship between group size and foraging success. The direct effects of risk and competition were not strong, contrary to our expectations. Group size-mediated effects of predation risk and competition merit further research. We assumed at the onset of the study that low-risk habitats would generate higher foraging returns, which is not always the case (Orrock et al. 2013). Future studies of animal foraging success in wild populations should also consider the costs to individuals in low-risk habitats (e.g., resource availability, within-refuge competition). Another broad question is why animals occupy groups with sub-optimal foraging returns. Future research of wild populations could consider tracking individuals as they sample groups of varying size across the foraging landscape. This may shed light on patch- or group-departure rules.

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