Variation in Social Environment Influences Susceptibility to an Evolutionary Trap in Western Mosquitofish

By

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Abstract

While it is well recognized that animals use social information (i.e., information gleaned from conspecifics) to guide behavior, little attention has been given to the role of social information use in shaping responses to novel situations, such as those introduced by rapid environmental change. The three chapters of my dissertation focus on how evolved decision-making strategies that use social information can become maladaptive in changing environments. I examined how something as simple and fluctuating as group size and composition can alter individual behaviors of fish, including the common evolutionary trap of eating plastic. The "group size effect" is a classic phenomenon found across taxa, in which animals in larger groups show less vigilance behavior and more foraging behaviors. I looked at whether this common effect could carry over into novel situations by presenting novel foods with varying fitness benefits and costs to fish shoals of different sizes. I studied these questions in Western mosquitofish (*Gambusia affinis*), an ideal system to test how variation in group size might influence behaviors because they naturally live within fission-fusion societies, and thus experience constant changes in social aggregations. By studying individual foraging behaviors toward both known and novel food items, I was able to directly compare how individuals changed in their responses across the different foraging situations. The experiments provide evidence that group dynamics can influence the severity of a socially-mediated evolutionary trap and that, regardless of the number of members, group identity can have a strong effect on individual behavior. Furthermore, while social roles vary within a group based on group size, within-group variation in susceptibility to an evolutionary trap can be associated with social position.

Chapter 1

Variation in plastic consumption: social group size influences individual susceptibility to an evolutionary trap

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Abstract:

Anthropogenic change forces wildlife to navigate novel conditions, including evolutionary traps formed by decoupling cues from their previously evolved meaning. One underexplored feature that could drive variation in response to traps is social context. We looked at how group size influences the behavior of Western mosquitofish (*Gambusia affinis*), including eating novel foods. Individuals in larger groups were faster to recover after experiencing a predator cue and faster to feed on known food items. Moreover, fish in larger groups were more likely to try novel foods, including microplastics, a common evolutionary trap. We also found evidence of a group-level behavioral syndrome, in which groups had consistent proportions of individuals perform a behavior across assays. Our data provides evidence that group size can influence the severity of an evolutionary trap and that, regardless of group size, group identity can have a strong effect on individual behavior.

Keywords: collective personality, evolutionary trap, group size, microplastic

Introduction:

Human-induced rapid environmental change (HIREC) compels wildlife to navigate unprecedented situations, often with detrimental consequences (Sih, Ferrari, & Harris, 2011). Since behavioral responses are often the key, immediate reaction an animal has towards a novel condition, maladaptive behavioral responses can be particularly damaging to individual fitness and population persistence. Evolutionary traps are a common type of behavioral pitfall, in which animals make decisions based on cues that have been decoupled from their previously associated high fitness outcome (Robertson, Rehage, & Sih, 2013; Schlaepfer, Runge, & Sherman, 2002). Examples include animals that oviposit on glass because it polarizes light similar to water (Horváth, Kriska, Malik, & Robertson, 2009) or beetles that mistake a beer bottle for a suitable mate (Gwynne & Rentz, 1983). Critically, the variation in susceptibility to traps both between and within species is still poorly understood (Hale, Morrongiello, & Swearer, 2016; Hale & Swearer, 2016; Robertson et al., 2013). Understanding why certain individuals and species fall for evolutionary traps, while others do not, can help formulate predictions for how HIREC will shape ecological communities in the future (Hale & Swearer, 2016).

One common evolutionary trap is plastic consumption by marine and freshwater species (Anbumani & Kakkar, 2018; Andrady, 2011). Of particular concern are microplastics, defined as plastic items less than 5 mm in diameter (Andrady, 2011). These pollutants enter water systems via multiple sources, including the breakdown of larger plastic products and the release of plastic beads from cosmetic products. Due to their chemical structure and high surface to volume ratio, microplastics adsorb toxicants (Rillig, 2012; Wagner et al., 2014), potentially becoming six times more contaminated than the surrounding water (Mato et al., 2001), although several mechanism likely affect plastics as a vector of pollutants (Koelmans, Bakir, Burton, & Janssen, 2016). The

negative effects of microplastic consumption can range from hepatic stress to death (Anbumani & Kakkar, 2018; Rochman, Hoh, Kurobe, & Teh, 2013). One hypothesis for widespread consumption of plastic is that these particles resemble natural food sources (Savoca, Tyson, McGill, & Slager, 2017; Savoca, Wohlfeil, Ebeler, & Nevitt, 2016). Yet, despite scientific focus on documenting these phenomena, little investigation has focused on understanding why certain individuals within a species might be more susceptible to this trap than others (see Nanninga, Scott, & Manica, 2020 for an exception).

Critically, variation in falling for an evolutionary trap might be due, in part, to the varying influences of social information (Barrett, Zepeda, Pollack, Munson, & Sih, 2019; Donelan et al., 2020). Many animals rely on group behavior to locate food sources and initiate foraging (Giraldeau & Caraco, 2018). There is an inherent tradeoff between waiting to learn about a new option from conspecifics and missing out on that option, such that individuals in a group are expected to balance individual sampling and social information. For example, waiting for personal detection of a food source might result in its depletion by conspecifics, such that social information might be too costly to ignore. Improved foraging in social situations has been observed in experiments with guppies (*Poecilia reticulata),* in which groups showed improved decision accuracy toward an edible stimulus compared to singletons (Clément et al., 2017). However, inaccurate social information can be misleading. Naive bison (*Bison bison*), for example, have been found to follow misguided conspecifics into risky agricultural habitat (Sigaud et al., 2017). In this case, social information caused other individuals to choose a suboptimal, even fatal, option. In addition, maladaptive behaviors might perpetuate in populations if the cost of the socially learned misinformation is delayed or subtle (Aplin,

Sheldon, & McElreath, 2017). This could be the case for consumption of plastics, where fitness costs (e.g., the bioaccumulation of toxicants) are decoupled from the immediate behavior.

One aspect of social context that has been consistently documented as having an influence on behavior is group or aggregation size (Elgar, 1989; Hellström, Heynen, Oosten, Borcherding, & Magnhagen, 2011). The "group-size effect" is a classic phenomenon observed across multiple taxa, in which individuals in larger groups forage more and spend less time vigilant (Magurran & Pitcher, 1983; Morgan, 1988). Notably, it is difficult to differentiate whether these shifts in behavior are due to perceived safety in numbers against potential predators (Pitcher & Parrish, 1993), perceived increased competition with conspecifics (Grand & Dill, 1999), or social conformity (Webster & Ward, 2011). Furthermore, if individuals can be heavily influenced by leaders or keystone individuals that exhibit extreme behaviors (e.g., particularly fast or bold individuals (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014), then a group size effect can be due to the fact that larger groups are more likely to contain at least one particularly bold individual (i.e., the 'pool-of-competence' effect; Ioannou, 2017; Morand-Ferron & Quinn, 2011). Analyses of group size effects often assume that the behavior is adaptive, with animals weighing individual and social information and making the best decisions based on the context. However, under HIREC, the relative usefulness of social information can change, leading animals that use social information to be at a disadvantage (Barrett et al., 2019). In other words, if following the crowd was an adaptive heuristic in the past, it could become outdated in a rapidly changing world (e.g., Thambithurai et al., 2018).

Moreover, social context does not only influence variation in individual behaviors, but also emergent group-level performance (Tang & Fu, 2019; Wilson et al., 2019). In many social species, the behavior of the group or colony can be just as important as the behavior of the

individual. Just like individuals, there are consistent differences among social groups in their collective responses to predator cues, foraging bouts, and other crucial activities (Bengston & Jandt, 2014; Jolles, Laskowski, Boogert, & Manica, 2018; Planas-Sitjà, Deneubourg, Gibon, & Sempo, 2015; Wright et al., 2019). Statistically, measuring the repeatability of group behavior could be evaluated on multiple levels. On one level, individuals within a group might be converging to behave similarly to each other (i.e., lower variation among individuals within groups and/or higher variation between groups). This could emerge if group behavior is driven by a keystone's response, since individuals would be expected to behave similarly to their group mates compared to others regardless of group size because everyone is following the leader. On another level, an emergent group trait (i.e., collective movement, social network, or mean behavior) could also be repeatable across time or context (Jolles et al., 2018). In this case, understanding the repeatability of group-level behaviors is essential for predicting group performance and potentially individual fitness.

The role of group behavioral syndromes is of particular interest, but has received little attention beyond the study of eusocial societies (Jandt et al., 2014; Wright et al., 2019). These syndromes are correlated clusters of group performance traits (i.e., that a group as a whole could be consistently bolder in the presence of a predator cue as well as more voracious toward food items) (Jandt et al., 2014). If group-level responses to predators are correlated with foraging behaviors, this could have major ramifications for how groups of individuals might respond in a changing world. That is, there could be a benefit to the whole group if being faster to consume familiar foods or adopt a novel edible food is correlated to a swifter recovery after exposure to a predator. However, it could be maladaptive if those same behaviors are correlated with a greater susceptibility to be perform a maladaptive behavior, like by consuming plastic. We know

surprisingly little about variation among groups in behavior for vertebrate societies (but see Jolles et al., 2018), since most studies of collective personality have focused on arthropods (Wright et al., 2019). To our knowledge, collective repeatability of behavior has never been studied in response to traps. Thus, one of the goals of this study was to examine the differences among groups in explaining individual behavior across several tasks and look for group-level behavioral syndromes, especially in connection to foraging for novel foods, including plastics.

In a series of controlled experiments, we examined how differences in the size of mosquitofish social groups influence how quickly individuals approach and sample novel foods. In natural settings, mosquitofish forage in groups that vary in both size and membership (Pyke, 2008), thus they are an ideal system to query how differences in social context influence behavior. We hypothesized that the group size effect would carry over into novel situations, such that individuals in larger groups would be both more likely to eat plastics, and faster to do so, compared to individuals in smaller groups. We investigated several explanatory mechanisms for this group-size effect in a novel situation. That is, we measured both individual recoveries after a predator cue (e.g., the influence of the dilution of risk) and latencies to eat known food particles (e.g., the influence of increased competition) in order to assess whether decreased predation risk, competition, or both might be driving differences in mosquitofish behavior across group sizes.

In order to assess the differences among groups in explaining individual behavior across ecological contexts, we examined how much variation within our data set was explained by within versus between-group variation. This can be interpreted as how similarly individuals behave to those within their group versus those outside of their group and provides an estimate of within-group behavioral convergence. In addition, we examined whether there were group-level

behavioral syndromes regardless of social group size. We hypothesized that groups that had a higher proportion of individuals that resumed movement post predator cue would also have a higher proportion of individuals eat both known and novel foods, and thus be more susceptible at the group-level to falling into socially-induced traps.

Methods:

Study system

We investigated how group size and composition influences anti-predator and foraging behaviors in Western mosquitofish (*Gambusia affinis*). Mosquitofish are a model system for social behavioral studies (Etheredge, Avenas, Armstrong, & Cummings, 2018; Hansen, Schaerf, & Ward, 2015; Polverino, Liao, & Porfiri, 2013), and respond to changes in group size by adjusting their dispersal and exploratory behavior (Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Ward, 2012). Generalist foragers, mosquitofish are one of the most widespread introduced species in the world and are found in a broad range of habitats (Pyke, 2008). Due to their widespread abundance, mosquitofish are an important trophic link between invertebrates and primary producers that they consume and larger aquatic predators in many freshwater systems. Critically, foraging behavior involves a significant social component in this species (e.g., Hansen, Schaerf, Simpson, Ward, & Lewis, 2016).

Fish care and behavioral assays

The behavioral experiments were performed between August and October 2017 at the Center for Aquatic Biology and Aquaculture (CABA) facilities at the University of California, Davis. Female mosquitofish, donated from the Sacramento-Yolo Mosquito and Vector Control District (CA, USA), were used for this study. Fish were housed in 37.8 L tanks of 40 individuals

for a week to acclimate to lab conditions (14:10 light:dark photoperiod, 22°C). During this acclimation period, fish were fed ad libitum with a mixture of fish flakes (Tetramin™) and surface floating krill-based feeding pellets (New Life Spectrum™).

For the subsequent behavioral assays, 532 individuals were randomly separated into 116 groups of either 2, 4, or 8 individuals, with 40 replicates of 2 individuals, 39 replicates of 4 individuals, and 37 replicates of 8 individuals. Groups were observed over 6 blocks of 5 days, totaling 30 days of trials. The first 5 blocks had either 7 or 8 groups of 2 fish, 6-8 groups of 4 fish and 5-8 groups of 8 fish. The final block had 1 group of 2, 2 groups of 4, and 4 groups of 8 fish. All groups were comprised of subsets of individuals from the same home tank, such that all fish had the opportunity to interact prior to being divided into groups. Groups were formed 24 hours before the start of observations and were housed together until the end of trials 5 days later. Each group experienced a set of four behavioral assays three times, performed every other day (i.e., on days 1, 3 and 5) in an observational arena (30 x 32 x 28 cm tank filled to a depth of 6 cm). To reduce visual stimuli from outside the arena, aquaria walls were lined with black plastic bags and then frosted with adhesive film on the inside to reduce reflectiveness. Observations were filmed from above for later analysis.

Behavioral assays for each group were performed in a series of 3 consecutive assays in the same order each day: predator cue, known food item, and novel food item. Groups were allowed 7 minutes of acclimation without an observer present in the room before behavioral observations began. The assays were sequentially performed as follows:

Predator cue assay: Groups were recorded for 5 minutes following the introduction of a predator cue (i.e., a simulated bird attack), which consisted of a wooden dowel weighted by galvanized steel hex nuts that struck the surface of the water and then was immediately removed

(similar to Barber, Walker, & Svensson, 2004). After the predator cue, fish performed a variety of anti-predator behaviors, including erratic movements and freezing. Therefore, we measured the latency until each individual in the group resumed general movement behavior (i.e., either stopped erratic movements or freezing).

Known food assay: Following the predator cue, groups were recorded for 5 minutes immediately following the introduction of known floating pellets (New Life Spectrum) through airline tubing. In order to standardize the level of competition, food was scaled for group size, such that there were 2 pellets per fish (i.e., 4 pellets for a group of 2 fish, 8 pellets for a group of 4, etc.). We measured the latency until each individual in the group took a bite of a pellet.

Novel food assay: Following the known food assay, groups were recorded for 5 minutes immediately following the introduction of a novel food though airline tubing. The novel food was varied for each trial, but introduced in the same sequence for each group to control for the effect of order of introduction across groups. The novel foods introduced were brine shrimp (frozen and then defrosted, highly palatable, trial 1), glass beads (similar in color and size to the brine shrimp, not palatable, trial 2), and biofouled microplastics (purple and white polyethylene particles distilled from facewash and kept in water from Putah Creek (Yolo County, CA) for 1 month to accumulate natural biofilm growth, trial 3). See Appendix 1A for more details on novel item size and source. The first two novel foods were scaled for group size (i.e., 2 brine shrimp or beads per fish); however, the same amount of biofouled microplastics suspended in water (i.e., 0.5 mL) were piped into the arena for all group sizes to control for both the intensity of the olfactory cue of added stream water and to maintain an ecologically relevant pollution concentration within the arena (~ 0.23 ppm) (Li, Busquets, & Campos, 2020). We measured the latency until each individual in the group attempted to take a bite of a novel item. At the

conclusion of the last assay, individuals were weighed and measured for standard length. These procedures were approved by the University California Davis Institutional Animal Care and Use Committee (protocol #19357).

Video scoring and statistical analysis

Behaviors were scored using Jwatcher software (Blumstein & Daniel, 2007). Individuals were not marked, so we were unable to track individual consistency across trials, but video was able to keep track of individuals within a given trial. For the statistical analysis of behavioral data, we used Bayesian generalized linear multilevel models, fitted with the R package brms (Bürkner, 2018), which is an interface to the MCMC sampler Stan (Carpenter et al., 2017). All models included varying intercepts for group ID, to account for consistent differences among groups, and tank ID, to account for potential differences in outcomes across assay tanks.

To assess how group size affects latency to: resume normal activity post predator cue, to eat familiar food, and to eat each of three novel foods, we used a hurdle negative binomial structure to jointly model a mixture of two processes: a binomial process for whether or not a fish responded during the 5-minute trial (i.e., resumed activity or ate), and a negative binomial process to model latency for fish that responded during the trial (i.e., how quickly an individual resumed activity or ate). Hurdle models are a type of zero-inflated model, where values of zero can arise only from a single source: not performing the behavior. We used group size and trial number as predictors, and used the same predictors and varying effect structures for both processes. In order to account for potentially biased outcomes, informative cluster sizes (i.e., group size) were included as a numerical predictor within these models (Silk, Harrison, & Hodgson, 2020). For the latency to respond to predator cue and known food models, trial was

treated as an integer; however for the latency to eat novel food, trial was treated as a categorical variable to account for the different items. For beta values of fixed effects, we used weakly informative, regularizing priors centered on 0, meaning the models were skeptical of high beta values.

To assess the degree to which individual behaviors vary within vs. between groups (i.e., estimate within-group behavioral convergence), we used a varying intercept structure for group ID to calculate the variance ratio for each model. The variance ratio is a statistic that describes the proportion of the total variance explained by group-level effects in a multilevel model. Its analogue, the intra-class correlation coefficient or ICC, has frequently been used to show individual behavioral repeatability or group cohesion (Nakagawa, Johnson, & Schielzeth, 2017). Within a Bayesian framework, the proportion of variance explained by grouping can be calculated by taking draws from the posterior distribution, a method used to calculate a Bayesian version of R^2 (Gelman, Goodrich, Gabry, & Vehtari, 2019; Lüdecke, Makowski, Waggoner, & Patil, 2020). For the hurdle models described here, the variance ratio is calculated for each portion of the mixture model separately (see Appendix 1B for details).

To address the possibility of a group-level behavioral syndrome (e.g., whether groups that had a higher proportion of individuals feed on familiar food also had a higher proportion feed on novel foods), we also conducted a multivariate analysis of relationships among several group-level outcomes, in contrast to the above univariate analyses. Because we did not track individuals across assay types, we used proportion of individuals that performed the behavior within the trials for this "group-level" model. For this model, each outcome is binomially distributed, describing the number of fish per group that performed the behavior during the assay, conditional on the number of fish in the group, with treatment and trial as predictors and

group ID and tank as varying intercepts. Trial was treated as a numeric predictor for the predation and known food assays, but as a categorical predictor for the novel food assay. For this multivariate model, we were focused on the correlations between a group's varying intercepts in each of the multivariate outcomes. That is, using varying intercepts as an index of the proportion of individuals in the group that performed a behavior, do groups with higher varying intercepts in one assay also have higher varying intercepts in another assay?

Results:

The influence of group size on anti-predator and foraging behaviors

Model structure and posterior parameter estimates are reported in Table 1.1. After a simulated aerial predator attack, almost all fish (97%) resumed movement within the 5-minute trial. Importantly, fish in larger groups had a higher tendency to resume normal movement (Fig. 1.1a,b) and to do so more quickly (i.e., had shorter latencies) (Fig. 1.2a,b); however, we are less confident in the former result since the credible intervals slightly overlap zero. To emphasize, this is not just that the first fish to resume activity did so sooner in larger groups, it is that in larger groups, the average individual resumed activity sooner. Fish also appeared to habituate to the simulated attack, as evidenced by the fact that fish in later trials were more likely to resume movement sooner (although the probability of resuming activity decreased with trial).

When offered a familiar food, almost all (94%) fish fed within the 5-minute trial. Fish in larger groups were both more likely to eat the known food during the assay (versus not eat at all) (Fig. 1.1c,d) and to begin feeding sooner (Fig. 1.2c,d); however, we are less confident in the former estimate since the credible interval slightly overlaps with zero. Fish also appeared to habituate to the feeding trials, since fish in later trials tended to begin feeding sooner. However,

trial did not affect the likelihood that a fish ate during the assay (versus not eat at all). This is likely because most fish ate known food during all trials (94% of observations).

Most interestingly, individuals in larger groups were more likely to eat the novel food (Fig. 1.1e,f), and to do so more quickly (Fig. 1.2e,f); however, the credible intervals again just included zero. The type of novel food also appeared to influence willingness to sample those foods; however, because we presented novel foods in a standardized order, the differences between food types could also reflect a trial order effect. In particular, fish were more likely to take a bite of brine shrimp (an edible, valuable novel food type, offered only on day 1) than glass beads (offered on day 3) (median odds ratio estimate = 1.71, 95%CI = 1.16 – 2.35); and, for those fish that took a bite of either of these novel foods, they were quicker to try brine shrimp than glass beads (median odds ratio estimate = 0.66, 95%CI = 0.50 – 0.84). However, when offered plastic particles on day 5, fish were as likely to try to feed on plastic (glass bead/plastic median odds ratio estimate = 0.86, 95%CI = 0.57 – 1.23; brine shrimp/plastic median odds ratio estimate = 1.47, 95%CI = 0.98 – 2.11) and as quick to feed on plastic (glass bead/plastic median odds ratio estimate = 1.31, 95%CI = 0.97 – 1.72; brine shrimp/plastic median odds ratio estimate = 0.87, 95%CI = 0.66 – 1.12) as they had earlier been on either brine shrimp or glass beads.

For a summary of raw latency data from all assays and trials, see Appendix 1C.

Table 1.1 Model structure and posterior parameter estimates for models of mosquitofish latency to resume movement post predator cue, latency to eat known food, and latency to eat novel food

Model Structure	Posterior parameter estimates for fixed effects			
	parameter	estimate	2.5% CI	97.5% CI
Latency to resume movement ~ 1 + group size + trial + (1| group ID) + (1 | tank) **hurdle** ~ 1 + group size + trial + (1| group ID) + (1 | tank)	hurdle intercept	-4.45	-6.77	-2.29
	hurdle group size	-0.29	-0.66	0.03
	hurdle trial	**0.91**	**0.44**	**1.40**
	intercept	3.53	3.13	3.92
	group size	**-0.10**	**-0.17**	**-0.03**
	trial	**-0.12**	**-0.19**	**-0.04**
	correlation between intercepts (group ID)	0.28	-0.25	0.80
	shape	1.37	1.22	1.53
Latency to sample known food ~ 1 + group size + trial + (1| group ID) + (1 | tank) **hurdle** ~ 1 + group size + trial + (1| group ID) + (1 | tank)	hurdle intercept	-2.48	-3.96	-0.99
	hurdle group size	**-0.20**	**-0.43**	**0.03**
	hurdle trial	0.08	-0.27	0.45
	intercept	4.52	3.87	5.14
	group size	**-0.19**	**-0.30**	**-0.09**
	trial	**-0.45**	**-0.57**	**-0.33**
	correlation between intercepts (group ID)	0.62	0.30	0.91
	shape	0.51	0.43	0.60
Latency to sample novel food ~ 1 + group size + trial + (1| group ID) + (1 | tank) **hurdle** ~ 1 + group size + trial + (1| group ID) + (1 | tank)	hurdle intercept	-0.98	-1.54	-0.46
	hurdle brine versus bead	**0.54**	**0.18**	**0.85**
	hurdle brine versus plastic	**0.39**	**0.01**	**0.76**
	hurdle group size	**-0.10**	**-0.19**	**-0.01**
	intercept	3.58	3.04	4.10
	brine versus bead	**0.41**	**0.15**	**0.65**
	brine versus plastic	0.14	-0.12	0.40
	group size	-0.07	-0.16	0.02
	correlation between intercepts (group ID)	-0.03	-0.51	0.46
	shape	0.50	0.42	0.58

Note that the hurdle estimates are of the probability of not performing the behavior (i.e., negative hurdle estimates for group size indicate that the probability of performing the behavior increases with group size.

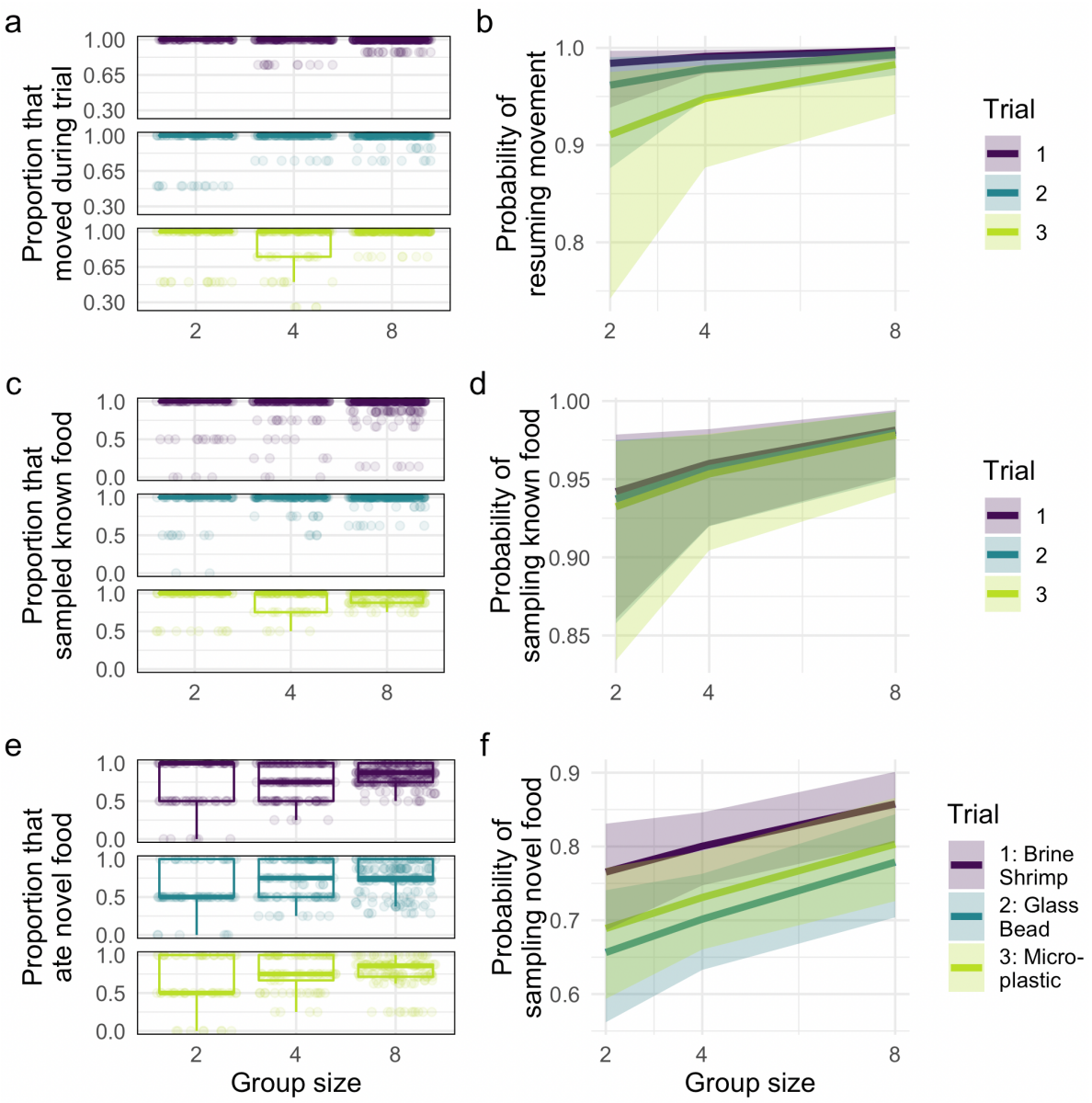

Figure 1.1 Raw proportion data and marginal effects of group size and trial on likelihood of mosquitofish to perform a behavior. Box plots include (a) proportion of individuals within a group that moved post predator cue, (c) proportion of individuals within a group that ate the known food, and (e) proportion of individuals within a group that ate the novel food. The boxplots are overlaid on top of raw data and include the mean latency and the interquartile range (IQR) with whiskers extending to +/- 1.5 IQR. The marginal effects plots are derived from the hurdle portion of posterior parameter estimates from mixture models indicating (b) individual probability of moving post predator cue, (d), probability of eating known food, and (f) probability of eating novel food. The marginal effects plots show the global effects of group size and trial on likelihood to perform a behavior using expected values from the posterior predictive distribution. The lines represent the median effects, while the bands show the 95% credible intervals. Note that the Y-axes have varying scales in this set of figures.

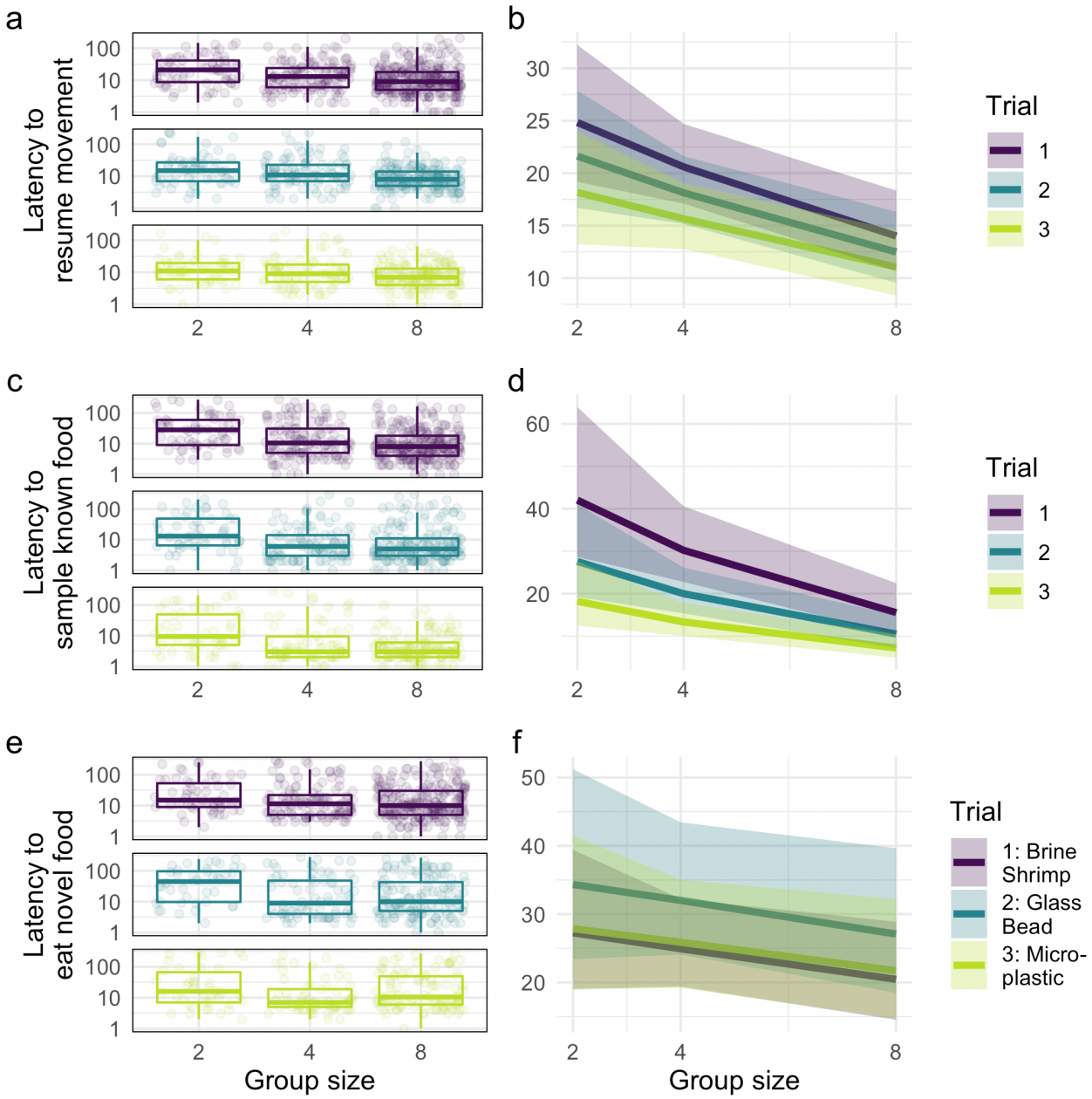

Figure 1.2 Raw latency data and marginal effects of group size and trial on mosquitofish latency behavior. Box plots of (a) latency to move post predator cue, (c) latency to eat known food, and (e) latency to eat novel food are on a log scale to aid in differentiating between group sizes and trials. The boxplots are overlaid on top of raw data and include the mean latency and the interquartile range (IQR) with whiskers extending to +/- 1.5 IQR. The marginal effects plots are derived from the latency portion of posterior parameter estimates from mixture models of (b) latency to move post predator cue, (d) latency to eat known food, and (f) latency to eat novel food. The marginal effects plots show the global effects of group size and trial on latency to perform a behavior using expected values from the posterior predictive distribution. The lines represent the median effects, while the bands show the 95% credible intervals. Note that the Y-axes have varying scales in this set of figures.

The influence of group identity on individual behavior across assay types

Which group an individual is part of (i.e., group identity) matters for predicting individual latency to resume activity after a predator cue (variance ratio = 0.59, 95%CI = 0.36 – 0.78), and for both tendency to eat known food (variance ratio = 0.38, 95%CI = 0.01 – 0.67), and for those that do, latency to eat known food (variance ratio = 0.65, 95%CI = 0.24 – 0.90). Since almost all individuals moved within the 5 minute trial, it is not surprising that group identity did not affect whether or not individuals moved post predator cue (variance ratio = 0.28, 95%CI = -0.25 – 0.76). Interestingly, for novel foods, while group identity did not influence tendency to take a bite (variance ratio = 0.03, 95%CI = -0.09 – 0.15), for those that did eat the novel food, it did influence latency to take a bite (variance ratio = 0.44, 95% CI = 0.00 – 0.77). However, the variance ratio based on group identity for latency to eat novel food had a broad credible interval that slightly overlapped with zero, indicating that we are less confident that group identity explains much of the variation in this posterior estimate.

Group-level behavioral syndromes

The outcome of the multivariate analysis (i.e., examining how many fish completed the activity as a binomial outcome) suggests that some groups consistently had fish that did not perform a behavior during the assay, regardless of assay type. There were strong correlations between known food and predation assays (estimate = 0.83, 95% CI = 0.57 – 1.00), between known food and novel food assays (estimate = 0.85, 95% CI = 0.63 – 1.00), and between novel food and predation assays (estimate = 0.59, 95% CI = 0.17 – 0.96). See Table 1.2 for full set of posterior parameter estimates.

Table 1.2 Posterior parameter estimates for multivariate model of proportion of mosquitofish that performed a behavior within a group across all assay types

	Posterior parameter estimates for fixed effects			
Model Structure	parameter	estimate	2.5% CI	97.5% CI
Number of fish that ate novel food / group size ~ group size + trial + (1| group ID) + (1 | tank)	known food - intercept	2.06	1.00	3.08
	known food - group size	0.16	0.01	0.32
	known food - trial	-0.35	-0.62	-0.08
	novel food - intercept	1.30	0.72	1.87
	novel food - group size	0.02	-0.08	0.11
	novel food - bead	-0.63	-0.98	-0.30
	novel food - plastic	-0.71	-1.10	-0.35
	movement - intercept	5.58	3.15	7.97
	movement - group size	0.24	-0.09	0.59
	movement - trial	-1.12	-1.69	-0.57
Number of fish that ate known food / group size ~ group size + trial + (1| group ID) + (1 | tank)	correlation between known food and movement intercepts (group ID)	**0.83**	**0.57**	**1.00**
	correlation between novel food and known food intercepts (group ID)	**0.85**	**0.63**	**1.00**
Number of fish that resumed normal movement / group size ~ group size + trial + (1| group ID) + (1 | tank)	correlation between novel food and movement intercepts (group ID)	**0.59**	**0.17**	**0.95**
	known food - sd (group ID)	1.22	0.88	1.60
	novel food - sd (group ID)	0.73	0.51	0.97
	movement - sd (group ID)	1.65	0.87	2.60
	known food - sd (tank)	0.27	1.33e-06	0.71
	novel food - sd (tank)	0.12	3.76e-05	0.37
	movement - sd (tank)	0.70	4.52e-07	1.85

Discussion:

In a controlled lab setting using mosquitofish as a model system, we found evidence that the classic group-size effect on activity and foraging carries over across multiple situations. Individuals in larger groups were both faster to resume activity (even with no food present) after exposure to a predator cue and, in a separate trial, faster to forage for known food. Of particular interest is the fact that individuals in larger groups were more likely to attempt to eat novel food items, including microplastics. This is compelling because we standardized per capita rations for most food types, but used a standardized volume for microplastics, implying that the group size effect is robust to the quantity of cues present. Not surprisingly, individuals were more likely to

eat novel brine shrimp (a palatable item) compared to novel glass beads (non-palatable) and to do so sooner. Interestingly, greater variation was shown in response to microplastics, such that individuals were neither more likely to try microplastics, nor approached microplastics faster, compared to both brine shrimp and beads.

Several non-mutually exclusive behavioral mechanisms might underlie the observed group size effects. One plausible mechanism is the "pool of competence" effect (Ioannou, 2017), by which larger groups are more likely to have one fast or bold individual, who then spreads information to other group members. In this case, certain key individuals would have an outsized effect on the behavior of the group as a whole, instead of all individuals conforming to the mean (Brown & Irving, 2014). If larger groups are more likely to have a highly bold individual, and individuals conform to match that boldest member of their group, then in general, individuals in larger groups would be expected to behave more boldly than those in smaller ones.

The group-size effect might, however, have limits. In some scenarios, larger groups respond slower to stimuli compared to smaller groups (Kao & Couzin, 2014). Having more leaders can be confusing. For example, in Arctic charr (*Salvelinus alpinus*), naïve individuals in groups with smaller proportions of conditioned predator-experienced demonstrators learned better socially about a predation threat compared to groups with a larger demonstrator-to-observer ratio (Vilhunen, Hirvonen, & Laakkonen, 2004). The overall result might be an upper limit for the group-size effect (e.g., (Ward & Webster, 2019)), which we did not observe in our system due to our relatively small upper maximum. In a follow-up study, if we continued testing individuals in even larger group sizes, we might then observe increasing individual latencies. Indeed, we tested group sizes much smaller than the upper limit of mosquitofish aggregations observed in the wild (A. Munson, personal observation).

Even more intriguing than the group size effect per se, we found that individuals behaved more similarly to others within their group than between groups. While our confidence in this is stronger for latency to recover post predator cue and latency to eat known food compared to latency to eat novel food, the within-group repeatability in the latency to eat novel food was still evident, although credible intervals did narrowly overlap zero. This finding is consistent with a scenario where across different group sizes and behavioral contexts, individuals in the group only begin a focal behavior after the initial keystone leader performs it. Similarly, if individuals are generally conditioned to the behavior of others in the group, they might learn to conform to their groupmate's behavior over time. This would explain why within-group behaviors seem to converge on similar latency values. Behavioral conformity may increase with group size, but this relationship is largely unexplored (Webster & Ward, 2011). Although we studied about 40 groups per group size treatment, even with our moderately high group-level repeatabilities, our sample size is likely insufficient to provide a strong test of this hypothesis.

Moreover, we found evidence of a group-level behavioral syndrome. Certain groups consistently had fish that did not perform a behavior (i.e., did not move post predator cue and did not eat the known or novel food). Groups that had a higher proportion of individuals eat known food also had a higher proportion of individuals eat novel food. In other words, groups were similarly voracious in both contexts. In parallel with the observation that individual-level behavioral syndromes can be associated with some maladaptive behavior (e.g., where more voracious individuals are also inappropriately bold, or too willing to engage in excess sexual cannibalism (Johnson & Sih, 2005; A Sih, Bell, & Johnson, 2004)), we find perhaps the first evidence of a group-level behavioral syndrome resulting in maladaptive behavior (i.e., consuming plastics). This finding is intriguing in that selection favoring higher voraciousness

(e.g., due to stronger food limitation or competition) and/or a beneficial tendency to rapidly sample and adopt edible novel foods can be associated with increased susceptibility to falling into an evolutionary trap. Although we documented a significant among-group correlation between proportion of fish that moved post predator cue and proportion that foraged for both foods, given that almost all fish moved during the assays (97%), this correlation is probably not of high ecological importance.

Overall, this study provides evidence that social context, in this case group size and group identity, can have an important influence on an individual's response to HIREC, in this case whether or not an organism attempts to eat plastic. While the role of social context depends on the social organization of the species in question, our findings indicate that social species might be more susceptible to certain types of evolutionary traps than more solitary species. While our study only hints at the potential role of a keystone, future studies should investigate whether certain traits, like size or dominance rank, might determine keystone status and a maladaptive leadership role when it comes to evolutionary traps. Depending on the scenario, the keystone could be a useful target of focus for conservation management for the mitigation of traps.

Lastly, environmental change can also influence the size and structure of groups in the wild (e.g., via harvesting, habitat fragmentation, change in habitat carrying capacity, etc.), which in turn influences how groups navigate new challenges. This potential feedback loop, between social context and responses to novel stressors, has the potential to mitigate the negative impacts of environmental change or drive deadly Allee effects (Gil, Hein, Spiegel, Baskett, & Sih, 2018). More research is needed to uncover the reciprocal relationship between how HIREC shapes the social environment and, in turn, how the social environment influences animal responses to novel environmental challenges.

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Data Availability: Data and code used to generate statistics and figures are available at: https://github.com/MCMaurer/Fish_GroupSize_Plastic.

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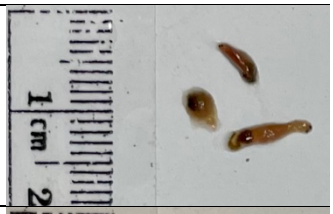
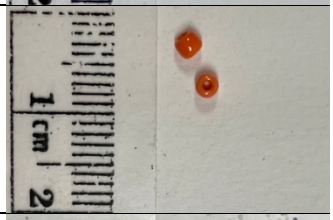
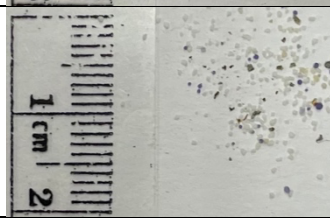
Supporting Information:

Appendix 1A.

Table 1A. Items for novel food assay

Novel Item	Trial	Source	Approximate Size Range	Image
Brine Shrimp	1	San Francisco Bay Frozen Brine Shrimp	3 – 5 mm	
Glass Beads	2	"Seed Beads", manufacturer unknown	1 – 4 mm	
Microplastics (Polyethylene)	3	Clean&Clear Deep Action Facial Scrub	0.1 – 1 mm	

Appendix 1B. Bayesian variance ratio and the intraclass correlation coefficient

The intraclass correlation coefficient (ICC) is a statistic used to describe the proportion of variance in a hierarchical model due to the grouping (random) effects. An ICC value of 0 means that the grouping variable gives no information, all of the variance is due to between-individual differences and not between-group differences. An ICC value of 1 means that all variation is due to the grouping variable, and all observations within a group are identical. In a frequentist framework, the ICC is calculated using the delta method, which involves an algebraic decomposition of the variance into discrete terms for the random and fixed effects.

In a Bayesian context, there is a comparable statistic referred to as the Bayesian variance ratio, or simply variance ratio. It is conceptually similar to the ICC, describing the proportion of variance due to grouping effects, but it is calculated somewhat differently. Rather than an algebraic decomposition of variance, we can utilize the posterior parameter distribution to generate predicted outcome values and calculate a variance ratio based on these outcomes. For every sample from the posterior parameter distribution, we generate an estimated outcome value for every row in the original data used to fit the model. If there were 1000 rows in the data and 5000 samples in the posterior distribution, we end up with a matrix of 1000 x 5000 predicted outcomes. We then calculate the variance of each set of 1000 predicted outcomes, yielding 5000 variance values, one for each posterior sample. The method of using posterior predictive distributions to estimate individual variance components has been used to calculate metrics similar to the ICC, such as a Bayesian R^2 (Gelman et al. 2019). The basic building blocks of the Bayesian R^2 and ICC are the same, they simply estimate different ratios of the same valid estimates of individual variance components.

In order to calculate the variance ratio, we carry out this process twice. First, we generate predictions conditional on random effects, which is to say we are considering every source of variation captured in our model. Next, we generate predictions unconditional on random effects, which is to say we are ignoring any variation that comes from the random effects. We now have two vectors of variance estimates, each of them containing estimates from every posterior distribution sample. We then take the ratio of variance unconditional on random effects / variance conditional on random effects. This yield a vector of ratios representing the proportion of variance due to sources other than random effects. In order to get the proportion of variance due to random effects, we subtract this vector from 1. Finally, we have a vector of Bayesian variance ratios, corresponding to samples from the posterior distribution. This gives us the benefit of including uncertainty in our variance ratio estimates, just as we can do with any Bayesian calculations derived from the posterior distribution.

If between-group differences are high, then a larger portion of the total variance in the data will be due to between-group effects, and less will be due to within-group effects. This would mean that variance from posterior predictive draws will be smaller when only within-group variation is taken into account, and higher when both within-group and between-group variation are taken into account. This will yield a variance ratio closer to 1, as more of the total variance is due to group-level effects. However, if most of the variance is due to within-group effects and there is little between-group variation, then the variance of predicted draws will be very similar whether group-level variation is taken into account or not. In this case, the distributions of predicted variance will be very similar between conditional and unconditional estimates.

Another benefit of the method using posterior predictions is that the variance ratio can be calculated while considering multiple random effects. For example, we fit models using both group ID and tank as random intercepts, but we are only interested in the variance ratios for group ID. Fitting random intercepts by tank is simply to capture any variation introduced by subtle differences in the tanks. When we calculate the variance ratio for group ID, what we really want to know is how much of the variance is due to group ID, once we have taken everything else into account. That means that rather than calculating 1- (variance conditional on no random effects / variance conditional on group ID), we want to calculate 1 – (variance conditional on tank only / variance conditional on group ID and tank). The actual measurement we care about is how much information we can get from knowing group ID once we have already taken into account all other sources of variation, including other random effects such as tank. All variance ratio estimates presented in the manuscript use this approach.

Sometimes, when the conditional and unconditional estimates are very similar, or they both vary widely, some unconditional variance estimates will be higher than the conditional variance estimates. In other words, while the numerator variance (which ignores a source of variance) is usually smaller than the denominator variance (which accounts for all sources of variation), the stochastic nature of generating predicted outcomes may yield a numerator larger than the denominator. Then, when we subtract these values to 1 to get our Bayesian variance ratio, those estimates will have a negative value. Conceptually, a negative proportion makes no sense, but it is simply a byproduct of this method of calculation. It could be considered further evidence for a variance ratio of 0, since the two values are so similar that either one could be higher than the other. In fact, if the group-level variance is actually 0, meaning the grouping variable tells you nothing, then we'd actually expect a distribution of Bayesian variance ratio

estimates centered around 0, but with about half of the density below 0. Again, these negative values are not representing negative proportions, but rather that across two vectors of variance estimates generated in the same way, each value has a 50% chance of being larger than its counterpart in the other vector. In Fig. 1B, we can see a visual representation of the process of calculating the Bayesian variance ratio.

References:

Gelman, A., Goodrich, B., Gabry, J., & Vehtari, A. (2019). R-squared for Bayesian regression models. *The American Statistician*, *73*(3), 307–309.

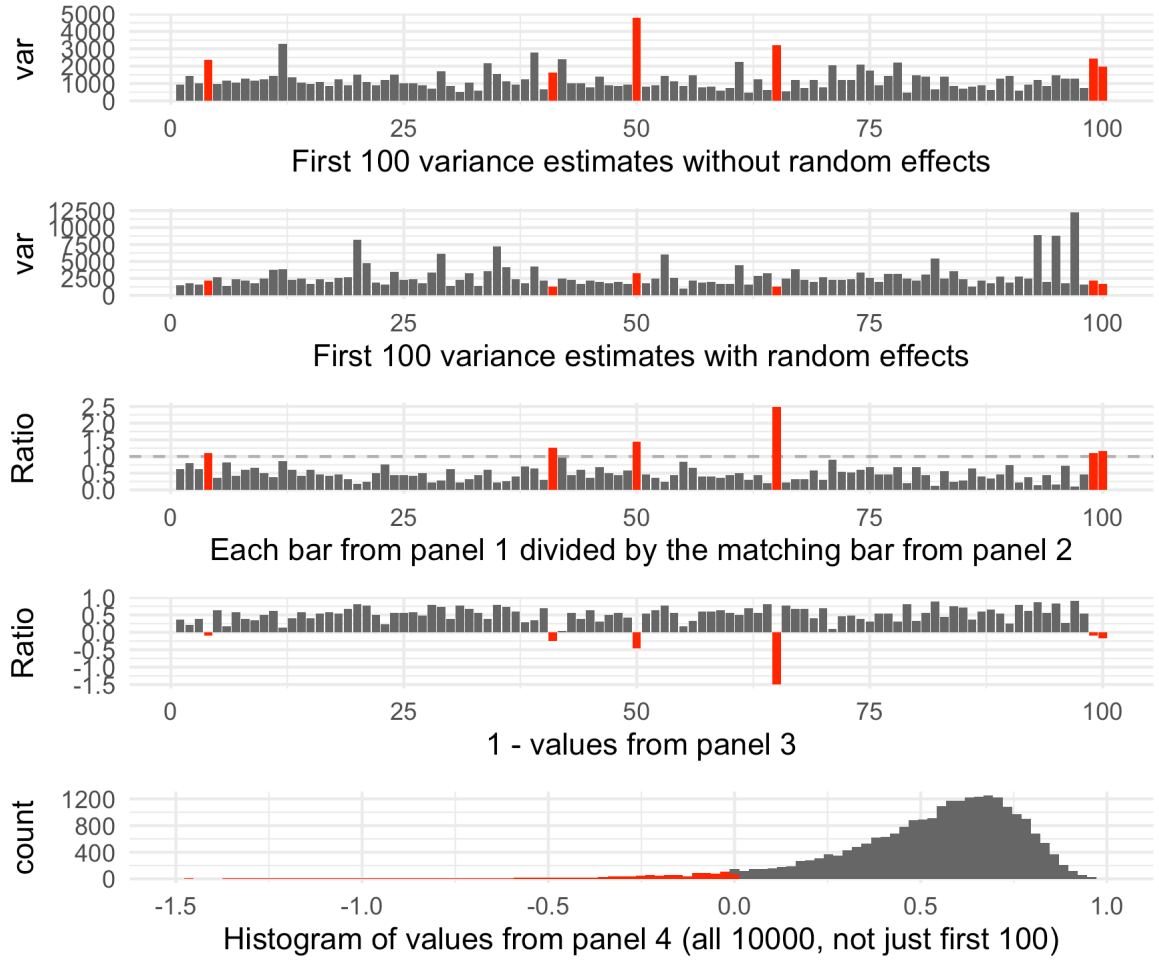


Figure 1B. In the first panel, we see variance estimates derived from posterior predictions from the first 100 samples from the posterior, unconditional on random effects. The second panel is similar, but the predictions are conditional on random effects, meaning they capture an additional source of variance. Notice that the y-axis scales differ between these two. Most of the time, the bars in the second panel are larger than the corresponding bars in the first panel, but the cases where it is the opposite are colored in red. For panel 3, we divide each bar from panel 1 by its corresponding bar in panel 2. The cases marked in red now yield values greater than 1, hitting the dashed line. These values correspond to the proportion of variance due to everything other than the random effects. Finally, to get our 4th panel, the Bayesian variance ratio, we subtract each value in panel 3 from 1. The red bars now correspond to negative values for the Bayesian variance ratio. In panel 5, we have a histogram of all 10000 variance ratio estimates, and we see that the tail in red extends below 0.

Appendix 1C. Raw Latency Data

Here we present plots of the raw data for each assay, in the form of plateau plots, which are essentially reversed survival plots. On the x-axis, we have time during the trial, and on the y-axis, the cumulative number of fish that have moved. The lines have a stepwise fashion, similar to survival plots, and once all fish in a group have moved, the endpoint is denoted with a circle. Trials where one or more fish never move will have a line trailing off to the far right of the plot, leveling off at the number of fish that moved during the trial.

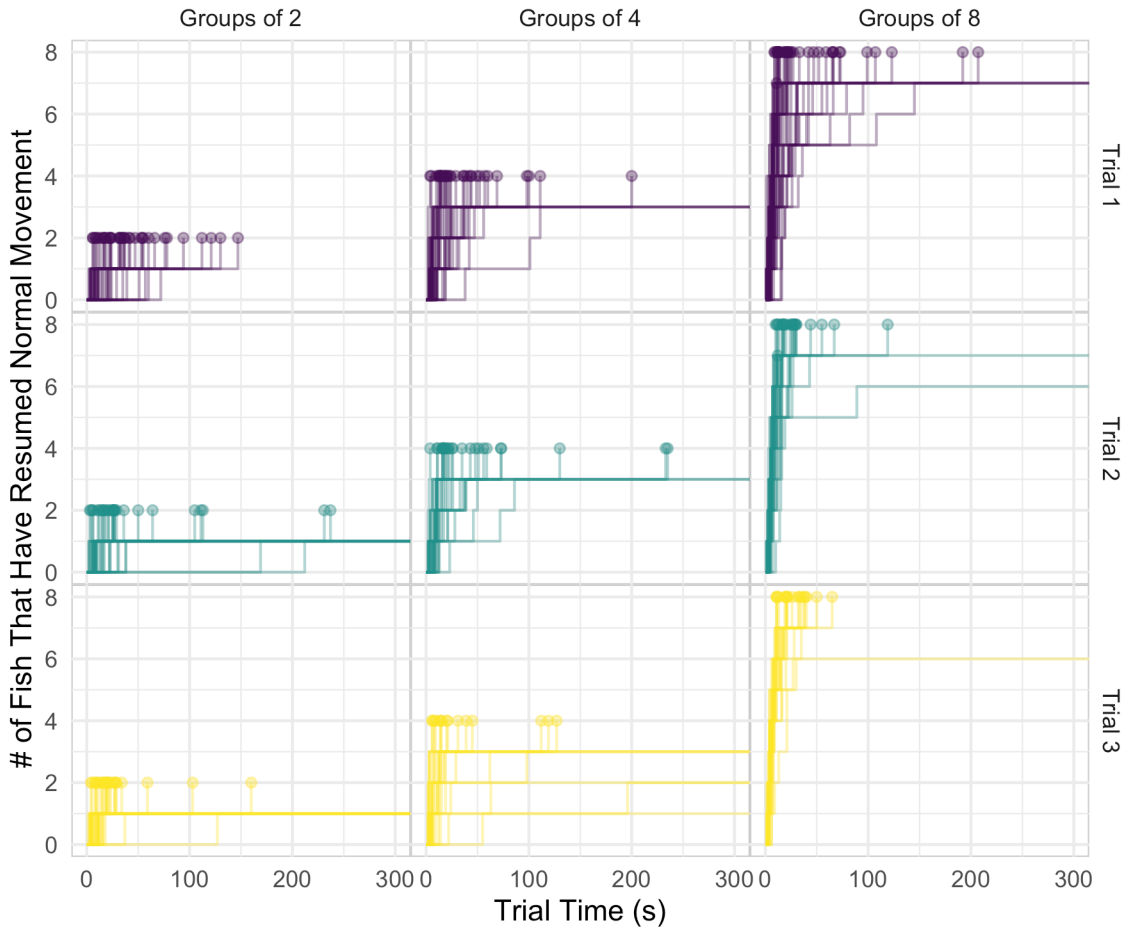


Figure 1.1C. Plateau plots for raw data of number of fish that resumed normal moved over the course of the predation cue trial.

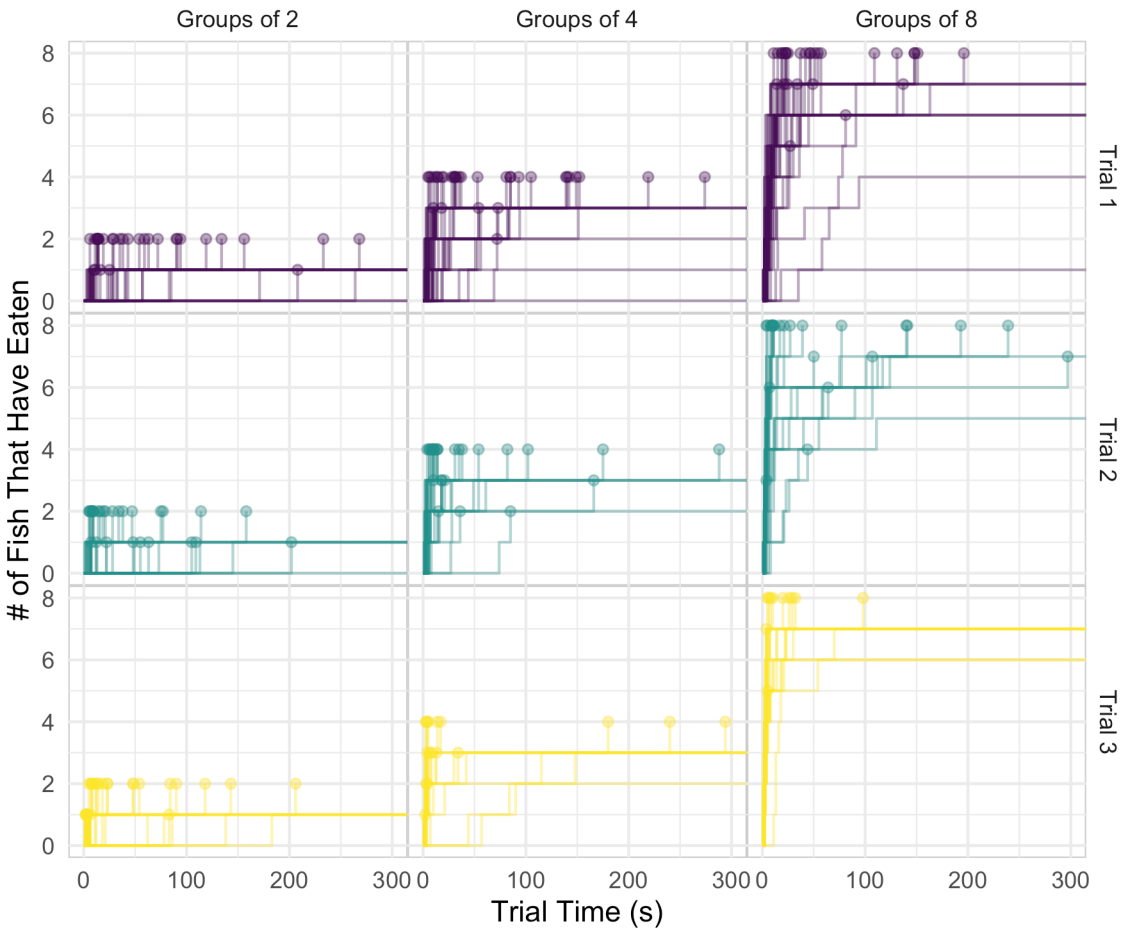


Figure 1.2C. Plateau plots for raw data of number of fish that took a bite of food over the course of the known food trial.

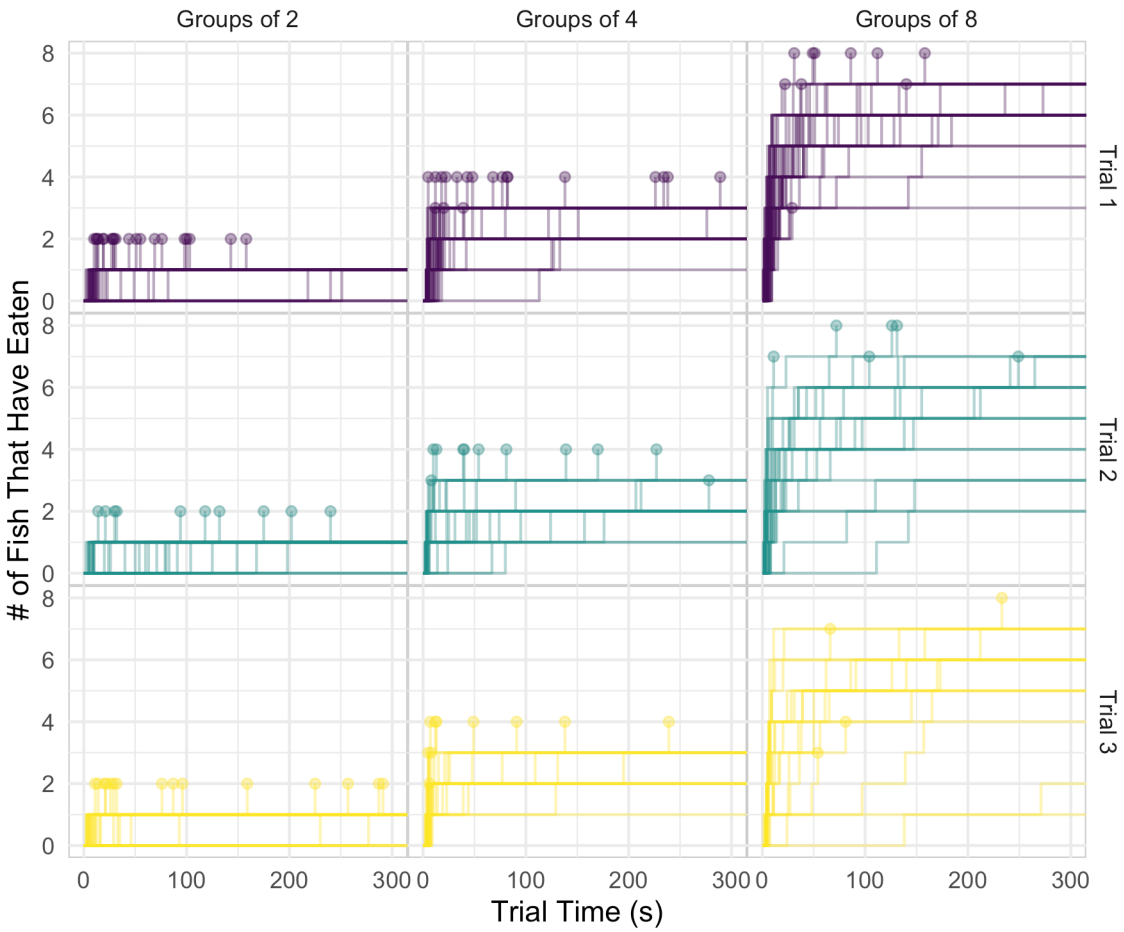


Figure 1.3C. Plateau plots for raw data of number of fish that took a bite of food over the course of the novel food trial.

Table 1C. Summary statistics of latency data

Assay	Trial	Group size	N	No action	Mean latency	SE
Predation	1	2	72	0	31.681	3.732
Predation	2	2	68	7	33.951	6.861
Predation	3	2	62	7	20.091	3.925
Predation	1	4	136	3	21.586	2.329
Predation	2	4	104	2	23.324	3.602
Predation	3	4	84	10	20.595	3.910
Predation	1	8	295	3	17.212	1.483
Predation	2	8	199	3	11.520	0.935
Predation	3	8	152	2	10.587	0.816
Known Food	1	2	71	10	50.885	8.230
Known Food	2	2	57	6	36.098	6.493
Known Food	3	2	53	5	35.167	7.303
Known Food	1	4	149	11	29.297	3.753
Known Food	2	4	109	4	18.581	3.823
Known Food	3	4	76	6	22.929	6.449
Known Food	1	8	280	15	18.411	1.801
Known Food	2	8	192	4	18.915	2.931
Known Food	3	8	147	9	7.181	1.035
Novel Food	Brine	2	76	21	43.109	7.927
Novel Food	Bead	2	66	26	65.625	10.294
Novel Food	Plastic	2	62	20	60.071	13.817
Novel Food	Brine	4	153	31	32.934	5.117
Novel Food	Bead	4	108	30	39.192	6.890
Novel Food	Plastic	4	83	18	26.308	5.848
Novel Food	Brine	8	279	43	27.864	2.732
Novel Food	Bead	8	175	42	38.113	4.927
Novel Food	Plastic	8	132	30	39.863	5.715

The "Assay" column indicates the assay type (i.e., the predator cue, known food, or novel food assay). The "Trial" column indicates which trial, either the order for the predation and known food trials, or the novel food type in the novel food assay. The "N" column indicates the number of individuals for which we have observations of for that group size and trial. Note that due to loss of a group member, technical difficulties, and corrupt video files, not all the groups have three observations and thus N varies between trials for each group size. The "No action" column indicates how many individuals did not perform the behavior (i.e., resume normal movement or consume known or novel food). The "Mean latency" column indicates the mean latency for all individuals that did perform the behavior, and is trial specific. That is, for the predation assay, the mean is for latency to resume normal movement; for the known food assay, the mean is for latency to eat known food; and for the novel food assay, the mean is for latency to eat the novel food presented (i.e., the food item in the trial column). Lastly, the "SE" column indicates the standard error for the mean latency value.

Chapter 2

Fish plastically adjust their behavior between different group sizes when foraging for familiar food

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Abstract:

With human-induced environmental change, wildlife must navigate novel conditions, including unfamiliar food items that could range from beneficial to deadly. One underexplored feature that could drive variation in response to these novel items is social context. Previous work found a group-size effect in groups of Western mosquitofish (*Gambusia affinis*), in which mosquitofish in larger groups were more willing to try known and novel foods in larger groups. This study aims to address how fine-tuned this shift in behavior is by examining whether individual fish plastically adjust their foraging behavior to different group sizes. While individuals were faster to feed on known food items when in a larger group, we did not find evidence of an effect of group size on foraging for novel foods. This might be due to a lack of familiarity between group mates in this study, which could diminish the likelihood that individuals use social information. Our data provides evidence that fish adjust their behaviour to novel social environments, but only under familiar contexts, like when foraging for familiar foods.

Keywords: evolutionary trap, group size, microplastic, fission-fusion societies

Introduction:

Human-induced environmental change (HIREC) is altering ecosystems around the world (Barnosky et al., 2012; Sih, Ferrari, & Harris, 2011). An increasingly common habitat modification is the introduction of novel food resources from non-native species, human refuse, and pollution (e.g., Bertheau, Brockerhoff, Roux-Morabito, Lieutier, & Jactel, 2010; Obbard et al., 2014; Stewart, Hill, Stephens, Whittingham, & Dawson, 2021; Ward-Fear, Brown, & Shine, 2020; Wilcox, Van Sebille, & Hardesty, 2015). While some novel items might be beneficial to consumers (e.g., Bartomeus, Fründ, & Williams, 2016), others can be toxic –yet many organisms continue to consume them (e.g., Kessler et al., 2015; Shine, 2010). This phenomenon can often be explained as an evolutionary trap, which occur when cues become decoupled from previously associated high fitness outcomes, causing animals to make maladaptive decisions (Robertson, Rehage, & Sih, 2013; Schlaepfer, Runge, & Sherman, 2002). So far, research on evolutionary traps has largely ignored a fundamental process that influences animal foraging decisions: social dynamics. Information gleaned from conspecifics, that is social information, can guide animals toward foraging in a dangerous patch or for a noxious food item (e.g., Sigaud et al., 2017). Thus, when trying to understand variation in response to novel food items, it is essential to consider the social context in which organisms are making their decisions (Greggor et al., 2016).

Organisms adjust their behavior in response to various group-level traits, including the phenotypic composition of the group (Jolles et al., 2015; Magnhagen & Bunnefeld, 2009; Wey et al. 2015), sex of the group (Piyapong et al., 2010; Schuett & Dall, 2009), and number of group members (Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Kareklas, Elwood, & Holland, 2018). Moreover, how individuals adjust their behavior when in a group depends on their own personal traits, such as behavioral type (Jolles et al., 2014; Montiglio et al. 2017; Webster, Ward,

& Hart, 2007), energetic requirements (Rands, Pettifor, Rowcliffe, & Cowlishaw, 2004), and source population (Wade, Ramnarine, & Ioannou, 2020). However, the literature is unclear as to the specific group-level traits that might induce individuals to forage more readily, particularly on novel foods. Some research indicates that individuals tend to behave more boldly, that is be more willing to take on risk, when in groups compared to when alone (Kareklas et al., 2018; Magnhagen & Bunnefeld, 2009; Rieucau, Morand-Ferron, & Giraldeau, 2010). Conversely, other studies have found that individuals behave more boldly when in isolation (Mainwaring, Beal, & Hartley, 2011; Schuett & Dall, 2009; Webster et al., 2007). This could impact how organisms interact with novelty in their environment, as boldness is expected to be correlated with neophilia in many individuals (Carere, Caramaschi, & Fawcett, 2010; Sih & Del Giudice, 2012). Thus, how social environments might affect foraging for novel items remains an open area for inquiry.

Group size has a well-documented effect on foraging behavior. One hypothesis for the adaptiveness of group living is that it improves foraging efficiency (Giraldeau & Caraco, 2018). Living in a social group helps individuals locate food sources and identify which foods to eat (Rapaport & Brown, 2008; Van de Waal, Borgeaud, & Whiten, 2013). Individuals in larger groups are often faster to locate food patches, more likely to eat once they find food, and take more bites once they start eating (Pollack et al., *chapter 1*; Snijders et al., 2021; Steinegger, Sarhan, & Bshary, 2020). Moreover, lower risk aversion when part of a group might cause individuals to approach novel foods faster and with less variability (Kareklas et al., 2018). However, decision-making efficiency might decrease when groups pass a size threshold (Ward & Webster, 2019). While having more individuals within the group might increase the likelihood that individuals avoid maladaptive decisions (Ward, Sumpter, Couzin, Hart, & Krause, 2008),

evolved heuristics might backfire if the true costs of the behavior is hidden (Pollack et al., *chapter 1*; Thambithurai et al., 2018). This might be acutely true under HIREC, where the riskiness of choices can be obfuscated in novel situations.

Critically, little is known about whether and how individuals adjust their behavior as they move through different group sizes (Webster & Ward, 2011), yet many species likely experience shifts in group size throughout their lifetime. This is especially relevant for organisms in fission-fusion societies, who by definition are introduced to novel social environments on a regular basis (Aureli et al., 2008). Thus, one of the goals of this study is to examine whether individuals are consistent in their foraging behavior across different group sizes. This includes not only their readiness to forage, but also their consistency in social foraging role. That is, are certain individuals always the initiators of foraging in a group, no matter the size?

Moreover, prior social experience has been shown to influence behavior in later social settings, including shoal group choice (Gómez-Laplaza, 2009), risk-taking behavior (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007; Jolles et al., 2014), leadership (Jolles et al., 2014), and aggression (Kilgour, Norris, & McAdam, 2020). That is, prior social experience can lead to a behavioral carry-over into a subsequent situation (Jolles, Aaron Taylor, & Manica, 2016; Kilgour et al., 2020; Stamps & Groothuis, 2010). Therefore, when trying to understand how foraging behaviors shift across different group sizes, we must also consider recent experiences. This includes both the impacts of previous foraging behavior and prior group size on subsequent behavior.

Using a series of controlled experiments with Western mosquitofish, we studied how shifts in group size within a fission-fusion society affects latency to forage on both known and novel food sources. To account for order-effects and the influence of habituation to the

experimental arena, we used a block design. Across blocks, individuals foraged in groups of 2, 4, and 8 in every possible order combination across a series of 3 trials. In a previous experiment, we found that fish more likely to eat and faster to eat both known and novel foods in the presence of more conspecifics (Pollack et al., *chapter 1*). Similarly, we hypothesized that individuals would adjust their behavior based on their current social context, although the effect would likely be smaller as constantly adjusting behavior to shifting social context is probably more cognitively demanding. Furthermore, we hypothesized that recent experiences would carry-over and influence subsequent foraging behavior in multiple ways. That is, (1) individuals' voraciousness for known food would carry-over for novel foods, such that fish who ate known food during a trial would be more likely to eat novel food when it appears later in that trial. Furthermore, if individuals ate both food types within a trial, individuals who were faster to eat known food would also be faster to eat novel food. Furthermore, (2) individuals would be more likely to eat and faster to eat both known and novel foods if they had previously foraged in a larger group. This assumes that the experience of a decrease in group size replicates a spontaneous group fissioning and not a predation event.

To account for differences in behavior based on novel food type, we presented fish with a series of novel items that ranged from highly palatable (brine shrimp), to neutral (wood chips), to potentially costly (microplastics). Plastic consumption is a familiar and increasingly prevalent evolutionary trap for many freshwater and marine species (Savoca, McInturf, & Hazen, 2021). In addition to lost opportunity costs of foraging for a more nutritious item, ingesting plastic debris is associated with various negative health effects (Anbumani & Kakkar, 2018; Andrady, 2011). We hypothesized that individuals would be more likely to consume microplastics in larger groups, even when groups were made up of unfamiliar group mates. To assess whether this

pattern is driven in part by behavioral conformity in larger groups (Webster & Ward, 2011), we examined how much variation within our data set was explained by within versus between-group variation.

Lastly, we assessed the consistency of individual foraging behavior across different group sizes. We had previously observed that within familiar groups, certain individuals consistently act as initiators in both known and novel foraging situations (Pollack et al., *chapter 3*). If this social role is consistent across group size treatments, we expect that individuals who initiated foraging behavior in groups of 8 were likely also initiators in groups of 2 and 4. Alternatively, since all groups were newly formed to control for familiarity affects, social roles might not have had time to solidify. In that case, we would not observe consistency in social role.

Methods:

System

We investigated how experiencing different group sizes influences foraging behaviors in Western mosquitofish (*Gambusia affinis*). In natural settings, mosquitofish forage in groups that vary in both size and membership (Fryxell, Arnett, Apgar, Kinnison, & Palkovacs, 2015; Pyke, 2008). Thus, they are an ideal system to study how changes in in social group size correspond to adjustments in behavior. A model system for the study of social behavior (Etheredge, Avenas, Armstrong, & Cummings, 2018; Hansen, Schaerf, & Ward, 2015; Polverino, Liao, & Porfiri, 2013), mosquitofish display different dispersal and exploratory behaviors in different group sizes (Cote et al., 2010; Ward, 2012). Although females prefer to shoal with larger groups in general, this preference depends on the personality composition of the group as well as the personality of the individual choosing the shoal (Cote, Fogarty, & Sih, 2012). Furthermore, research on sister

species *Gambusia holbrooki* suggests that mosquitofish can discriminate between small differences in groups sizes (Agrillo, Dadda, Serena, & Bisazza, 2008). As one of the most widespread introduced species in the world (Pyke, 2008), mosquitofish are likely at the forefront of experiencing a vast array of human-induced environmental change, including plastic pollution.

In order to mimic natural plastic pollution, microplastics were allowed to biofoul (i.e., accumulate natural biofilm growth) before being presented to fish in this study. Since misleading cues from the biofouling process can cause plastics to smell like natural food sources (Savoca, Tyson, McGill, & Slager, 2017; Savoca, Wohlfeil, Ebeler, & Nevitt, 2016), biofouling also increases the evolutionary trap-like nature of this novel item. In particular, polyethylene particles were used because it is the most commonly found plastic debris type (Andrady, 2011). In addition, polyethylene adsorbs greater concentrations of toxicants compared to other plastics (Rochman, Hoh, Kurobe, & Teh, 2013), increasing the evolutionary trap-like nature of the item. Using postmortem dissections, we have previously confirmed that mosquitofish ingest biofouled polyethene particles during lab-based foraging assays (Pollack L., unpublished observation).

Fish care and housing

For this experiment, we used female mosquitofish donated from the Sacramento-Yolo Mosquito and Vector Control District. We housed fish in groups of 40 individuals for 1 month to acclimate them to lab conditions before further handling. After this initial acclimation period, we individually marked 320 individuals with VIE tags (Northwest Marine Technologies) and randomly separated them into 32 home tanks of 10 individuals. Unique tags within home tanks allowed us to track all fish across experimental trials. Fish were allowed to acclimate post

tagging for at least 2 weeks in their home tanks before any behavioral observations. During this acclimation period, fish were fed *ad libitum* with a mixture of fish flakes and surface floating krill-based pellets (Tetramin^{TM}) and kept in 37.8 L tanks (14:10 light:dark photoperiod, 22°C). In between assays, individuals were housed in their original home tank. In total, we assayed 192 fish for this experiment, all (except for one) of whom had previously experienced a 3-day social exploration experiment at least one month prior to the described experiment (Pollack et al., *in prep*).

Behavioral assays

For each trial, individuals were randomly placed into experimentally manipulated groups of 2, 4, and 8 individuals within a novel empty arena (51.4 cm x 26.7 cm x 32.1 cm tank filled to a depth of 20 cm). Individuals experienced each of the group sizes over the course of 3 trials with approximately 24 hours between trials. Each assay group was composed of unacquainted individuals to control for the effect of familiarity on behavior. To control for the effect of order of experience, blocks of individuals experienced group sizes in different orders (Table 2.1). All assays were filmed from the side for later scoring of behaviors.

Table 2.1 Blocks of fish experienced group size treatments in different orders over 3 trials

Treatment Blocks	Novel Item	A	B	C	D	E	F
Trial 1	Brine shrimp	4	8	2	2	8	4
Trial 2	Wood chips	2	4	8	4	2	8
Trial 3	Microplastics	8	2	4	8	4	2

Each block consisted of 32 individuals, such that a given block and trial will either have 16 groups of 2, 8 groups of 4, or 4 groups of 8. In the next trial, all 32 individuals in a given block were re-allocated into one of the other group size treatments; e.g., for block A, in trial 1, the 32 fish were in 8 groups of 4, in trial 2, those same fish were re-allocated into 16 groups of 2, and in trial 3, those fish were combined into 4 groups of 8. Each individual experienced a completely new set of groupmates for each trial. Overall, the design provides data on behavior of fish in 96 groups of 2 fish, 48 groups of 4 fish and 24 groups of 8 fish, feeding on both familiar and novel foods.

For each trial, individuals experienced the same set of behavioral assays in the same order. Individual fish were first gently placed into the assay arena one at a time to aid in identifying individually marked fish during video playbacks. Individuals were given a 5 minute period to acclimate to the novel arena and their new group-mates before food items were introduced. Behavioral assays for each group were performed in the same order each time: introduction of known food followed by introduction of a novel food item (both assays were consecutive). To reduce handling stress, leftover known food was not removed from the arena before the introduction of novel food, however fish rarely interacted with the known food in the 5 minutes following the introduction of novel items.

Known food assay: Groups were recorded for 5 minutes immediately following the introduction of known brown floating surface food particles. In order to standardize the level of competition, food amount was scaled for group size, such that there were 2 pellets per fish. In post-trial video scoring, we recorded every individual's latency to take a bite of a pellet.

Novel food assay: Groups were recorded for 5 minutes immediately following the introduction of a novel food. Novel foods differed between trials, but were introduced in the same sequence across trial days to control for the effect of order of introduction across groups. The novel foods on trials 1, 2 and 3, respectively, were dried brine shrimp (floating, highly palatable), wood shavings (Aspen snake bedding, floating, not palatable), and biofouled microplastics (polyethylene particles distilled from facewash (XtraCare Oil-Free Foaming Acne Wash Facial Scrub) and then kept in Putah Creek (Yolo County, CA) water for 1 month to accumulate natural biofilm growth). See Appendix Table 2.1A for details on novel food items. The first two novel foods were scaled for group size – 3 mg per fish (i.e., the same mass per fish as the familiar food pellets). Biofouled microplastics were piped into arenas in a standardized volume of biofouled water (i.e., 0.5 mL) for all group sizes to control for both the intensity of the olfactory cue of added stream water and to maintain an ecologically relevant freshwater pollution concentration of microplastics within the arena (~ 0.5 g/L) (Li, Busquets, & Campos, 2020). We recorded every individual's latency to take a bite of a novel food in post-trial video scoring.

At the conclusion of the last assay, individuals were weighed and measured for standard length. These procedures were approved by the University California Davis Institutional Animal Care and Use Committee (protocol #19357). Due to camera malfunctioning, we did not include data from 7 out of the 168 groups in our final analyses (i.e., 4 groups of 2, 2 groups of 4, and 1 group of 8).

Statistical analysis

We used Bayesian generalized linear multilevel models, fitted with the R package brms (Bürkner, 2018), to analyze all behavioral data. In all models, we used weakly informative,

regularizing priors centered on 0, meaning the models were skeptical of high beta values.

To assess how switching between group sizes affects latency to eat familiar and novel foods, we used a hurdle negative binomial structure to jointly model two processes: (i) a binomial process for whether or not a fish ate during the 5-minute trial, and (ii) a negative binomial process for how quickly an individual took a bite. Both models of known and novel food latencies included varying intercepts for (i) individual ID nested in block, to account for consistent differences between individuals; (ii) group ID nested in block, to account for consistent differences between groups; (iii) block, to account for potential differences between time blocks; and (iv) tank ID, to account for potential differences in outcomes across assay tanks. The nested structure of individual and group ID reflects the experimental design, since unique individuals and groups were only found within a single block. To determine whether behaviors differed based on group size differently due to trial, we included group size by trial number interaction as a predictor. For the latency to eat known food models, trial was treated as an integer (e.g., to test for habituation); however, for the latency to eat novel food, trial was treated as a categorical variable to account for the different items presented in each trial. In order to account for the possibility of biased estimates for fixed effect parameters, informative cluster sizes (i.e., group size) was treated as a numerical predictor (Silk, Harrison, & Hodgson, 2020).

In addition, to determine if prior social experience (i.e., group size) impacts individual foraging behavior within the current group size, additional hurdle negative binomial models were run only on data from trials 2 and 3 (i.e., those that had a prior social experience), with group size by prior group size and trial as predictors and the same random effects structure as described above. To assess the impact of previous foraging experience for known food on responses to novel food, we ran two separate models. To determine if whether an individual ate known food

impacted subsequent foraging on novel food within the same trial, we ran another hurdle negative binomial model of latency to eat novel food, with whether an individual ate the known food as an interaction with trial as an additional predictor of behavior. To determine if the latency to eat known food then impacted latency to eat novel food within the same trial, we ran a separate negative binomial model only of latency to eat novel food as predicted by an interaction between latency to eat known food and trial. The interaction term in both these models allowed us to incorporate the possibility that these prior foraging experiences could be item (i.e., trial) specific. For example, consuming known food might increase the chances an individual consumes brine shrimp, but not wood chips. Both these models included group size by trial as an additional predictor with the same random effects structure as described above.

To assess the degree to which individual foraging behavior was consistent between group sizes (i.e., estimate individual repeatability), we used a varying intercept structure for individual ID to calculate the variance ratio for both latency models. The variance ratio is a statistic that describes the proportion of variance in a hierarchical model due to the grouping (random) effects (Lüdecke, Makowski, Waggoner, & Patil, 2020). Its analogue, the intra-class correlation coefficient or ICC, is often used to express individual repeatability or group cohesion (Holtmann, Santos, Lara, & Nakagawa, 2017). The proportion of variance explained by grouping can be calculated by taking draws from the posterior distribution, a method used to calculate a Bayesian version of R^2 (Gelman, Goodrich, Gabry, & Vehtari, 2019). A byproduct of this method is that sometimes estimates can be negative, even though the statistic itself is conceptually between zero and 1 (See Pollack et al., *chapter 1,* Appendix A for a detailed explanation). For the hurdle models described here, the variance ratio is calculated for each portion of the mixture model separately. Similarly, to assess the relative degree to which individual behaviors vary within vs.

between groups (i.e., as an estimate of within-group behavioral conformity), we used a varying intercept structure for group ID to calculate the variance ratio for each model as well (following Pollack et al., *chapter 1*).

Furthermore, to determine if individuals were more likely to be initiators in groups of 8 if they were also initiators in groups of 2 or 4, we used a Bernoulli structure to model whether an individual ate first. Body length and trial were included as predictors in these models to account for the potential role of body size and habituation (or novel food type) on the likelihood to be an initiator within a group. To account for potential differences between arenas and time blocks, tank and block were included as varying intercepts in these models.

Results:

Individuals adjust their foraging behavior based on group size, but only for known food

Model structure and posterior parameter estimates are reported in Table 2.2. Across all observations, approximately half of the fish (51%) fed on known food, while 63% fed on novel foods. While 78% of fish fed on brine shrimp (an edible, valuable novel food type, offered only in trial 1), 54% of fish fed on wood chips (an inedible, neutral novel food type, offered only in trial 2), and 58% of fish fed on biofouled microplastics (an inedible, potential evolutionary trap, offered only in trial 3). When in larger groups, individuals were more likely to eat the known food (Fig. 2.1a,b), and to do so more quickly (Fig. 2.2a,b); however, we are less confident in the latter result since the credible intervals slightly overlap zero. We did not observe an interaction between group size and trial.

We did not find strong evidence for an impact of group size on whether individuals ate novel food (Fig. 2.1c,d) or their latency to eat novel foods (Fig. 2.2c,d). We observed differences

in foraging for the various novel food items; however, because we presented novel foods in a standardized order, the differences between food types could also reflect a trial order effect. Fish were more likely to take a bite of brine shrimp (trial 1) than wood chips (trial 2) (median odds ratio estimate = 6.08, 95%CI = 1.75 – 14.8); and, for fish that did take bites of novel foods, they were quicker to try brine shrimp than wood chips (median odds ratio estimate = 0.61, 95%CI = 0.39 – 0.87). Fish were also more likely to try brine shrimp than microplastics (trial 3) (median odds ratio estimate = 3.76, 95%CI = 1.11 – 8.68); and quicker to try brine shrimp than microplastics (median odds ratio estimate = 0.32, 95%CI = 0.21 – 0.45). Fish were as likely to eat woods chips as plastic (median odds ratio estimate = 0.62, 95%CI = 0.19 – 1.26), but quicker to try woods chips compared to plastic (median odds ratio estimate = 0.52, 95%CI = 0.32 – 0.75).

Table 2.2 Model structure and posterior parameter estimates for models of latency to eat both known and novel food

Model structure	**Posterior parameter estimates for fixed effects**			
	parameter	estimate	2.5% CI	97.5% CI
Latency to sample known food ~ 1 + group size * trial + (1| tank) + (1| block) + (1 | block:id) + (1| block:group) hurdle ~ 1 + group size * trial + (1| tank) + (1| block) + (1 | block:id) + (1| block:group)	intercept	5.55	4.83	6.25
	hurdle intercept	1.60	-1.32	4.64
	group size	**-0.13**	**-0.25**	**0.00**
	trial	-0.25	-0.55	0.07
	group size * trial	0.04	-0.02	0.10
	hurdle group size	**-0.71**	**-1.38**	**-0.12**
	hurdle trial	-0.20	-1.51	1.08
	hurdle group size * trial	0.21	-0.06	0.51
Latency to sample novel food ~ 1 + group size * trial + (1| tank) + (1| block) + (1 | block:id) + (1| block:group) hurdle ~ 1 + group size * trial + (1| tank) + (1| block) + (1 | block:id) + (1| block:group)	intercept	4.16	3.42	4.88
	hurdle intercept	-2.02	-3.81	-0.40
	group size	-0.06	-0.17	0.05
	brine vs. wood	0.46	-0.40	1.31
	brine vs. plastic	**0.78**	**0.00**	**1.59**
	group size * brine vs. wood	0.01	-0.16	0.18
	group size * brine vs. plastic	0.09	-0.08	0.25
	hurdle group size	0.04	-0.26	0.36
	hurdle brine vs. wood	**2.99**	**1.06**	**5.16**
	hurdle brine vs. plastic	1.62	-0.25	3.74
	hurdle group size * brine vs. wood	-0.27	-0.72	0.15
	hurdle group size * brine vs. plastic	-0.06	-0.51	0.36

Note that the hurdle estimates are of the probability of not performing the behavior (i.e., negative hurdle estimates for group size indicate that the probability of eating food during the trial increases with group size).

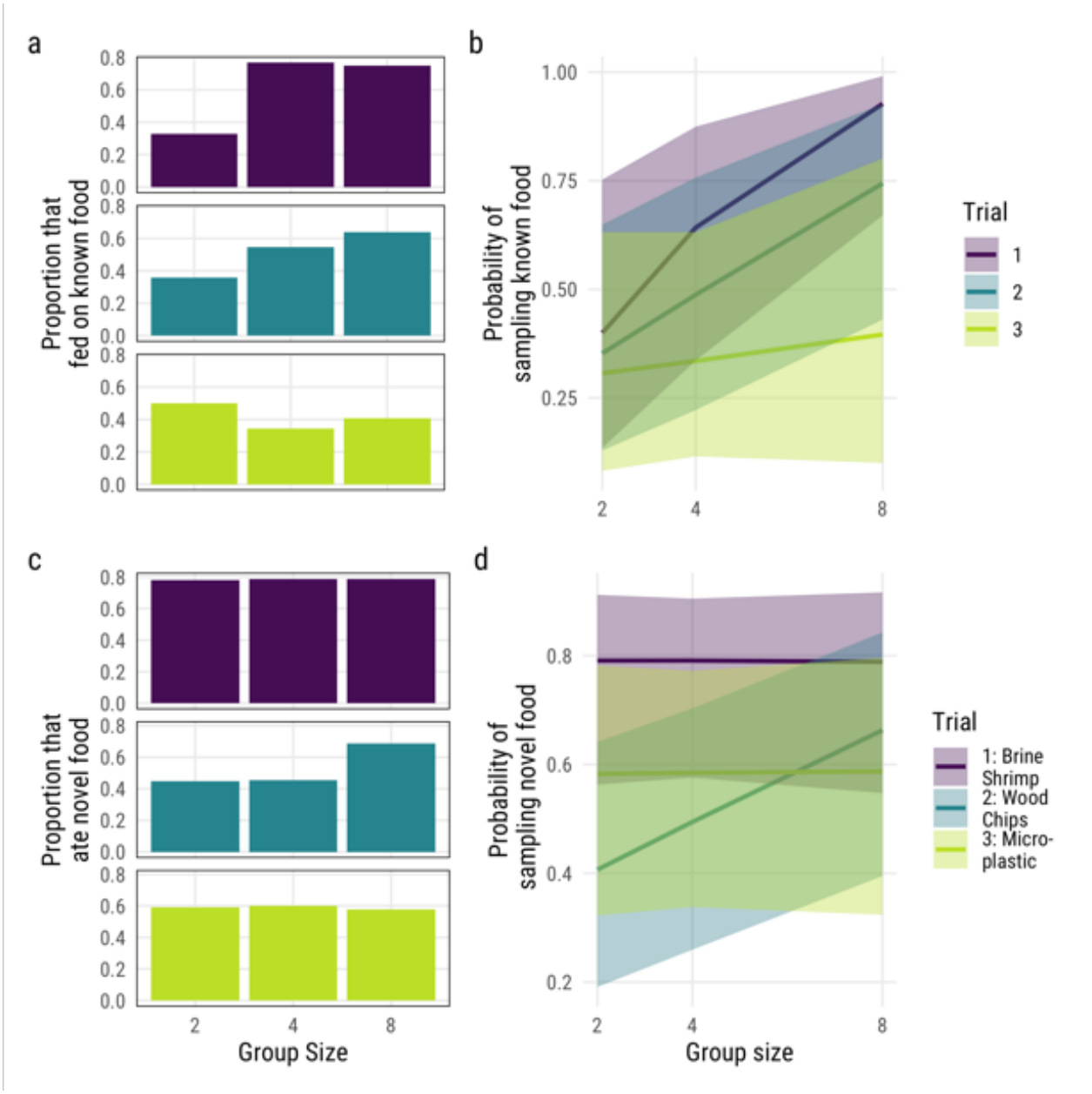

Figure 2.1 Raw proportion data and marginal effects of group size and trial on likelihood to eat known and novel foods in replicated, newly formed groups of female mosquitofish (Gambusia affinis) observed in aquaria. Bar plots display the raw data, with (a) proportion of individuals that ate the known food, and (c) proportion of individuals that ate the novel food across different group sizes. The marginal effects plots are derived from the hurdle portion of posterior parameter estimates from mixture models indicating the (b) probability of eating known food, and (d) probability of eating novel food for an individual across different group sizes. The marginal effects plots show the global effects of group size and trial on likelihood to perform a behavior using expected values from the posterior predictive distribution. The lines represent the median effects, while the bands show the 95% credible intervals. Note that the Y-axes have varying scales in this set of figures.

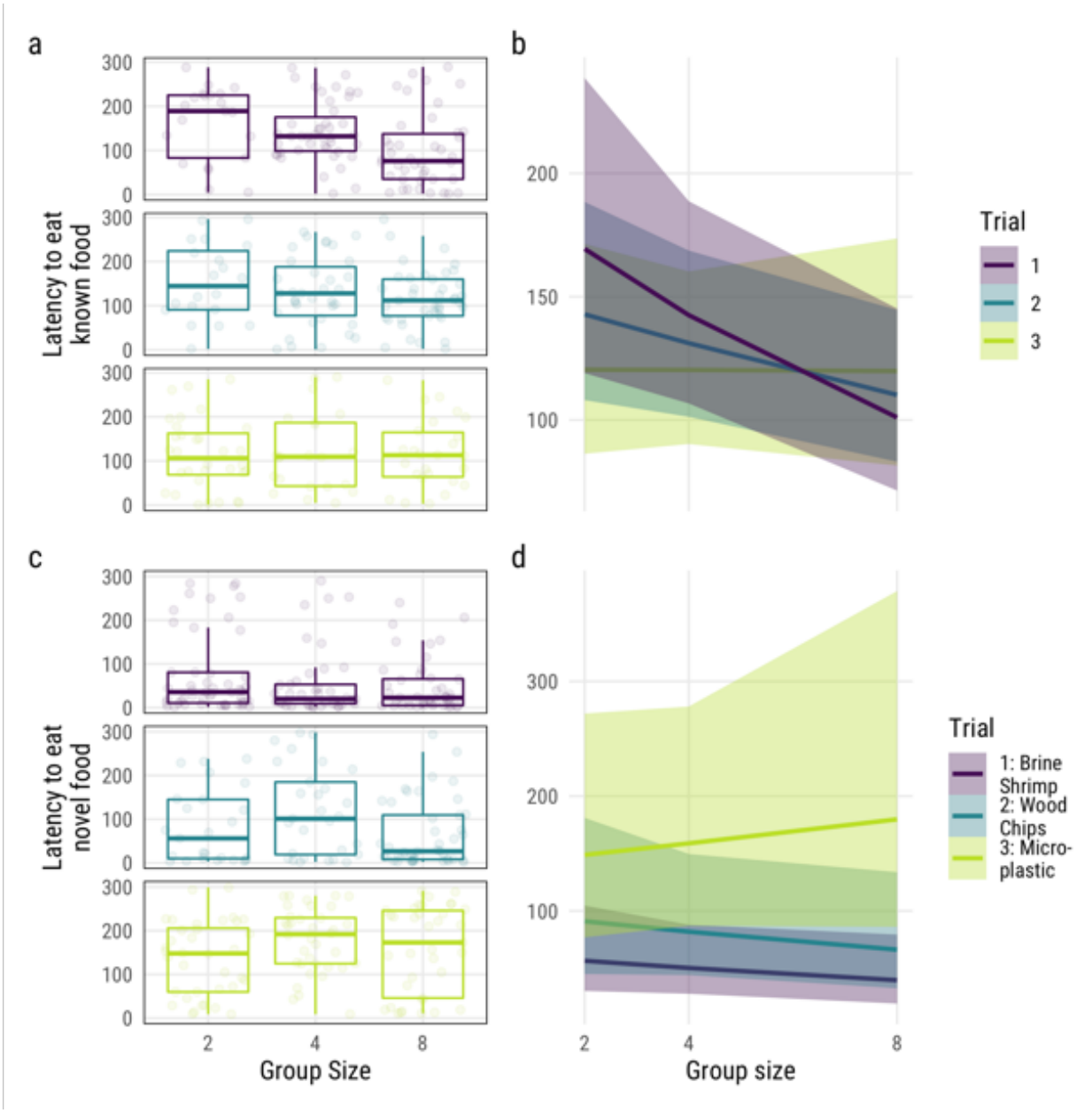

Figure 2.2 Raw latency data and marginal effects of group size and trial on latency behavior in replicated, newly formed groups of female mosquitofish (Gambusia affinis) observed in aquaria. Box plots display the raw data for (a) latency to eat known food, and (c) latency to eat novel food. The boxplots are overlaid on top of raw data and include the mean latency and the interquartile range (IQR) with whiskers extending to +/- 1.5 IQR. The marginal effects plots are derived from the latency portion of posterior parameter estimates from mixture models, indicating the (b) latency to eat known food, and (d) latency to eat novel food for an individual across different group sizes. The marginal effects plots show the global effects of group size and trial on latency to perform a behavior using expected values from the posterior predictive distribution. The lines represent the median effects, while the bands show the 95% credible intervals. Note that the Y-axes have varying scales in this set of figures.

Recent social and foraging experience does not have a carry-over effect on foraging behavior

Posterior parameter estimates are reported in Appendix Tables 2.2A and 2.3A. Overall, previous group size experience did not influence subsequent foraging behavior for either known or novel food. Furthermore, prior foraging experience on known food did not impact whether an individual ate novel food, nor how quickly they were to sample novel food.

Individual behavior was not consistent across different group sizes

Individuals did not maintain consistent behavioral differences across treatments. Individuals were neither consistent in whether they ate (known food variance ratio = 0.00, 95%CI = -0.01 – 0.03; novel food variance ratio = 0.04, 95%CI = -0.05 – 0.6) nor were they consistent in their latency to eat across the different group sizes (known food variance ratio = 0.04, 95%CI = -0.46 – 0.44; novel food variance ratio = 0.08, 95%CI = -0.89 – 0.74). Moreover, being an initiator in a group of 2 or 4 did not predict whether an individual was an initiator in a group of 8 in either known or novel food contexts (Table 2.3).

Moreover, individuals did not conform their behaviors to others in their group. Group identity did not predict whether an individual ate (known food variance ratio = 0.00, 95%CI = -0.10 – 0.02; novel food variance ratio = 0.03, 95%CI = -0.05 – 0.14) nor individual latency to eat (known food variance ratio = 0.08, 95%CI = -0.43 – 0.49; novel food variance ratio = 0.25, 95%CI = -0.62 – 0.81).

Table 2.3 Model structure and posterior parameter estimates for models of first to eat in a group of 8 as predicted by behavior in other group sizes

Model structure	**Posterior parameter estimates for fixed effects**			
	parameter	estimate	2.5% CI	97.5% CI
first to eat known food in a group of 8 ~ length + trial + first to eat in a group of 4 + first to eat in a group of 2 + (1| tank) + (1| block)	intercept	-2.18	-3.96	-0.46
	length	0.39	-0.05	0.82
	trial	0.08	-0.67	0.84
	first group of 4	0.06	-1.14	1.14
	first group of 2	0.17	-0.87	1.16
first to eat novel food in a group of 8 ~ length + trial + first to eat in a group of 4 + first to eat in a group of 2 + (1| tank) + (1| block)	intercept	-2.09	-3.32	-0.91
	length	-0.19	-0.70	0.27
	brine vs. wood	0.10	-1.23	1.44
	brine vs. plastic	-0.16	-1.57	1.23
	first group of 4	0.44	-0.60	1.40
	first group of 2	0.18	-0.75	1.10

Discussion:

Overall, individuals adjusted their foraging behavior based on group size toward a known food item. When in larger groups, individuals were more likely to eat the known food, and to do so more quickly, as previously observed in stable groups of mosquitofish (Pollack et al., *chapter 1*). This behavioral pattern aligns with expectations from the "group-size effect," a classic phenomenon observed across multiple taxa, in which individuals in larger groups forage more readily and spend less time vigilant (Magurran & Pitcher, 1983; Morgan, 1988). However, we did not find strong evidence that group size impacts whether individuals eat novel food or their latency to eat novel foods, even though previous work on stable social groups of mosquitofish had found that individuals in larger groups were more likely to eat novel foods (Pollack et al., *chapter 1*). This might be due to a lack of statistical power, as the posterior parameter estimates in the novel food models had wide distributions, preventing us from making concrete conclusions.

However, because we did observe differences between group sizes in response to known food, this lack of group-size effect toward novel foods might indicate that the familiarity of groupmates impacts behavior toward novel food differently than it does toward known food. Under this scenario, in a completely novel situation (i.e., unfamiliar group mates and novel items), organisms may rely more on personal information than social information. Thus, we might fail to observe an effect of social context on individual behavior when mosquitofish forage for novel foods. Similarly, we did not find evidence of behavioral conformity within these newly formed groups, even though it has been previously observed in familiar groups (Pollack et al., *chapter 1*). While the increased number of known food items might be objectively more detectable, such that it might impact latencies in larger groups, the lack of increased latency toward highly palatable novel food items like brine shrimp supports our interpretation that this reflects increased readiness to forage and not purely increased detection. Furthermore, all items were surface floating such that fish had to swim upward toward them to interact and introduced with the same 30 mL injection of water, allowing olfactory information to quickly spread throughout the arena at the moment of introduction.

Moreover, we did not observe that recent experience of a particular group size carried over into how an individual behaved in a subsequent group. It is possible that the differences between group sizes were not great enough to observe clear differences. Other studies that have found a carry-over effect of prior social experience in shoaling fish have compared individuals that experienced social isolation to those that had previously been housed in a social group (i.e., Munson, Michelangeli, & Sih, 2021). In this case, being isolated is likely more influential than being in a smaller group, leading to observable changes in behavior. Furthermore, other studies that have observed a carry-over effect have found this effect after individuals experienced a

social contest (e.g., Frost et al., 2007; Oldham et al., 2020), which is likely more important than previous social group size. It also might be that slight differences in home tank experience between experiments might affect or mask these carry-over effects within the arena. Lastly, in a fission-fusion society, where individuals are experiencing a constant turnover of social partners and social group sizes, the relative importance of previous group experience on current behavior may be lower. That is, behavioral carry-over from recent social group size is just maladaptive in a more dynamic social environment, where recent social experience is not reflective of near future social environments.

Unsurprisingly, fish were more likely to take a bite of, and faster to forage, for highly palatable brine shrimp compared to wood chips and microplastics. Yet, in a previous experiment where stable groups of mosquitofish were fed brine shrimp on trial 1 and microplastics on trial 3 (Pollack et al., *chapter 1*), we failed to observe clear differences in foraging behavior between brine shrimp and microplastics. This could also similarly be occurring because fish are relying less on social information to make foraging decisions when paired with unfamiliar groupmates. Indeed, familiarity with a demonstrator might be critical for individuals to socially learn about novel foods (Figueroa, Solà-Oriol, Manteca, & Pérez, 2013; Valsecchi, Choleris, Moles, Guo, & Mainardi, 1996). Thus, because of the lack of familiarity in this study, fish are just less likely to following the behavior of the crowd. In this case, fish might be better equipped to differentiate between palatable and unpalatable food items by disregarding potential sources of social information. Indeed, other studies suggest that organisms should be skeptical of social information, particularly in in a rapidly changing world (reviewed in Barrett, Zepeda, Pollack, Munson, & Sih, 2019; Rieucau & Giraldeau, 2011).

While fish generally prefer familiar shoal mates (Griffiths & Magurran, 1997; Krause et al., 2000), there are cases when unfamiliar group mates might be beneficial and even preferable. Thus, the assigned unfamiliar groupmates in this study are not wholly unrealistic. For example, knowledge about foraging site spreads most quickly through groups with a mix of familiar and unfamiliar guppies, and not in completely familiar groups (Hasenjager & Dugatkin, 2017). Furthermore, fish might prefer unfamiliar shoal mates if their food resources are subpar (Frommen, Luz, & Bakker, 2007), and especially if unfamiliar conspecifics have had access to higher quality food sources (Morrell, Hunt, Croft, & Krause, 2007). For example, while satiated sticklebacks prefer to shoal with familiar fish, hungry sticklebacks preferred unfamiliar individuals, which the authors posit is because fish wish to reduce competition with close relatives –the most likely source of familiar shoal mates (Frommen et al., 2007). However, it might also be that familiar individuals would also be hungry and less knowledgeable about alternative food sources. Along those lines, when foraging in unfamiliar situations, it might be beneficial to forage with unfamiliar individuals who might have complementary knowledge of alternative food sources (the 'novel social partner hypothesis', Ramakers, Dechmann, Page, & O'Mara, 2016). In this case, group mate knowledge and not group size per say should have a stronger impact on individual behavior.

Individuals did not consistently take initiator roles between different groups in this study, even though the individual initiator role has been shown to be consistent in stable groups of mosquitofish (Pollack et al., *chapter 3*) and other systems (e.g., Nagy et al., 2013; Nakayama, Harcourt, Johnstone, & Manica, 2012; Tuliozi, Camerlenghi, & Griggio, 2021). This might just be due to the lack of familiarity in newly formed groups, such that social roles have not had time to solidify through repeated interactions (Bergmuller & Taborsky, 2010; P. O. Montiglio, Ferrari,

& Reale, 2013). Moreover, information sharing might be a more important driver in who leads than an innate trait of an individual in some species (Harel, Spiegel, Getz, & Nathan, 2017). In order to differentiate between the relative influence of group size versus familiarity in this system, a follow-up study manipulating the size of familiar groups would be necessary. However, deciding which individual within a stable group to remove when manipulating group size introduces additional sources of variation within the experimental design. If social roles establish within a familiar group, removing certain individuals might influence behavior of the group more strongly than others. For example, the loss of a keystone individual, like an initiator or dominant, might have a stronger impact on group-wide behavior than the removal of a less influential member (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014).

Changes in grouping patterns and group stability are only expected to increase as HIREC increases in the future (Fisher, Eiracusa, & Kilgour, 2021). However, the influence of environmental change on social grouping depends on the species and the type of change occurring. For example, increased temperatures might lead to reduced grouping in some organisms for whom aggregations might be important for thermoregulation in cooler months (e.g., Australian skinks; Lanham, 2001), while increased dryness is expected to lead to increased grouping in other species (e.g., decreased foraging bouts in harvester ants leads to greater short-term aggregations; Gordon, 2013). Similarly, higher frequency of storms could to lead to increased grouping as individuals increase their collective use of shelter (Adams, Hooper-Bùi, Strecker, & O´Brien, 2011). With increased group instability, familiarity within groups will likely decrease, which might lead individuals to rely more heavily on personal information than social information. Furthermore, an increase in reliance on personal information might be even more evident when interacting with novel items, which are also projected to increase with

HIREC. This might be adaptive for responses to novel noxious foods if ignoring social pressures helps organisms avoid socially-mediated evolutionary traps. However, if social information could help organisms avoid maladaptive behavior by through a pooling of information (Ward et al., 2008), decreased aggregating behavior might lead organisms to become even more severely trapped in the future.

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Supporting Information:

Appendix 2A.

Table 2.1A. Items for novel food assay.

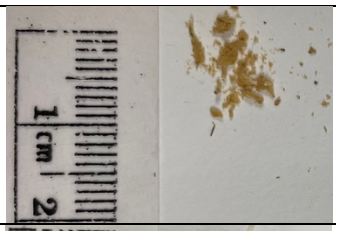
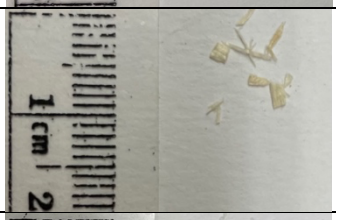
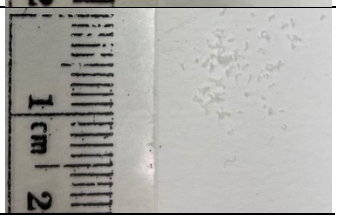
Novel Item	Trial	Source	Approximate Size Range	Image
Brine Shrimp	1	Omega One Freeze Dried Brine Shrimp	0.1 – 3 mm	
Wood Chips	2	Zoo Med Aspen Snake Bedding	0.5 – 4 mm	
Microplastics (Polyethylene)	3	XtraCare Oil-Free Foaming Acne Wash Facial Scrub	0.1 – 1 mm	

Table 2.2A. Model structure and posterior parameter estimates for models of latency to eat both known and novel food as predicted by current and prior group size experience.

Model structure	**Posterior parameter estimates for fixed effects**			
	parameter	estimate	2.5% CI	97.5% CI
Latency to sample known food ~ 1 + group size * prior group size + trial + (1| tank) + (1| block) + (1 | block:id) + (1| block:group) **hurdle** ~ 1 + group size * prior group size + trial + (1| tank) + (1| block) + (1 | block:id) + (1| block:group)	intercept	5.01	3.90	6.12
	hurdle intercept	-2.13	-7.04	2.41
	group size	-0.01	-0.17	0.15
	prior group size	0.04	-1.12	0.20
	trial	-0.13	-0.40	0.13
	group size * prior group size	0.00	-0.04	0.04
	hurdle group size	0.05	-0.62	0.75
	hurdle prior group size	0.29	-0.33	0.98
	hurdle trial	0.76	-0.33	1.97
	hurdle group size * prior group size	-0.06	-0.24	0.10
Latency to sample novel food ~ 1 + group size * prior group size + trial + (1| block) + (1 | block:id) + (1| block:group) **hurdle** ~ 1 + group size * prior group size + trial + (1| tank) + (1| block) + (1 | block:id) + (1| block:group)	intercept	4.26	3.05	5.40
	hurdle intercept	-0.58	-3.87	2.53
	group size	-0.01	-0.21	0.19
	prior group size	0.02	-0.17	0.22
	wood vs. plastic	**0.69**	**0.37**	**1.03**
	group size * prior group size	0.00	-0.04	0.05
	hurdle group size	0.17	-0.43	0.80
	hurdle prior group size	0.29	-0.25	0.90
	hurdle wood vs. plastic	-0.65	-1.78	0.33
	hurdle group size * prior group size	-0.09	-0.25	0.06

Note these models were run on individual latency to sample foods for trials 2 and 3 only. Thus, some findings differ from the model outcomes in Table 2 in the main manuscript. For example, group size is no longer a strong predictor of latency to consume known food when we longer include data from trial 1. Furthermore, since trial 1 (i.e., brine shrimp) is not part of the data, the comparison between categorical trials for the reported posterior parameter space is "wood vs. plastic" (i.e., trial 2 vs. 3) and not "brine vs. plastic" (i.e., trial 1 vs. 2), as reported in Table 2 in the main manuscript. Also note that the hurdle estimates are of the probability of not performing the behavior (i.e., negative hurdle estimates for group size indicate that the probability of eating food during the trial increases with group size).

Table 2.3A. Model structure and posterior parameter estimates for models of latency to eat novel food as predicted by prior foraging experience on known food.

Model structure	**Posterior parameter estimates for fixed effects**			
	parameter	estimate	2.5% CI	97.5% CI
Latency to sample novel food ~ 1 + group size * trial + ate known food * trial + (1| tank) + (1| block) + (1 | block:id) + (1| block:group) **hurdle** ~ 1 + 1 + group size * trial + ate known food * trial + (1| tank) + (1| block) + (1 | block:id) + (1| block:group)	intercept	4.13	3.32	4.89
	hurdle intercept	-1.87	-3.73	-0.13
	group size	-0.06	-0.18	0.05
	brine vs. wood	0.53	-0.36	1.42
	brine vs. plastic	0.80	-0.04	1.66
	ate known (true)	0.04	-0.45	0.51
	group size * brine vs. wood	0.02	-0.15	0.20
	group size * brine vs. plastic	0.10	-0.08	0.27
	ate known food (true) * brine vs. wood	-0.22	-0.91	0.48
	ate known food (true) * brine vs. plastic	-0.04	-0.70	0.61
	hurdle group size	0.10	-0.22	0.43
	hurdle brine vs. wood	**3.14**	**1.11**	**5.45**
	hurdle brine vs. plastic	**2.06**	**0.06**	**4.31**
	hurdle ate known food (true)	-0.73	-1.91	0.39
	hurdle group size * brine vs. wood	-0.29	-0.76	0.16
	hurdle group size * brine vs. plastic	-0.14	-0.61	0.31
	hurdle ate known (true) * brine vs. wood	-0.17	-1.60	1.29
	hurdle ate known (true) * brine vs. plastic	-0.61	-2.08	0.84
Latency to sample novel food ~ 1 + group size * trial + latency to sample known food * trial + (1| block) + (1 | block:id) + (1| block:group)	intercept	3.43	2.37	4.50
	group size	0.02	-0.12	0.16
	brine vs. wood	1.17	-0.22	2.58
	brine vs. plastic	**1.44**	**0.12**	**2.78**
	latency to eat known food	0.00	0.00	0.01
	group size * brine vs. wood	-0.04	-0.25	0.17
	group size * brine vs. plastic	-0.03	-0.25	0.18
	latency to eat known food * brine vs. wood	0.00	-0.01	0.00
	latency to eat known food * brine vs. plastic	0.00	0.00	0.01

Note that the hurdle estimates are of the probability of not performing the behavior. Interaction terms indicate the interaction between either group size or prior foraging behavior (i.e., whether an individual ate or their previous latency to eat) and the trial food type (i.e., brine shrimp, wood chips, or microplastics). The interaction term acknowledges the possibility that the impact of prior foraging experiences on behavior could be item (i.e., trial) specific.

Chapter 3

Dominance hierarchies and evolutionary traps: outcompeting subordinates could disadvantage dominants when foraging for novel noxious foods

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Abstract:

Anthropogenic change creates novel challenges for wildlife, including evolutionary traps that occur when cues are decoupled from their previously associated high fitness outcomes. A common facet of social aggregations across taxa, dominance hierarchies, could affect individual responses to evolutionary traps across social environments. We looked at how variation between group sizes influences the formation of dominance relationships, and in turn, how this could drive differences in foraging behavior in Western mosquitofish (*Gambusia affinis*). Overall, dominant individuals were often the first to eat and had higher bites rates compared to subordinates, including when foraging for microplastics, a common evolutionary trap. However, differences in foraging behavior between ranks varied among group sizes and whether groups were presented with familiar or novel foods. Furthermore, individuals were consistent in their foraging behavior across trials, indicating the formation of social roles in these social groups. Our findings suggest that within-group variation in susceptibility to an evolutionary trap can be strongly associated with social position, but that it is also crucial to consider within-population variation in dominance structures when making this assessment.

Keywords: evolutionary trap, group size, microplastic, dominance hierarchy

Introduction:

Environmental change is exposing many animals to unfamiliar and often dangerous situations. Since behavioral responses are often the most immediate reactions an animal can have toward a novel condition, maladaptive behavioral responses can be highly damaging to individual fitness and population persistence (Sih, Ferrari, & Harris, 2011). Evolutionary traps are a common type of behavioral pitfall, in which animals make decisions based on cues that have been decoupled from their previously associated high fitness outcome (Robertson, Rehage, & Sih, 2013; Schlaepfer, Runge, & Sherman, 2002). However, most studies of evolutionary traps miss a critical aspect behavioral variation by ignoring the social context in which species experience traps. A common source of within-group differences is the hierarchical structure of the social group. Dominance hierarchies, in which individuals have a rank that designates their position within a network of competitive relationships, are a consistent feature of many animal societies (e.g., Bush, Quinn, Balreira, & Johnson, 2016; Grosenick, Clement, & Fernald, 2007; Strauss & Holekamp, 2019; Tibbetts & Dale, 2004). Critically, dominance rank position is associated with differences in physiology, morphology and behavior, such that behavioral phenotypes differ between organisms experiencing the same environment, down to the same tank or cage in a controlled laboratory setting (Varholick et al., 2019). Thus, social dynamics must be considered when trying to understand variation in animal responses to environmental change.

Social dominance is often associated with priority access to resources, such as food (Clutton-Brock, Albon, & Guinness, 1984; Lee & Cowlishaw, 2017; Robbers, Tersteeg, Meijer, & Coomans, 2021) or mates (Chen, Beekman, & Ward, 2011; D. G. Smith, 1993; Wroblewski et al., 2009). In addition, hierarchy status likely influences foraging behavior because rank is associated with different energetic demands (Castro, Ros, Becker, & Oliveira, 2006; Killen et al.,

2014). However, the literature is divided on whether subordinate or dominant individuals incur greater metabolic costs (e.g., Grobler & Wood, 2013; Sloman, Motherwell, O'connor, & Taylor, 2000), and thus which rank should be more motivated to feed (i.e., more voracious). Since dominants often control preferential access to food sources, subordinates frequently forage in riskier situations, and are thus less neophobic and more likely to consume novel foods compared to dominants (Heinrich, Marzluff, & Adams, 1995; Reader & Laland, 2001; Seok An, Kriengwatana, Newman, MacDougall-Shackleton, & MacDougall-Shackleton, 2011; Stahl, Tolsma, Loonen, & Drent, 2001). Therefore, subordinates might be particularly susceptible to evolutionary traps, since they are more likely to take on more risk for reward, especially when foraging around dominant individuals. Conversely, subordinates might be more likely to benefit when the group encounters an undervalued resource if the unfamiliarity of cues leads dominants to avoid novel but nutritious food sources.

Furthermore, patterns of dominance structure are not phylogenetically constrained, and different groups within the same species can have different structural patterns (Hobson, Mønster, & DeDeo, 2021). Critically, behavior and physiology are expected to depend both on the type of dominance hierarchy as well as the individual's position within that hierarchical structure (Varholick et al., 2019). For example, subordinate mice in highly despotic groups (i.e., one defined dominant individual with undefined subordinate ranks) have much lower testosterone and higher levels of cortisone compared to the dominant (Williamson, Lee, Romeo, & Curley, 2017). However, mice in a linear hierarchy structure, in which all individuals have a unique rank, have similar levels of both hormone no matter their dominance position (Williamson et al., 2017). Thus, is it important when studying the influence of rank on behavior to consider multiple potential hierarchy structures. Even something as simple as changes in overall group size can

affect the number of positions within a relationship network, effectively altering hierarchy structure.

Dominant individuals are often influential leaders or initiators within their groups (King, Douglas, Huchard, Isaac, & Cowlishaw, 2008; Peterson, Jacobs, Drummer, Mech, & Smith, 2002; J. E. Smith et al., 2015). Initiators usually have greater access to encountered food, since arriving first at a food patch allows a greater opportunity to exploit it (Krause, Hoare, Krause, Hemelrijk, & Rubenstein, 2000). However, being the first could also be costly, since being the first in an unfamiliar situation increases the risk of error (Greenberg & Mettke-Hofmann, 2001). This could be especially harmful when encountering an evolutionary trap if it results in monopolizing a harmful resource, like a noxious food item or a deadly nesting site. Furthermore, being the first is not only costly for the initiator. Following an initiator could be problematic for the group in general if uninformed leaders provide outdated or misguided information (Barrett, Zepeda, Pollack, Munson, & Sih, 2019).

Who takes on the initiator or leadership role might change depending on the context. While there is some evidence that individuals maintain consistent leadership-followership roles within a group (Nakayama, Harcourt, Johnstone, & Manica, 2012), individuals might take different social roles depending on the situation (Tuliozi, Camerlenghi, & Griggio, 2021). Moreover, consistency in a social role, like leadership, might be lower in a novel scenario. For example, shoals of *Gambusia holbrooki* experienced a greater number of changes in leadership when swimming in an unfamiliar environment compared to a relatively familiar one (Burns, Herbert-Read, Morrell, & Ward, 2012). The authors argue that this reflects an absence of any preference in direction by any one individual, resulting in a decreased motivation to lead (and thus be the first in the group). A similar phenomenon might occur with environmental change, if

lack of information about novel conditions leads to decreased preferences, ultimately resulting in an absence of leadership. In this case, no social dominance position might be more or less likely to interact with an evolutionary trap.

In a series of controlled experiments, we examined how differences in dominance rank, as determined by aggressive interactions, influences social roles and subsequent differences in foraging for both familiar and novel foods in groups of mosquitofish. We hypothesized that higher ranked individuals would act as initiators in familiar foraging situations, and that this would translate into greater exploitation of food resources compared to subordinates. Alternatively, if lower ranked individuals acted as initiators, we did not expect that this would lead to greater exploitation of food resources by the subordinates. This is because we expected that higher ranked individuals would still be able to outcompete lower ranked individuals once they began foraging, effectively nullifying the subordinate's head start. This might then lead to dominants continuing to outcompete subordinates or perhaps a more equal sharing of food amongst ranks.

In order to account for the interaction between rank and dominance structure, we ran identical experiments with different group sizes, controlling for the number of available social roles within a dominance network. We did not have a priori hypotheses for the influence of group size on different dominance rank's foraging behavior. It might be that with larger group sizes, clearer differences between ranks would become more apparent. Thus, smaller groups might be more egalitarian in their foraging, while larger groups have greater skew in resource access. On the other hand, it might be more difficult for a single individual to dominate the more members there are in a social group. In this case, while smaller groups have a single dominant outcompeting subordinates for resources, larger groups become more egalitarian between all

members. Alternatively, it might be that structures remain relatively similar (i.e., despotic or linear hierarchy structure in all group sizes). This would be especially apparent if all groups have an underlying despotic structure, in which all lower ranked individuals would be expected to behave similarly subordinate no matter the group size.

We had competing hypotheses for the relationship between leadership and dominance regarding foraging for novel foods. If foraging in general is perceived by individuals as having similar risk levels, it might be that dominant individuals are the first to eat and eat more than their subordinate counterparts regardless of the familiarity of the resource. On the other hand, subordinate individuals could be more likely to eat novel foods first if dominant individuals hang back from initiating foraging because they are either (1) less energetically motivated (i.e., more satiated from high consumption of familiar food) or (2) less motivated to lead due to lack of information. We predicted that these mechanisms would also influence the consistency of the initiator role across and between trials that differ in whether food is familiar or novel.

Lastly, differences in behaviors between ranks could depend on the type of novel food. That is, while dominants might take more bites of a beneficial novel food compared to subordinates, this pattern could change if the food item was less appealing or even costly. To account for these differences, we presented fish with a series of novel food items that ranged from highly palatable (brine shrimp), to inert (glass beads and wood chips), to potentially costly (microplastics, a common evolutionary trap for freshwater and marine organisms). Fish were presented with both virgin and biofouled plastics in order to examine differences in foraging based on the nature of the evolutionary trap. Misleading cues from the biofouling process can cause plastics to smell like natural food sources (Savoca, Tyson, McGill, & Slager, 2017;

Savoca, Wohlfeil, Ebeler, & Nevitt, 2016), making it a potentially more misleading trap than virgin plastic alone.

To test these hypotheses, we examined the differences between groupmates across three different group sizes in four behaviors: likelihood to eat first when foraging for either familiar or novel foods and number of bites when foraging for either familiar or novel foods. We quantified (i) individual consistency in these four behaviors and compared between dominance ranks, assuming (ii) despotic and (iii) transitive dominance structures. Lastly, (iv) we assessed whether differences between ranks depended on novel food type.

Methods:

Study system

We examined the influence of dominance rank on foraging behaviors in Western mosquitofish (*Gambusia affinis*) in different sized social groups. Dietary generalists, mosquitofish are one of the most widespread introduced species in the world (Pyke, 2008), thriving in human-dominated landscapes and thus likely encountering novel items in their environment. A model system for social behavioral studies (Etheredge, Avenas, Armstrong, & Cummings, 2018; Hansen, Schaerf, & Ward, 2015; Polverino, Liao, & Porfiri, 2013), mosquitofish form fission-fusion shoals in the wild of various sizes and compositions (Fryxell, Arnett, Apgar, Kinnison, & Palkovacs, 2015). While research indicates that group size influences mosquitofish behavior (Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Reding & Cummings, 2019), no studies have investigated how changes in group size influences intra-specific differences in social roles and foraging behavior.

The features and consequences of dominance rank are well studied in the sister species *Gambusia holbrooki* (Chen et al., 2011; Liss, Lopez, Donelson, & Wong, 2020; Matthews & Wong, 2015). While some work has linked size disparity as a prominent basis of social dominance in this species (Matthews & Wong, 2015), others have found that size and dominance status are not always linked (Chen et al., 2011). Multiple studies have assumed a despotic (also called monarchic) structure in *Gambusia holbrooki* hierarchies, with one dominant and multiple subordinates of indistinguishable rank (Burns et al., 2012; Chen et al., 2011). Others have considered a linear (also called a transitive hierarchy or pecking-order structure), with differences between all individuals (Liss et al., 2020; Matthews & Wong, 2015). Since there has not been a definitive characterization of *Gambusia affinis* hierarchy structure, we considered both types of potential hierarchy types in our analysis.

Plastic debris was used as the evolutionary trap for this study because plastic ingestion is common and associated with various negative health effects in many freshwater and marine species (Anbumani & Kakkar, 2018; Andrady, 2011). We used polyethylene particles, which are the most common plastic debris (Andrady, 2011). Furthermore, polyethylene sorbs greater concentrations of toxicants compared to other common plastics (Rochman, Hoh, Kurobe, & Teh, 2013). In a prior study, we observed that mosquitofish consume polyethylene beads in the lab (Pollack et al. *in prep*) and confirmed with postmortem dissections that particles were ingested (Pollack unpublished observation).

Group formation and determination of dominance rank

Observations of fish groups were performed between August 2019 and April 2020 at the Center for Aquatic Biology and Aquaculture (CABA) facilities at the University of California,

Davis. Adult female fish were donated from the Sacramento-Yolo Mosquito and Vector Control District. Females were individually tagged with VIE tags (Northwest Marine Technologies) and then randomly sorted into groups of 10 that were housed in 37.8 L tanks (14:10 light:dark photoperiod, 22°C) for at least 4 months prior to experiments. During this period, fish were fed *ad libitum* with a mixture of fish flakes (Tetramin) and floating pellets (New Life Spectrum). For the following experiment, 156 fish (mean standard length = 28.5 ± 3.2 mm) were randomly assigned to groups of 2, 3, or 4 individuals, with 16 replicates of 2, 20 replicates of 3, and 16 replicates of 4. To control for the influence of familiarity on behavior, all fish assigned to a social group were from different housing tanks. Observation tanks consisted of a 37.8L tank with a 15 cm long PVC pipe (3.81 cm diameter) refuge and airline tubing through which food items could be introduced to the tank. All foods were introduced through the tubing with a flush of 30 mL of water to limit associations between human handling of food and the introduction of food at the surface of the water. Fish were then observed at a random time between 0900 and 1800 for 10 subsequent days to evaluate dominance relationships and quantify foraging behavior.

Focal observations of each group commenced after a 24 hour acclimation period plus a 5 minute adjustment to the presence of the observer (as in Liss et al., 2020; Lopez, Davis, & Wong, 2018). Animals could not be observed blind, since group size treatments were familiar to the observer. However, observers were blind to previous days observations. Immediately following the adjustment period, the observer recorded all chasing events, the identity of both the chaser and the chased fish for 5 minutes. It is standard practice to consider aggression received, in this case chases, as an indicator of subordinate status of social fish in general (Fitzpatrick et al., 2008; Matthews & Wong, 2015).

Daily ranking was determined from average daily Elo scores (EloRating; Neumann et al., 2011). To account for the dynamic nature of dominance hierarchies, each fish's dominance rank was re-evaluated and reassigned each day depending on their updated Elo score, informed by data from the prior period of observation. If ties in score occurred, both individuals were assigned the lower rank (e.g., two individuals tied within a group of 2 were both given a rank of 2, two individuals tied within a group of 3 were both given a rank of 3 if there was an individual with a higher score above them or both given a rank of 2 if there was an individual with a lower score below them, etc.). This allowed for higher ranks to emerge as interactions progressed over the course of the 10-day observation period.

Social foraging assays

Familiar food assay: Directly after the 5-minute observation period of intragroup aggression, groups were observed for the 5 minutes immediately following the introduction of familiar floating pellets (New Life Spectrum). In order to standardize the level of competition, food was scaled for group size, such that there were 2 pellets per fish. The observer would then record the feeding order and number of bites taken of pellets by all fish in the group.

Novel food assay: For the last five days of observations, a novel food was introduced to the groups immediately following the daily familiar food assay. Groups were observed for the 5 minutes immediately following the introduction of novel food through airline tubing. The novel food was varied for each day, but introduced in the same sequence across days to control for the effect of order of introduction across groups. The novel foods introduced were brine shrimp (highly palatable, day 6), glass beads (not palatable, day 7), aspen woods chips (not palatable, day 8), virgin microplastics (polyethene particles distilled from facewash, day 9) and biofouled

microplastics (polyethylene particles distilled from facewash and kept in unfiltered water from Putah Creek (Yolo County, CA] for 1 month to accumulate natural biofilm growth, day 10). Novel foods (except for glass beads) were scaled for group size – 3 mg per fish (i.e., the same mass per fish as the familiar food pellets). Instead of scaling for weight, glass beads were scaled to count (2 beads per fish). Biofouled microplastics were piped into arenas in a standardized volume of biofouling water (i.e., 0.5 mL) for all group sizes to control for the intensity of the olfactory cue of added stream water. Furthermore, it allowed us to maintain the same ecologically relevant freshwater concentration of microplastics within the assay tanks (~ 0.05 ppm) (Li, Busquets, & Campos, 2020). See Appendix Table 3A for details on source and size of novel items.

At the conclusion of the last observation day (trial day 10), individuals were weighed and measured for standard length. These procedures were approved by the University California Davis Institutional Animal Care and Use Committee (protocol #19357).

Statistical analysis

We used Bayesian generalized linear multilevel models, fitted with the R package brms (Bürkner, 2018), to analyze all behavioral data. Out of the 520 trials in this study, 18 were not included in the final data set due to scheduling error.

In order to evaluate the influence of social rank on an individual's likelihood to eat familiar and novel foods first out of the entire group (i.e., initiate foraging for the group), we used a Bernoulli structure. To assess how individual rank affects the count of bites for familiar food we used a zero-inflated negative binomial structure, while we used a zero-inflated Poisson structure for the count of bites for novel food. The zero-inflated structure allows us to account

for the fact that multiple processes could be causing fish to take zero bites during a trial (e.g., fish that were never going to take a bite given infinite time versus those were prevented from taking a bite by other fish). For all models, daily dominance rank, group size, and trial number were included as predictors. To account for the potential that larger individuals are simply the strongest competitors (i.e., bigger, faster swimmers, etc.) and will always be first and eat more, we included body length as a predictor in all our models. All models included varying intercepts for fish ID nested within group ID, to account for consistent differences among individuals within different groups. For the familiar food models, trial was treated as an integer; however for the novel food models, trial was treated as a categorical variable to account for differences in novel items. For beta coefficients of fixed effects, we used weakly informative, regularizing priors centered on 0, meaning the models were skeptical of high beta values.

First, to assess differences in foraging behavior between overall dominant and subordinate individuals, models were run across the entire data set with rank 1 individuals as "dominant" and rank 2-4 individuals as "subordinate." Second, to consider differences across all ranks, models were run with all ranks included (i.e., ranks 1-3 in groups of 3, 1-4 in groups of 4). Since differences in relative rank are likely group size dependent, separate models were run for each group size without group size as a predictor. Third, to assess differences in number of bites between ranks for each novel food type, separate models were run for each novel food trial, with daily rank as a predictor and varying intercepts for fish ID nested within group ID.

In order to quantify repeatability of behaviors, the intra-class correlation coefficient (ICC, Nakagawa, Johnson, & Schielzeth, 2017) was calculated for individual fish ID seperately for all the models described above (with unnested varying intercept for fish ID) using the rptR package in R (citation), with 1000 bootstrapping in order to determine 95% CI. For this analysis, a

Poisson structure was used to assess the repeatability for the number of both familiar and novel bites (instead of zero-inflated). To assess whether the same individual initiated foraging in both familiar and novel foods contexts, an additional model was run with an individual's likelihood of eating novel food first as the outcome (Bernoulli structure) and whether they ate first during the familiar food trial, group size, and trial as predictors. The model also included varying intercepts for fish ID nested within group ID.

Results:

Across all trials, 80% of individuals took at least one bite of familiar food and 79% of individuals took at least one bite of novel food. Group hierarchy structure over the 10 day trial period was quite stable, as only 7 out of 52 groups had a stability index less than 0.81 (the cut-off considered to indicate high stability, McDonald & Shizuka, 2013).

The consistency of individual foraging behaviors

ICC values are reported in Table 3.1. Overall, individuals were consistent in whether they were the first to eat familiar and novel foods across all trials. Furthermore, individuals were consistent in the number of familiar food bites taken across trials. However, number of novel food bites was not repeatable, which is likely because novel foods were different between trials. These patterns held true across all group sizes, except for the largest groups, where individual consistency to be the first to eat novel food was not repeatable in groups of 4.

In addition to being consistent across trials, the initiator role was also consistent across assay types within the same trial. That is, an individual was more likely to to eat first in a novel

food trial if they ate first in the familiar food trial that day (estimate = 0.81, 95%CI = 0.39 – 1.22). See Appendix 3B for all posterior parameter estimates for this analysis.

Table 3.1. Intra-class correlation coefficients (ICC) across several trials assessing how likely mosquitofish individuals are to be the first in their group to consume a food item

		Group Size							
		All Groups		**Group of 2**		**Group of 3**		**Group of 4**	
		ICC	95% CI	ICC	95% CI	ICC	95% CI	ICC	95% CI
First to eat	Familiar food	**0.26**	**[0.17 - 0.33]**	**0.38**	**[0.20 - 0.48]**	**0.28**	**[0.16 - 0.41]**	**0.20**	**[0.08 - 0.32]**
	Novel food	**0.16**	**[0.05 - 0.21]**	**0.31**	**[0.05 - 0.48]**	**0.14**	**[0.01 - 0.23]**	0.06	[0.00 - 0.13]
Number of bites	Familiar food	**0.33**	**[0.23 - 0.38]**	**0.24**	**[0.09 - 0.38]**	**0.37**	**[0.24 - 0.47]**	**0.31**	**[0.20 - 0.41]**
	Novel food	0.10	[0.00 - 0.18]	0.11	[0.00 - 0.26]	0.08	[0.00 - 0.18]	0.10	[0.00 - 0.22]

CI is the credible interval from posterior parameter estimates.

Differences between dominant and subordinates in foraging behaviors

Model structure and posterior parameter estimates are reported in Table 3.2 (posterior parameter estimates for the zero-inflated portion of the models can be found in Appendix 3C). Assuming a despotic dominance structure (i.e., one dominant within a group with subordinates with indistinct rank differences between them), a simple pattern emerges across all group sizes, where the dominant fish within a group is more likely to eat first and take more bites of both familiar and novel foods (Fig. 3.1). Individual likelihoods to eat first decreased with group size simply reflecting the increased number of individuals within larger groups (i.e., more individuals who could not be first). The number of bites of familiar food decreased with trial, potentially due to satiation or habituation (i.e., lack of interest in pellets over time). For the novel food trials, individuals tended to take the most bites of aspen wood chips, followed by glass beads, then

brine shrimp, biofouled plastic, and finally virgin plastic (Table 3.3). However, we are unable to assess preference from this observation, since these findings are confounded by trial sequence, ease of consumption, and item apparency. While for most of the behaviors, length did not have a significant affect, length did have a positive influence on number of novel food bites.

Table 3.2 Model structure and posterior parameter estimates for models of foraging behavior that assume a despotic structure in dominance hierarchy

Model Structure	**Posterior parameter estimates for fixed effects**			
	parameter	estimate	2.5% CI	97.5% CI
Likelihood to eat familiar food first ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID)	intercept	0.40	0.25	2.57
	subordinate vs. dominant	**-0.96**	**-1.32**	**-0.59**
	trial	0.00	-0.04	0.05
	length	0.08	-0.17	0.34
	group size	**-0.54**	**-0.89**	**-0.20**
Likelihood to eat novel food first ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID)	intercept	1.38	0.23	2.54
	subordinate vs. dominant	**-0.96**	**-1.45**	**-0.47**
	trial 6 vs.7	-0.41	-0.93	0.11
	trial 6 vs.8	-0.07	-0.59	0.44
	trial 6 vs.9	-0.11	-0.64	0.41
	trial 6 vs.10	-0.04	-0.56	0.49
	length	-0.11	-0.36	0.15
	group size	**-0.49**	**-0.83**	**-0.16**
Familiar food bites ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID)	intercept	1.28	0.81	1.74
	subordinate vs. dominant	**-0.28**	**-0.39**	**-0.17**
	trial	**-0.03**	**-0.04**	**-0.01**
	length	0.01	-0.09	0.10
	group size	-0.01	-0.15	0.14
Novel food bites ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID)	intercept	1.92	1.49	2.34
	subordinate vs. dominant	**-0.20**	**-0.35**	**-0.06**
	trial 6 vs.7	0.37	0.26	0.49
	trial 6 vs.8	0.68	0.58	0.78
	trial 6 vs.9	-0.29	-0.43	-0.16
	trial 6 vs.10	-0.12	-0.23	0.00
	length	**0.13**	**0.04**	**0.22**
	group size	-1.13	-0.25	0.00

CI is the credible interval from posterior parameter estimates.

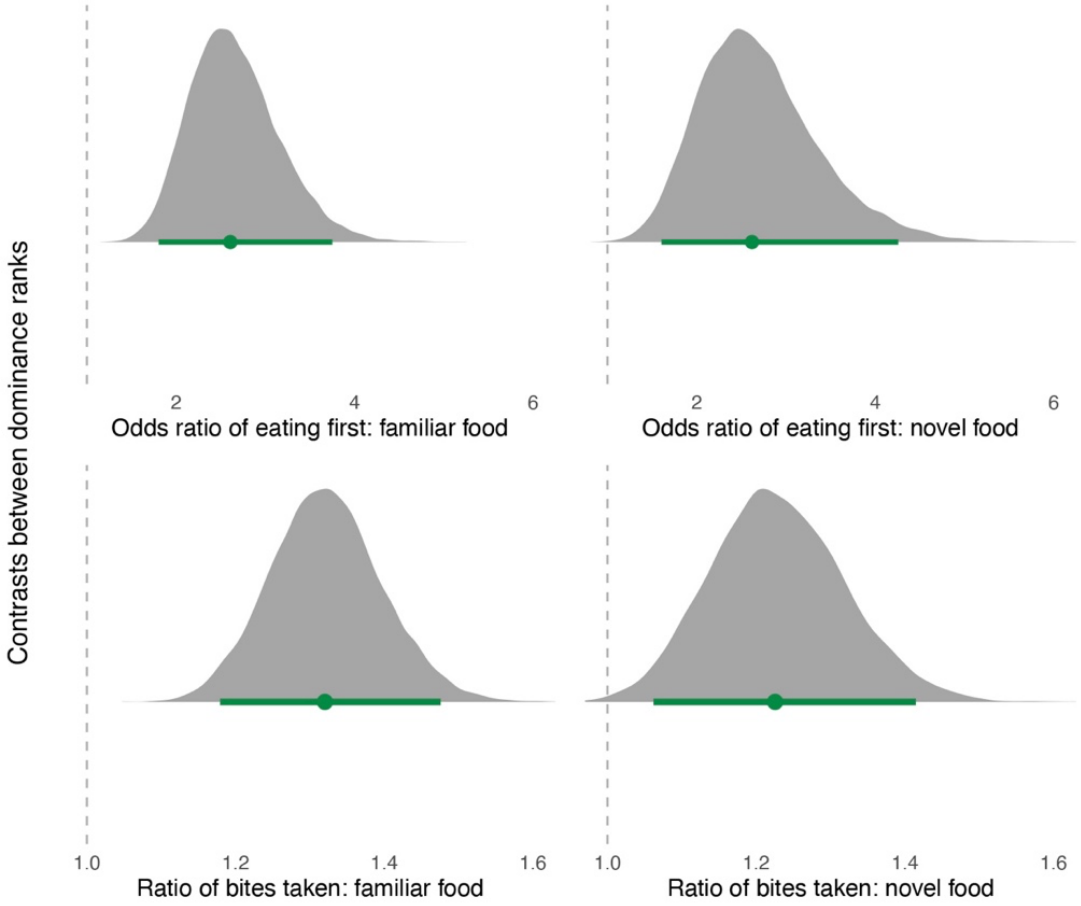

Figure 3.1 Odds ratio distributions between dominant and subordinates for likelihood to eat first and number of bites, for both familiar and novel foods. Odds ratio values greater than 1 indicate higher values for the more dominant individual. Odds ratio distributions are derived from the posterior parameter estimates of multilevel models and are estimates of the differences in dominance ranks for their median likelihood to take a bite first or median number of bites, respectively. Green denotes that the credible intervals do not overlap 1. Dashed lines indicate when the odds ratio is equal to 1.

Table 3.3 Odds ratios for number of bites between different novel food types. Odds ratio greater than 1 indicates that first listed food type was eaten more

contrast between trials	estimate	2.5%CI	97.5% CI
brine vs.biofouled	1.12	1.00	1.26
brine vs.bead	0.69	0.62	0.77
brine vs.wood	0.51	0.46	0.56
brine vs.virgin	1.34	1.17	1.52
bead vs.biofouled	1.63	1.45	1.84
bead vs.wood	0.74	0.67	0.81
bead vs.virgin	1.94	1.70	2.21
wood vs.biofouled	2.22	1.99	2.47
wood vs.virgin	2.64	2.34	2.99
virgin vs.biofouled	0.84	0.73	0.96

Odds ratio distributions are derived from the posterior parameter estimates of multilevel models and are estimates of the differences in the median number of bites between food types. CI is the credible interval from posterior parameter estimates.

Differences between all ranks in likelihood to be initiators

Model structure and all posterior parameter estimates, including odds ratios, are reported in Appendix 3D. When we incorporated all possible ranking in our analysis, we still found that rank affects likelihood to eat familiar food first, but only for the highest ranked individuals in the larger group sizes (Fig. 3.2). That is, for groups of 2, differences were not observed between rank 1 and 2 individuals. However, for groups of 3, individuals ranked 1 were more likely to eat first compared to individuals ranked 3. Differences were not observed between the other closer together ranks. Similarly, for groups of 4, individuals ranked 1 were more likely to eat first compared to lower ranked individuals. However, differences were not observed between individuals in the lower dominance ranks.

Similarly, rank differences did not affect likelihood to eat novel food first, except for the lowest ranked individuals in the largest group sizes (Fig. 3.3). For groups of 2 and 3, rank did not appear to influence feeding order for novel food. For groups of 4, there was no observed

differences between most ranks. The exception to this pattern was that rank 4 fish were less likely to eat novel food first compared to those ranked 3 and those ranked 1.

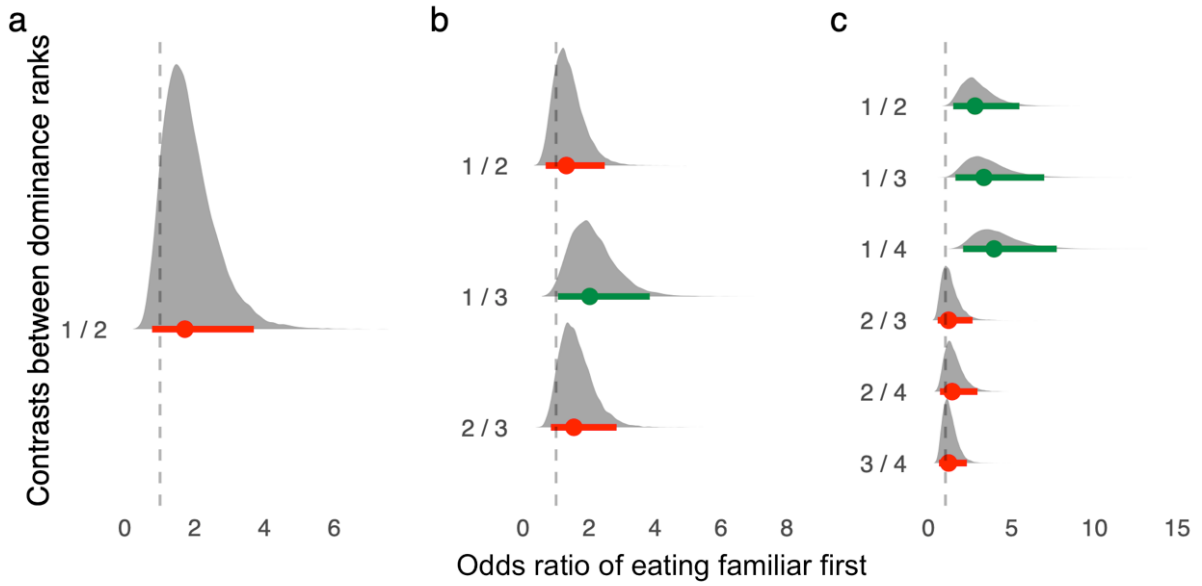

Figure 3.2 Odds ratio distributions of eating familiar first for (a) groups of 2, (b) groups of 3, and (c) groups of 4 based on differences in ranks. Odds ratio distributions are derived from the posterior parameter estimates of multilevel models and are estimates of the differences in dominance ranks for their mean likelihood to take a bite first. Red and green dots represent the estimated mean, while lines represent the 95% credible intervals. Red denotes that the credible intervals overlap with 1, while green denotes that the credible intervals do not overlap 1. Dashed lines indicate when the odds ratio is equal to 1.

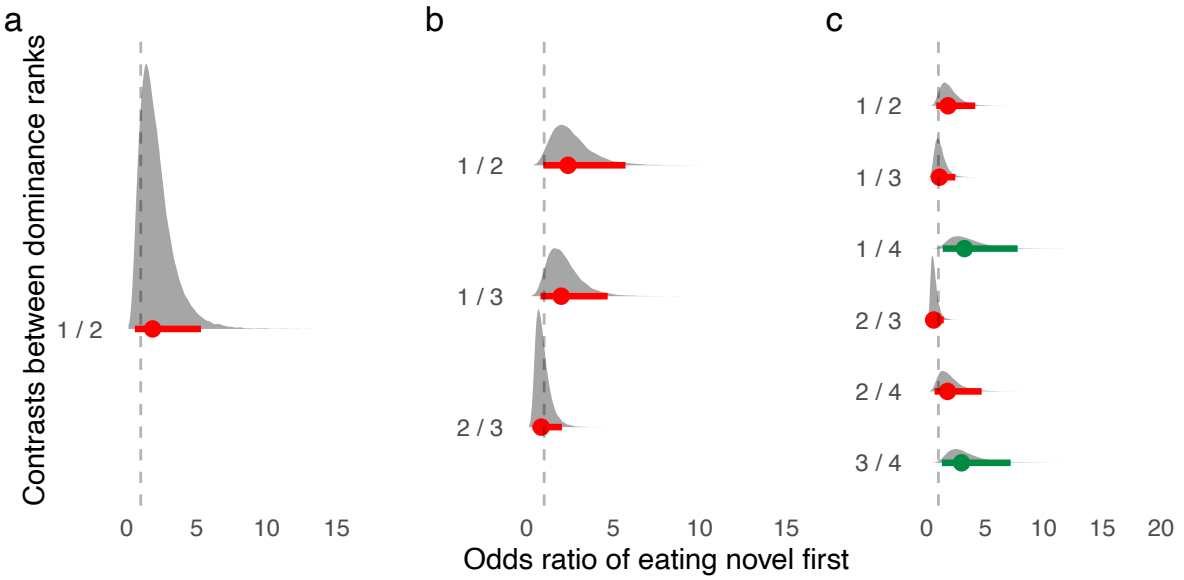

Fig 3.3 Odds ratio distributions of eating novel food first for (a) groups of 2, (b) groups of 3, and (c) groups of 4 based on differences in ranks. Odds ratio distributions are derived from the posterior parameter estimates of the multilevel models and are estimates of the differences in dominance ranks for their mean likelihood to take a bite first. Red and green dots represent the estimated mean, while lines represent the 95% credible intervals. Red denotes that the credible intervals overlap with 1, while green denotes that the credible intervals do not overlap 1.

Differences between all ranks in number of bites

Model structure and all posterior parameter estimates, including odds ratios, are reported in Appendix 3E. When we incorporated all possible ranking in our analysis, rank affects familiar food bite frequency, although the exact pattern depends on groups size (Fig. 3.4). For groups of 2, rank 1 individuals took more bites than rank 2. For groups of 3, rank 1 individuals took more bites than rank 2 and rank 3. However, differences were not observed between rank 2 and 3 individuals. For groups of 4, individuals took a similar number of bites with those of neighboring rank, including the most dominant individual, but more bites than those at least 2 ranks lower than them. Although we are less confident in the difference between ranks 1 and 2, ranks 2 and

3, and ranks 3 and 4, the trend indicates that higher ranked individuals potentially take more bites (since the 95% confidence intervals barely overlap zero).

When foraging for novel food, differences between ranks again depended on group size (Fig 3.5). For groups of 2, individuals ranked 1 took more bites than those ranked 2, as observed in the familiar food trials. However, the familiar food pattern did not hold when the larger groups foraged for novel food. For groups of 3, there were no differences in novel bites between ranks. For groups of 4, individuals ranked 1 took more bites than those ranked 2 and 4. However, differences were not observed between other ranks.

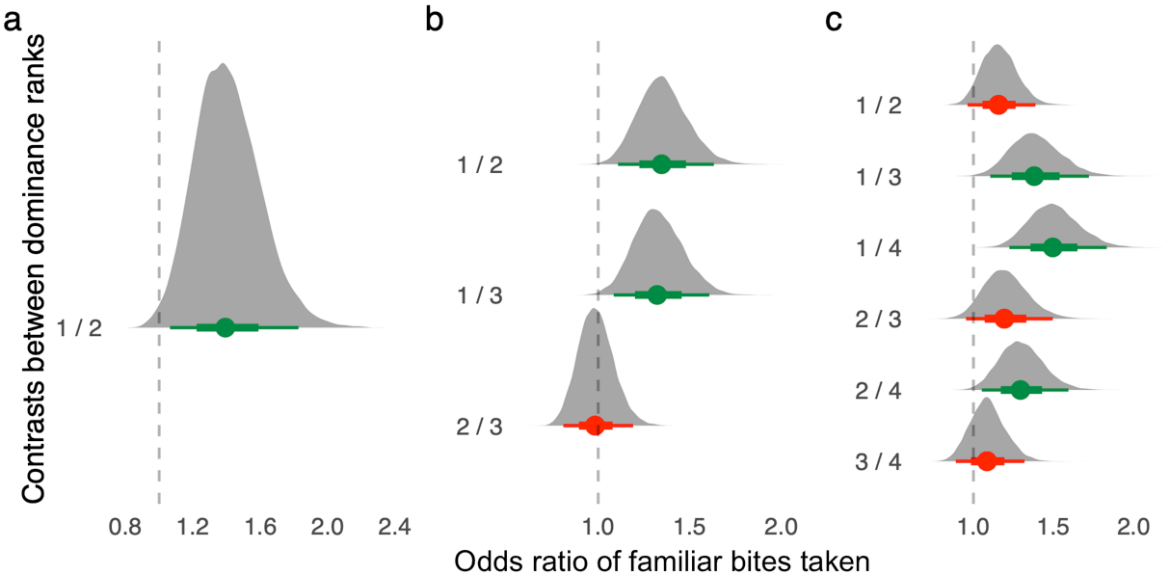

Figure 3.4 Odds ratio distributions of bites of familiar food taken for (a) groups of 2, (b) groups of 3, and (c) groups of 4. Odds ratio distributions are derived from the posterior parameter estimates of the multilevel models and are estimates of the differences in dominance ranks for their mean bite rate. Red and green dots represent the estimated mean, while lines represent the 95% credible intervals. Red denotes that the credible intervals overlap with 1, while green denotes that the credible intervals do not overlap 1.

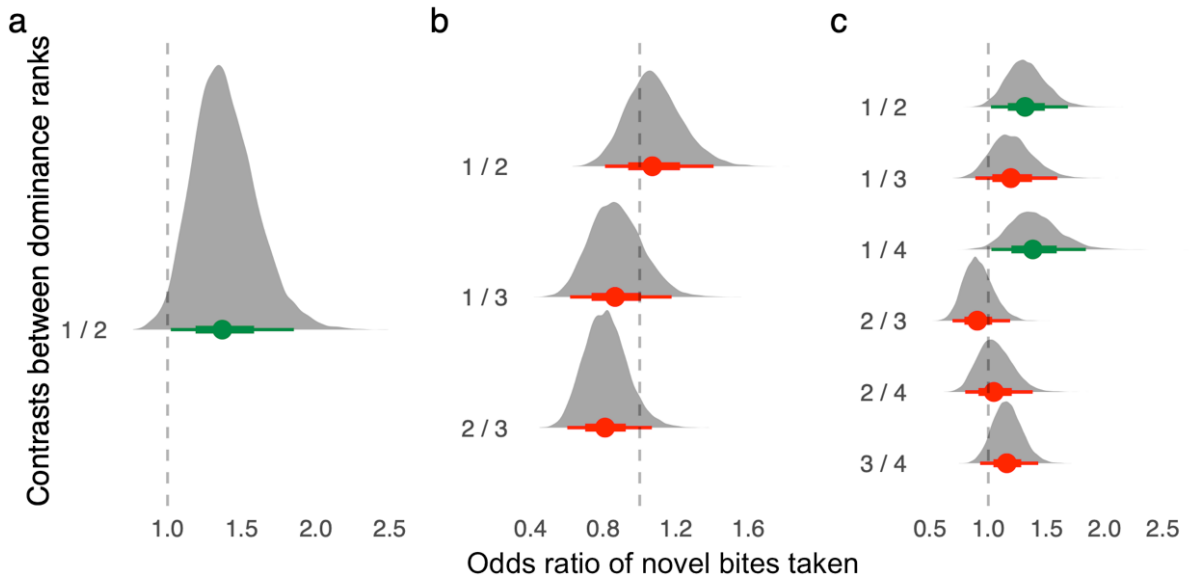

Figure 3.5 Odds ratio distributions of bites of novel food taken for (a) groups of 2, (b) groups of 3, and (c) groups of 4. Odds ratio distributions are derived from the posterior parameter estimates of the multilevel models and are estimates of the differences in dominance ranks for their mean bite rate. Red and green dots represent the estimated mean, while lines represent the 95% credible intervals. Red denotes that the credible intervals overlap with 1, while green denotes that the credible intervals do not overlap 1.

Differences between ranks in foraging for novel food types

Model structure and posterior parameter estimates are all reported in Appendix 3F. We did not observe differences between ranks in likelihood to eat first for any of the novel food types (Appendix Table 3F). Overall differences in foraging for items based on rank were supported only in the larger groups, where either the highest ranked individual took more bites or the lowest ranked individual took fewer bites compared to other ranks in the group (Table 3.4). When groups were presented with brine shrimp on day 6 (i.e., a palatable and nutritious novel food), rank 4 individuals took less bites than rank 1 and 3 individuals. When groups were presented with microplastics on trial day 9 (virgin) and day10 (biofouled), differences between ranks in number of bites were observed only in groups of 4. In both cases, top ranked individuals

took more bites of both plastic types than most other ranks in the group, regardless of whether the plastic was treated or not (i.e., has an additional attractive olfactory cue).

Table 3.4 Odds ratio of novel bites taken between different ranks

		Brine shrimp			Glass beads			Wood chips		
contrast between ranks		**estimate**	**2.5% CI**	**97.5% CI**	**estimate**	**2.5% CI**	**97.5% CI**	**estimate**	**2.5% CI**	**97.5% CI**
Group of 2	1 vs.2	0.95	0.61	1.58	3.5	0.82	21.4	1.29	0.68	2.48
Group of 3	1 vs.2	1.24	0.86	1.82	1.2	0.65	2.32	**1.84**	**1.02**	**3.28**
	1 vs.3	1.18	0.82	1.73	1.37	0.8	2.34	1.54	0.88	2.74
	2 vs.3	0.95	0.65	1.4	1.14	0.57	2.18	0.84	0.46	1.57
Group of 4	1 vs.2	1.25	0.79	2.03	0.81	0.42	1.54	1.26	0.67	2.47
	1 vs.3	1.01	0.67	1.56	0.6	0.3	1.16	**1.83**	**1.02**	**3.32**
	1 vs.4	**1.69**	**1.09**	**2.7**	1	0.52	1.98	1.79	0.98	3.41
	2 vs.3	0.81	0.48	1.37	0.75	0.37	1.41	1.45	0.74	2.77
	2 vs.4	1.35	0.78	2.36	1.25	0.65	2.38	1.42	0.73	2.77
	3 vs.4	**1.68**	**1.07**	**2.67**	1.67	0.86	3.45	0.99	0.54	1.84

		Virgin microplastics			Biofouled microplastics		
contrast between ranks		**estimate**	**2.5% CI**	**97.5% CI**	**estimate**	**2.5% CI**	**97.5% CI**
Group of 2	1 vs.2	0.55	0.23	1.3	1.36	0.41	4.95
Group of 3	1 vs.2	1.3	0.7	2.33	1.58	0.9	2.86
	1 vs.3	1.45	0.76	2.72	1.19	0.71	2.01
	2 vs.3	1.12	0.59	2.13	0.75	0.41	1.35
Group of 4	1 vs.2	**2.69**	**1.29**	**5.79**	1.52	0.95	2.49
	1 vs.3	**2.34**	**1.02**	**5.47**	**1.66**	**1.02**	**2.74**
	1 vs.4	**2.18**	**1**	**4.71**	**2.64**	**1.53**	**4.68**
	2 vs.3	0.87	0.35	2.16	1.09	0.64	1.53
	2 vs.4	0.81	0.34	1.92	1.73	0.97	3.13
	3 vs.4	0.93	0.36	2.38	1.6	0.88	2.89

Odds ratio distributions are derived from the posterior parameter estimates of the multilevel models and are estimates of the differences in the median number of bites between individuals. CI is the credible interval from posterior parameter estimates.

Discussion:

Generally, dominant individuals (i.e., those that had the highest Elo score within their group based on agonistic dyadic interactions) outcompeted their group mates for both familiar and novel food sources. Consistent with a despotic dominance hierarchy in our analysis, we found that the top ranked individual within a group was more likely to be the first to begin foraging and to take more bites of both familiar and novel food options. Given that in most groups, dominance positions were quite stable between trial days, this consistency in leadership and resource acquisition by the dominant is reflected in the repeatability of individual behavior. That is, individuals were consistent in their likelihood to initiate foraging in both contexts and in the number of familiar food bites taken within a trial. Similarly, individuals that were first to eat familiar food during a trial day were then more likely to be the first to eat novel food, indicating overall consistency in social role by the same individual within the group across foraging contexts.

Overall, our findings suggests that while dominant individuals may benefit from greater access to high quality resources, they also may pay higher costs when foraging for novel foods if those foods are noxious. We found that in groups of 4, dominant fish took more bites of two different types of microplastic, a costly evolutionary trap, compared to their subordinate groupmates. These findings indicate that, at least in some dominance structures, dominant individuals might be disproportionally hurt by novel risks, especially if novel items emit similar cues as safe or beneficial familiar objects. While in many systems subordinates tend to be less neophobic by necessity (Heinrich et al., 1995; Reader & Laland, 2001; Stahl et al., 2001), in other systems, dominant individuals might take on more risks or costs to the benefit of subordinates (Chiarati, Canestrari, Vera, & Baglione, 2012). For example, in cooperatively

breeding carrion crows, dominants may be more likely to approach novel resources first, so that closely related subordinates then benefit from decreased risk when foraging for the same novel foods (Chiarati et al., 2012). In this case, dominants may investigate the potential toxicity of novel foods by trying it first, alleviating the risks for offspring to try it after them. We were unable to track whether fish tasted and rejected novel foods, such that subordinates might have the opportunity to learn about potentially noxious food sources. However, rapid environmental change might increase the risks of trying novel items and even obfuscate the risks, benefiting none of the group. This is especially concerning with evolutionary traps like consumption of microplastics, where fitness costs (i.e., the bioaccumulation of toxicants, Anbumani & Kakkar, 2018) are decoupled from the immediate behavior.

Moreover, differences in behavior between ranks across different group sizes within our study indicates that it is crucial to consider both the hierarchy structure and individual rank within that structure when formulating hypotheses about the relationship between dominance rank and social role (Amici et al., 2020; Varholick et al., 2019). In the larger groups, we observed a despotic structure for access to familiar resources, where dominants were the first to feed and took more bites compared to subordinates. In contrast, there were no differences in likelihood to initiate foraging for either familiar or novel foods between ranks within groups of 2 fish. However, top ranked individuals still took more bites of familiar and novel foods compared to their subordinate group mates. In essence, dominant individuals were making up for this lack of priority access to food resources and still outcompeting subordinates for bites. One potential explanation is that leadership or initiator roles are just independent of social dominance, as has been observed in other systems (Bousquet & Manser, 2011; Nagy et al., 2013). However, with only one other individual to compete with for food, priority access to food might not matter at

much as it does in larger groups. In this case, there is no incentive to being the initiator in either a familiar or novel context. However, when the number of competitors increases, even as the amount of food is scaled, relative ability to outcompete groupmates could decrease and thus priority access to food (i.e., being the first) could therefore become more important. Thus, we see in groups of 3 and 4 fish, that the top ranked individual is more likely to eat first, at least within a familiar foraging context.

Critically, dominants were not necessarily more likely to initiate foraging and eat more when larger groups foraged for novel food. In groups of 3 fish, we did not observe differences in likelihood to initiate foraging or number of bites between any of the ranks. While in groups of 4, we still saw some evidence that more dominant individuals took more bites than their subordinates, it was only for the top ranked individual (and not the second ranked individual as observed with familiar food). This indicates that in unfamiliar settings, the heuristics of social roles might fall apart, and dominants no longer take such a strong initiator role as when foraging for familiar food sources (Burns et al., 2012). Surprisingly, we did not find that subordinates predominately take that initiator role either, indicating lack of information drives this pattern (i.e., no individual has a preference to lead) over differences in energetic demands (i.e., that subordinates are eating less food in general and thus showing greater initiative since hungrier). Similarly, studies of other systems have failed to observe differences in approaching novel objects between dominant and subordinates (Amici et al., 2020; Greggor, Jolles, Thornton, & Clayton, 2016).

For the most part, body size did not predict foraging behaviors, indicating that rank more than size affected exploitation of resource. However, size differences were purposefully kept to a minimum when forming groups in this experiment, and larger differences between group

members might reveal stronger sized-based differences (Matthews & Wong, 2015). Moreover, size was a strong predictor of one behavior, that of number of novel food bites taken. This might be due to greater metabolic demands of larger fish leading to a greater frequency of bites or morphological ability to take more bites within the 5 minute trial. Or it might indicate that in novel situations, traits other than previously established dominance ranks might play an important role in competition within a social foraging context. Indeed, neophobia levels may easily shift in many systems, like with seasonal changes in metabolic demand, resource availability, or predation pressure (Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013; Greggor et al., 2016).

In addition to dominance, other factors might drive differences in foraging behaviors between group mates. For example, in a study comparing dominance styles across different species of macaques, Amici et al. (2020) found that centrally located individuals within the group's social network were more likely to approach novel items, but only in less despotic groups. While in this study, rank did not influence differences in neophobia, hierarchy structure was important for both neophobic behavior and food sharing within the group. Furthermore, innate differences in individual behavioral traits, regardless of group composition, may drive differences in leadership and voraciousness (Nagy et al., 2013; Nakayama et al., 2012). This might be most applicable in rapidly shifting groups, where dominance relationships have not solidified. If groups are constantly changing membership, then individual traits, not relationships between individuals, might more reliably drive differences in foraging behavior.

This work adds to our understanding of what might drive variation in consumption of microplastics. While there has been extensive study on interspecific variation in plastic consumption by birds, fish, and sea turtles in the wild and in the lab (Roman, Bell, Wilcox,

Hardesty, & Hindell, 2019; Savoca et al., 2016; Schuyler, Hardesty, Wilcox, & Townsend, 2014; Wilcox, Van Sebille, & Hardesty, 2015), research on intraspecific patterns of plastic ingestion is limited. Some studies indicate that prior experience with plastic (Baird & Hooker, 2000; Coppock et al., 2019) and age-class (Denuncio et al., 2011; Scherer, Brennholt, Reifferscheid, & Wagner, 2017) might drive differences in consumption patterns in some species. Research on lab-reared fish suggests that activity-level and boldness behavior is positively related to plastic ingestion (Nanninga et al., 2021; Nanninga, Scott, & Manica, 2020). While a previous study of mosquitofish indicated that differences between social groups might also drive differences in foraging for plastics (Pollack et al. *in prep*), this work is the first to demonstrate the potential for differences within social groups driven by social relationships.

While our paper explores how variation in how social structures influence responses to environmental change (i.e., novel foods), environmental change also affects social structures in and of itself. For instance, warming temperatures have been linked to changes in patterns aggression and pollution can hinder social communication, likely leading to less stable hierarchies in the short term (Fisher et al., 2021). Increasingly variable environmental conditions might also disrupt dominance hierarchies. For example, groups of three spined stickleback had decreased hierarchy stability when exposed to simulated turbulence and drought in laboratory experiments (Sneddon, Hawkesworth, Braithwaite, & Yerbury, 2006). Furthermore, various environmental changes are often simultaneous, and multiple stressors could have an antagonistic or synergistic effect on aggression patterns and subsequent hierarchy formation (Orr et al., 2020; Wong & Candolin, 2015). Thus, groups are likely experiencing multiple stressors at the same time as they are encountering novel items. If, as suggested, these abiotic stressors destabilize dominance hierarchies, then dominants may not necessarily consistently outcompete

subordinates for foraging. This might lead to a greater shared cost of consuming an evolutionary trap across all group members, instead of concentrating costs at the top of the hierarchy. Future research on the effects of various stressors on social structures, and the subsequent effects of these changes on responses to other aspects of environmental change is therefore needed.

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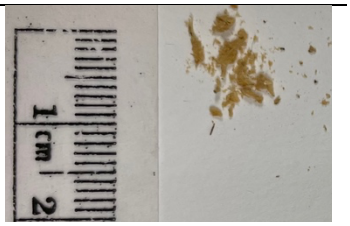
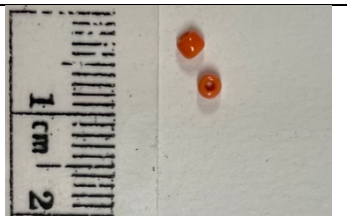
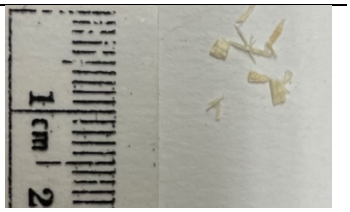
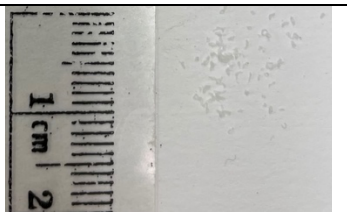
Supporting Information:

Appendix 3A. Novel Foods

Table 3A. Items for novel food assay.

Novel Item	Trial	Source	Approximate Size	Image
Brine Shrimp	6	Omega One Freeze Dried Brine Shrimp	0.1 – 3 mm	
Glass Beads	7	"Seed Beads", manufacturer unknown	1 – 4 mm	
Wood Chips	8	Zoo Med Aspen Snake Bedding	0.5 – 4 mm	
Microplastics (Polyethylene)	9 & 10	XtraCare Oil-Free Foaming Acne Wash Facial Scrub	0.1 – 1 mm	

Appendix 3B. Likelihood to eat novel food first across all group sizes

Table 3.1B. Posterior parameter estimates for model of likelihood to be first to eat novel food across all group sizes as predicted by whether an individual ate familiar food first during that day's trial.

parameter	estimate	2.5%	97.5%
intercept	0.37	-0.79	1.51
first to eat familiar food	0.81	0.39	1.22
group size	-0.48	-0.82	-0.15
trial 6 vs.7	-0.40	-0.92	0.12
trial 6 vs.8	-0.01	-0.52	0.50
trial 6 vs.9	-0.06	-0.58	0.46
trial 6 vs.10	-0.03	-0.55	0.50

Table 3.2B. Median odds ratios for the model of likelihood to be first to eat novel food across all group sizes as predicted by whether an individual ate familiar food first during that day's trial.

Contrast between trials	estimate	2.5%	97.5%
brine vs.biofouled	1.03	0.609	1.73
brine vs.bead	1.49	0.883	2.52
brine vs.pine	1.01	0.608	1.69
brine vs.virgin	1.06	0.633	1.79
bead vs.biofouled	0.692	0.395	1.22
bead vs.pine	0.679	0.398	1.16
bead vs.virgin	0.716	0.404	1.26
pine vs.biofouled	1.02	0.588	1.77
pine vs.virgin	1.05	0.612	1.83
virgin vs.biofouled	0.967	0.551	1.68

Contrasts are calculated from posterior parameter estimate quantile intervals for each trial.

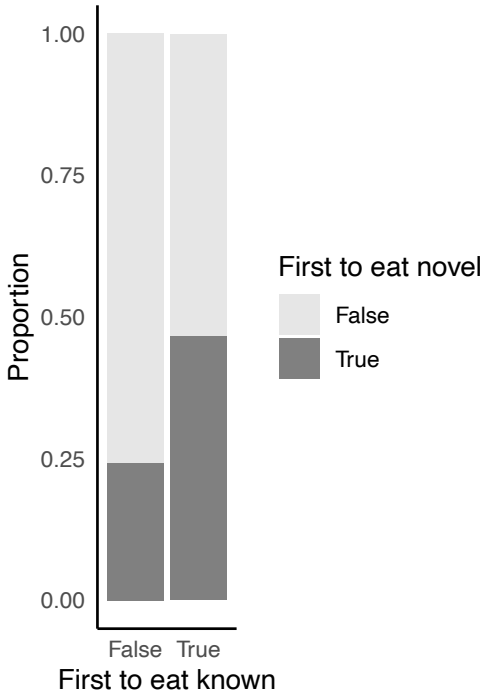


Figure 3B. Proportion of individuals who ate first for both familiar and novel food during the same day's trials.

Appendix 3C. Differences between dominant and subordinates in foraging behaviors

Table 3C. Complete model structure and posterior parameter estimates for models of foraging behavior that assume a despotic dominance structure.

Model Structure	Posterior parameter estimates for fixed effects			
	parameter	estimate	2.5% CI	97.5% CI
Likelihood to eat familiar food first ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID)	intercept	0.40	0.25	2.57
	subordinate vs. dominant	-0.96	-1.32	-0.59
	trial	0.00	-0.04	0.05
	length	0.08	-0.17	0.34
	group size	-0.54	-0.89	-0.20
Likelihood to eat novel food first ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID)	intercept	1.38	0.23	2.54
	subordinate vs. dominant	-0.96	-1.45	-0.47
	trial 6 vs.7	-0.41	-0.93	0.11
	trial 6 vs.8	-0.07	-0.59	0.44
	trial 6 vs.9	-0.11	-0.64	0.41
	trial 6 vs.10	-0.04	-0.56	0.49
	length	-0.11	-0.36	0.15
	group size	-0.49	-0.83	-0.16
Familiar food bites ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID) **zero inflated** ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID)	intercept	1.28	0.81	1.74
	subordinate vs. dominant	-0.28	-0.39	-0.17
	trial	-0.03	-0.04	-0.01
	length	0.01	-0.09	0.10
	group size	-0.01	-0.15	0.14
	zero inflated intercept	0.17	-0.30	0.65
	zero inflated dominant vs. subordinate	4.14	2.08	7.11
	zero inflated trial	0.12	-0.07	0.31
	zero inflated length	-0.49	-1.43	0.33
	zero inflated group size	-1.00	-2.44	0.32
	shape	10.19	7.33	14.45
Novel food bites ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID) **zero inflated** ~ 1 + daily dominance position + length + trial + group size + (1| group / fish ID)	intercept	1.92	1.49	2.34
	subordinate vs. dominant	-0.20	-0.35	-0.06
	trial 6 vs.7	0.37	0.26	0.49
	trial 6 vs.8	0.68	0.58	0.78
	trial 6 vs.9	-0.29	-0.43	-0.16
	trial 6 vs.10	-0.12	-0.23	0.00
	length	0.13	0.04	0.22
	group size	-1.13	-0.25	0.00
	zero inflated intercept	-4.89	-14.07	-1.61
	zero inflated dominant vs. subordinate	1.29	0.58	2.06
	zero inflated trial 6 vs.7	5.38	2.71	14.30
	zero inflated trial 6 vs.8	3.28	0.62	12.32
	zero inflated trial 6 vs.9	3.72	1.02	12.72
	zero inflated trial 6 vs.10	3.30	0.61	12.27
	zero inflated length	0.02	-0.31	0.35
	zero inflated group size	-0.62	-1.20	-0.07

Appendix 3D. Likelihood to eat familiar and novel foods for all ranks

Table 3.1D. Model structure and posterior parameter estimates for all models of familiar bite order.

Model Structure	Posterior parameter estimates for fixed effects			
	parameter	estimate	2.5% CI	97.5% CI
Likelihood to eat familiar food first for group of 2 ~ 1 + daily rank + length + trial + (1| group / fish ID)	intercept	-0.14	-1.23	0.90
	daily rank 1 vs. 2	-0.54	-1.32	0.25
	trial	0.05	-0.05	0.15
	length	-0.04	-0.76	0.67
Likelihood to eat familiar food first for group of 3 ~ 1 + daily rank + length + trial + (1| group / fish ID)	intercept	-0.53	-1.32	0.23
	daily rank 1 vs. 2	-0.27	-0.91	0.37
	daily rank 1 vs. 3	-0.70	-1.35	-0.06
	trial	-0.01	-0.08	0.07
	length	0.08	-0.33	0.49
Likelihood to eat familiar food first for group of 4 ~ 1 + daily rank + length + trial + (1| group / fish ID)	intercept	-0.36	-1.15	0.41
	daily rank 1 vs. 2	-1.03	-0.69	-0.38
	daily rank 1 vs. 3	-1.20	-1.93	-0.46
	daily rank 1 vs. 4	-1.37	-2.04	-0.72
	trial	-0.02	-0.11	0.06
	length	0.17	-0.30	0.65

Table 3.2D. Median odds ratios of contrasts between ranks for each model of likelihood to be first to eat familiar food.

contrast between ranks		estimate	2.5%CI	97.5% CI
Group of 2	1 vs.2	1.71	0.77	3.69
Group of 3	1 vs.2	1.31	0.69	2.47
	1 vs.3	2.02	1.06	3.84
	2 vs.3	1.54	0.84	2.83
Group of 4	1 vs.2	2.79	1.65	4.83
	1 vs.3	3.31	1.82	6.07
	1 vs.4	3.93	2.32	6.79
	2 vs.3	1.19	0.61	2.27
	2 vs.4	1.40	0.77	2.56
	3 vs.4	1.19	0.69	2.03

Contrasts are calculated from posterior parameter estimate quantile intervals for each rank.

Table 3.3D. Model structure and posterior parameter estimates for all models of novel bite order.

Model Structure	**Posterior parameter estimates for fixed effects**			
	parameter	estimate	2.5% CI	97.5% CI
Likelihood to eat novel food first for group of 2 ~ 1 + daily rank + length + trial + (1| group / fish ID)	intercept	0.32	-0.89	1.47
	daily rank 1 vs. 2	-0.59	-1.64	0.53
	trial 6 vs. 7	-0.75	-1.76	0.24
	trial 6 vs. 8	-0.06	-1.03	0.91
	trial 6 vs. 9	-0.06	-1.05	0.92
	trial 6 vs. 10	0.09	-0.90	1.09
	length	-0.37	-1.22	0.44
Likelihood to eat novel food first for group of 3 ~ 1 + daily rank + length + trial + (1| group / fish ID)	intercept	-0.34	-1.19	0.45
	daily rank 1 vs. 2	-0.85	-1.72	0.05
	daily rank 1 vs. 3	-0.67	-1.54	0.25
	trial 6 vs. 7	-0.34	-1.12	0.44
	trial 6 vs. 8	-0.06	-0.86	0.73
	trial 6 vs. 9	-0.14	-0.92	0.64
	trial 6 vs. 10	0.04	-0.72	0.82
	length	0.05	-0.35	0.44
Likelihood to eat novel food first for group of 4 ~ 1 + daily rank + length + trial + (1| group / fish ID)	intercept	-0.75	-1.54	0.00
	daily rank 1 vs. 2	-0.60	-1.43	0.22
	daily rank 1 vs. 3	-0.08	-0.89	0.75
	daily rank 1 vs. 4	-1.17	-2.06	-0.29
	trial 6 vs. 7	-0.20	-0.99	0.56
	trial 6 vs. 8	-0.01	-0.77	0.73
	trial 6 vs. 9	-0.03	-0.86	0.79
	trial 6 vs. 10	-0.14	-0.99	0.68
	length	-0.18	-0.62	0.25

Table 3.4D. Median odds ratios of contrasts between ranks for each model of likelihood to be first to eat novel food

contrast between ranks		**estimate**	**2.5%CI**	**97.5% CI**
Group of 2	1 vs.2	1.85	0.58	5.30
Group of 3	1 vs.2	2.38	1.13	4.81
	1 vs.3	1.98	0.94	3.99
	2 vs.3	0.83	0.41	1.72
Group of 4	1 vs.2	1.82	0.94	3.56
	1 vs.3	1.08	0.55	2.08
	1 vs.4	3.22	1.60	6.57
	2 vs.3	0.60	0.28	1.23
	2 vs.4	1.78	0.81	3.93
	3 vs.4	2.97	1.51	6.03

Contrasts are calculated from posterior parameter estimate quantile intervals for each rank.

Appendix 3E. Number of familiar and novel bites for all ranks

Table 3.1E. Model structure and posterior parameter estimates for all models of familiar food bites.

Model Structure	Posterior parameter estimates for fixed effects			
	parameter	estimate	2.5% CI	97.5% CI
Familiar food bites for group of 2 ~ 1 + daily rank + length + trial + (1| group / fish ID) **zero inflated** ~ 1 + daily rank + length + trial + (1| group / fish ID)	zero inflated intercept	-8.40	-13.95	-4.29
	zero inflated daily rank 1 vs. 2	3.20	0.22	7.17
	zero inflated length	-0.87	-3.35	1.19
	zero inflated trial	0.25	-0.11	0.66
	intercept	1.26	0.81	1.69
	daily rank 1 vs. 2	-0.33	-0.61	-0.06
	trial	-0.02	-0.05	0.02
	length	-0.17	-0.44	0.07
	shape	4.74	3.05	7.27
Familiar food bites for group of 3 ~ 1 + daily rank + length + trial + (1| group / fish ID) **zero inflated** ~ 1 + daily rank + length + trial + (1| group / fish ID)	zero inflated intercept	-13.34	-23.98	-7.44
	zero inflated daily rank 1 vs. 2	7.57	2.39	17.68
	zero inflated daily rank 1 vs. 3	7.37	2.12	17.54
	zero inflated length	-0.10	-1.15	0.80
	zero inflated trial	0.37	0.13	0.69
	intercept	1.20	0.97	1.43
	daily rank 1 vs. 2	-0.30	-0.49	-0.11
	daily rank 1 vs. 3	-0.28	-0.47	-0.08
	trial	-0.03	-0.05	-0.01
	length	-0.01	-0.13	0.11
	shape	38.43	10.64	139.71
Familiar food bites for group of 4 ~ 1 + daily rank + length + trial + (1| group / fish ID) **zero inflated** ~ 1 + daily rank + length + trial + (1| group / fish ID)	zero inflated intercept	-10.22	-25.55	1.06
	zero inflated daily rank 1 vs. 2	-0.19	-20.07	17.77
	zero inflated daily rank 1 vs. 3	10.36	1.48	32.22
	zero inflated daily rank 1 vs. 4	8.97	0.51	28.61
	zero inflated length	0.96	-1.18	3.98
	zero inflated trial	-0.78	-1.68	-0.30
	intercept	1.41	1.16	1.66
	daily rank 1 vs. 2	-0.15	-0.33	0.04
	daily rank 1 vs. 3	-0.32	-0.54	-0.10
	daily rank 1 vs. 4	-0.40	-0.61	-0.20
	trial	-0.05	-0.07	-0.03
	length	0.13	-0.02	0.28
	shape	15.60	7.43	36.50

Table 3.2E. Median odds ratios of contrasts between ranks for each model of familiar food bites.

contrast between ranks		estimate	2.5%CI	97.5% CI
Group of 2	1 vs.2	1.39	1.06	1.83
Group of 3	1 vs.2	1.35	1.11	1.63
	1 vs.3	1.32	1.08	1.61
	2 vs.3	0.98	0.81	1.19
Group of 4	1 vs.2	1.16	0.95	1.38
	1 vs.3	1.38	1.10	1.71
	1 vs.4	1.50	1.20	1.80
	2 vs.3	1.19	0.95	1.47
	2 vs.4	1.29	1.05	1.59
	3 vs.4	1.08	0.89	1.31

Contrasts are calculated from posterior parameter estimate quantile intervals for each rank.

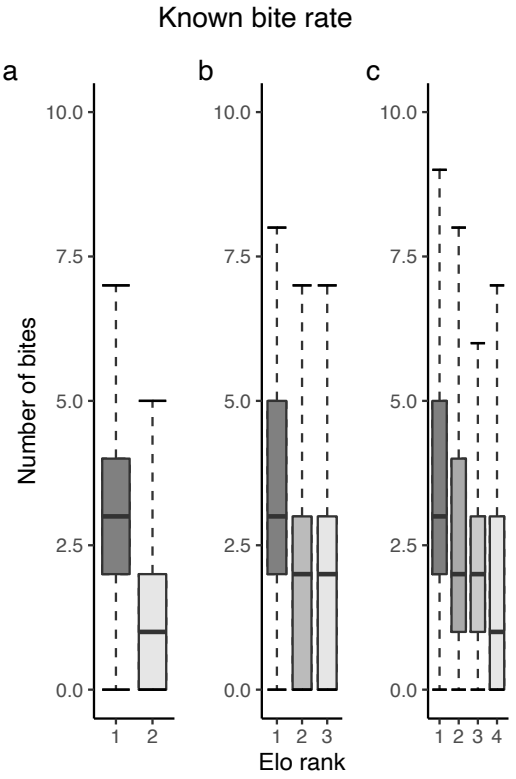


Figure 3.1E. Raw count data for bites of familiar food for (a) groups of 2, (b) groups of 3, and (c) groups of 4. Box plots include the mean latency and interquartile range (IQR) with whiskers extenting to +/1 1.5 IQR. Outliers have been removed from these plots to improve visualization.

Table 3.3E. Model structure and posterior parameter estimates for models of novel food bites.

Model Structure	Posterior parameter estimates for fixed effects			
	parameter	estimate	2.5% CI	97.5% CI
Novel food bites for group of 2 ~ 1 + daily rank + length + trial + (1| group / fish ID) **zero inflated** ~ 1 + daily rank + length + trial + (1| group / fish ID)	zero inflated intercept	-8.45	-21.85	-3.39
	zero inflated daily rank 1 vs. 2	0.99	-1.23	2.90
	zero inflated length	-0.49	-2.04	0.57
	zero inflated trial 6 vs. 7	8.48	3.23	22.10
	zero inflated trial 6 vs. 8	4.08	-1.20	17.22
	zero inflated trial 6 vs. 9	6.05	1.22	19.41
	zero inflated trial 6 vs. 10	5.86	1.02	19.07
	intercept	1.85	1.52	2.19
	daily rank 1 vs. 2	-0.31	-0.61	-0.02
	trial 6 vs. 7	0.94	0.73	1.15
	trial 6 vs. 8	-0.10	-0.32	0.11
	trial 6 vs. 9	-0.22	-0.45	0.00
	trial 6 vs. 10	-0.11	-0.33	0.12
	length	0.02	-0.23	0.26
Novel food bites for group of 3 ~ 1 + daily rank + length + trial + (1| group / fish ID) **zero inflated** ~ 1 + daily rank + length + trial + (1| group / fish ID)	zero inflated intercept	-12.09	-26.65	-5.43
	zero inflated daily rank 1 vs. 2	3.12	0.67	8.68
	zero inflated daily rank 1 vs. 3	2.88	0.47	8.52
	zero inflated length	-0.09	-0.84	0.57
	zero inflated trial 6 vs. 7	8.80	3.00	22.59
	zero inflated trial 6 vs. 8	6.66	0.96	20.20
	zero inflated trial 6 vs. 9	6.58	0.52	20.11
	zero inflated trial 6 vs. 10	5.50	-0.54	19.06
	intercept	1.36	1.08	1.62
	daily rank 1 vs. 2	-0.07	0.14	-0.34
	daily rank 1 vs. 3	0.15	-0.17	0.49
	trial 6 vs. 7	0.01	-0.20	0.20
	trial 6 vs. 8	0.85	0.69	1.00
	trial 6 vs. 9	-0.50	-0.72	-0.28
	trial 6 vs. 10	-0.11	-0.30	0.07
	length	0.17	0.03	0.31
Novel food bites for group of 4 ~ 1 + daily rank + length + trial + (1| group / fish ID) **zero inflated** ~ 1 + daily rank + length + trial + (1| group / fish ID)	zero inflated intercept	-10.02	-22.92	-3.83
	zero inflated daily rank 1 vs. 2	0.31	-1.62	2.09
	zero inflated daily rank 1 vs. 3	1.86	0.06	3.95
	zero inflated daily rank 1 vs. 4	1.55	-0.24	3.58
	zero inflated length	0.86	-0.05	2.00
	zero inflated trial 6 vs. 7	7.98	2.22	20.96
	zero inflated trial 6 vs. 8	5.74	0.12	18.55
	zero inflated trial 6 vs. 9	5.63	-0.22	18.61
	zero inflated trial 6 vs. 10	5.48	-0.42	18.49
	intercept	1.36	1.07	1.64
	daily rank 1 vs. 2	-0.28	-0.52	-0.03
	daily rank 1 vs. 3	-0.18	-0.48	0.12
	daily rank 1 vs. 4	-0.33	-0.62	-0.03
	trial 6 vs. 7	0.33	0.14	0.52
	trial 6 vs. 8	0.93	0.77	1.09
	trial 6 vs. 9	-0.14	-0.35	0.08
	trial 6 vs. 10	-0.15	-0.37	0.07
	length	0.16	-0.02	0.34

Table 3.4E. Median odds ratios of contrasts between ranks for each model of novel food bites.

contrast between ranks		estimate	2.5%CI	97.5% CI
Group of 2	1 vs.2	1.37	1.02	1.85
Group of 3	1 vs.2	1.07	0.81	1.41
	1 vs.3	0.86	0.62	1.18
	2 vs.3	0.81	0.60	1.07
Group of 4	1 vs.2	1.32	1.07	1.61
	1 vs.3	1.19	0.94	1.51
	1 vs.4	1.38	1.09	1.75
	2 vs.3	0.91	0.73	1.13
	2 vs.4	1.05	0.84	1.31
	3 vs.4	1.16	0.97	1.37

Contrasts are calculated from posterior parameter estimate quantile intervals for each rank.

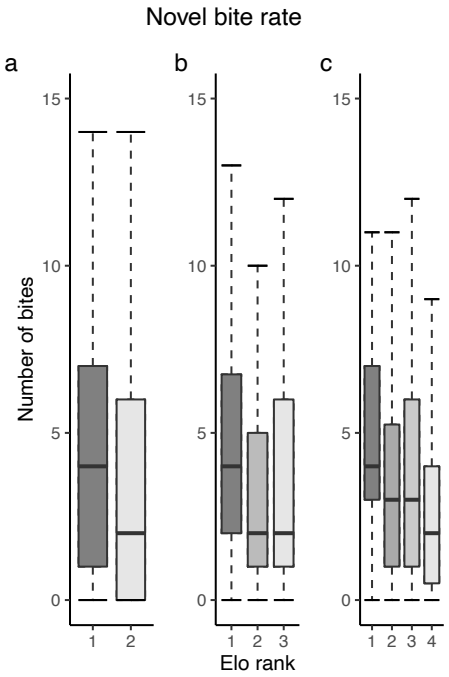


Figure 3.2E. Raw count data for bites of novel food for (a) groups of 2, (b) groups of 3, and (c) groups of 4. Box plots include the mean latency and interquartile range (IQR) with whiskers extenting to +/1 1.5 IQR. Outliers have been removed from these plots to improve visualization.

Appendix 3F. Differences between ranks in foraging for specific novel foods

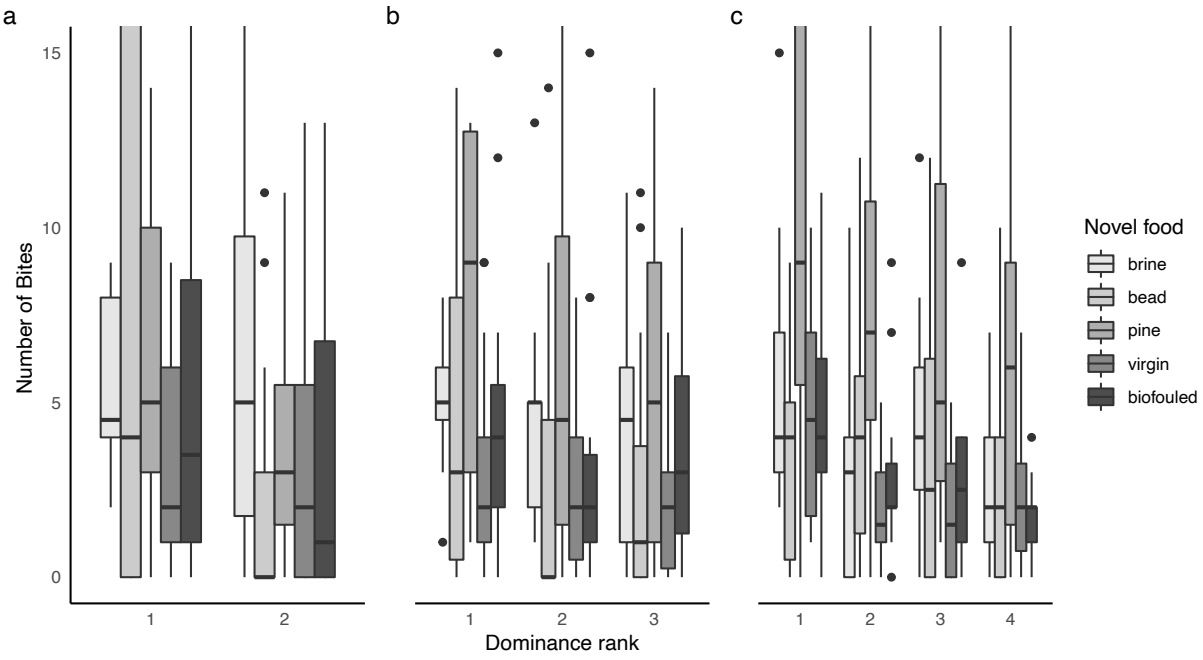


Figure 3F. Raw count data for bites of novel food for (a) groups of 2, (b) groups of 3, and (c) groups of 4. Box plots include the mean latency and interquartile range (IQR) with whiskers extenting to +/1 1.5 IQR. Plots have been zoomed in on the y-axis to improve visualization of differences, not all outliers are shown. Plots have been zoomed in on the y-axis to improve visualization of differences, not all outliers are shown.

Table 3.1F. Posterior parameter estimates for all models of number of bites for each novel food type organized by group size.

		Number of novel food bites								
		brine shrimp			glass bead			pine chips		
	parameter	estimate	2.5%	97.5%	estimate	2.5%	97.5%	estimate	2.5%	97.5%
Group of 2	intercept zero inflated	1.7	1.2	2.1	2.1	0.3	3.3	1.7	1.2	2.2
	intercept	-6.1	-13.7	-1.8	-3	-12.6	1.9	-5	-12.1	-1.2
	daily rank 1 vs. 2 zero inflated	0	-0.5	0.5	-1.3	-3.1	0.2	-0.3	-0.9	0.4
	rank 1 vs. 2	3	-2.1	10.9	4.1	-4.3	19.8	2.5	-2.4	9.9
Group of 3	intercept zero inflated	1.6	1.3	1.8	1.3	0.5	1.9	2	1.4	2.6
	intercept	-7.2	-16.3	-2.7	-6.8	-24.9	-0.4	-7.5	-16.4	-2.7
	daily rank 1 vs. 2	-0.2	-0.6	0.2	-0.2	-0.8	0.4	-0.6	-1.2	0
	daily rank 1 vs. 3 zero inflated	-0.2	-0.5	0.2	-0.3	-0.8	0.2	-0.4	-1	0.1
	rank 1 vs. 2 zero inflated	0.1	-9.9	10.3	11	0.5	51.5	2.6	-7	12.3
	rank 1 vs. 3	3.1	-4.5	12.7	4	-4.7	22	3.5	-4.7	13.1
Group of 4	intercept zero inflated	1.6	1.3	1.9	1.3	0.8	1.8	2.3	1.8	2.8
	intercept	-9.6	-22.6	-2.8	-9.7	-33.4	0.8	-5.9	-16.5	-1.5
	daily rank 1 vs. 2	-0.2	-0.7	0.2	0.2	-0.4	0.9	-0.2	-0.9	0.4
	daily rank 1 vs. 3	0	-0.4	0.4	0.5	-0.2	1.2	-0.6	-1.2	0
	daily rank 1 vs. 4 zero inflated	-0.5	-1	-0.1	0	-0.7	0.7	-0.6	-1.2	0
	rank 1 vs. 2 zero inflated	8.4	1.1	21.7	0.6	-12.2	25.3	2.6	-4.4	13.7
	rank 1 vs. 3 zero inflated	5.9	-2.4	19.2	20.1	-0.3	67.7	-2.6	-15.1	9.6
	rank 1 vs. 4	6.1	-1.9	19.5	9.4	-3.9	40.5	2.7	-4.1	13.8

		Number of novel food bites					
		virgin microplastic			biofouled microplastic		
	parameter	estimate	2.5%	97.5%	estimate	2.5%	97.5%
Group of 2	intercept	1.1	0.3	1.7	1.4	0.4	2.2
	zero inflated intercept	-5.7	-13.7	-1.2	-5.3	-13.1	-0.9
	daily rank 1 vs. 2	0.6	-0.3	1.5	-0.3	-1.6	0.9
	zero inflated rank 1 vs. 2	5.5	0.1	15.2	3.8	-2.5	13
Group of 3	intercept	1	0.5	1.5	1.3	0.8	1.7
	zero inflated intercept	-4	-11.6	-0.8	-6.7	-15.3	-2.3
	daily rank 1 vs. 2	-0.3	-0.8	0.4	-0.5	-1	0.1
	daily rank 1 vs. 3	-0.4	-1	0.3	-0.2	-0.7	0.3
	zero inflated rank 1 vs. 2	-0.7	-9.9	7.8	1.9	-8.1	11.5
	zero inflated rank 1 vs. 3	0.1	-7.8	8.6	1.4	-7.4	10.6
Group of 4	intercept	1.5	0.9	2	1.4	0.8	1.9
	zero inflated intercept	-8.2	-20.6	-2.3	-0.4	-0.9	0
	daily rank 1 vs. 2	-1	-1.8	-0.2	-0.5	-1	0
	daily rank 1 vs. 3	-0.8	-1.7	0	-1	-1.5	-0.4
	daily rank 1 vs. 4	-0.8	-1.5	0	0.6	0.3	1.3
	zero inflated rank 1 vs. 2	1.8	-10.8	16.1	0.2	0	0.6
	zero inflated rank 1 vs. 3	4.7	-7.1	19	0.1	-0.6	0.8
	zero inflated rank 1 vs. 4	3.5	-9.4	17.9	-0.1	-0.7	0.6

Table 3.2F. Posterior parameter estimates for all models of likelihood to eat first for each novel food type organized by group size.

		Likelihood to eat novel food first								
		brine shrimp			glass bead			wood chips		
	parameter	estimate	2.5%	97.5%	estimate	2.5%	97.5%	estimate	2.5%	97.5%
Group of 2	intercept	0.2	-1.7	2	-0.3	-1.9	1.2	0.4	-1.5	2.0
	daily rank 1 vs. 2	-0.3	-2.0	1.5	-0.9	-2.4	0.8	-0.9	-2.5	1.0
Group of 3	intercept	-0.7	-2.2	0.5	-1.3	-2.8	-0.1	0.1	-1.1	1.1
	daily rank 1 vs. 2	-0.3	-1.8	1.4	-0.3	-1.8	1.2	-1.4	-2.6	0.0
	daily rank 1 vs. 3	-0.7	-2.2	0.9	0.0	-1.5	1.5	-1.5	-2.8	-0.2
Group of 4	intercept	-1.7	-3	-0.6	-1.8	-3.1	-0.8	-1.1	-2.6	0.1
	daily rank 1 vs. 2	0.0	-1.5	1.4	0.5	-1.0	1.9	-0.4	-1.8	1.2
	daily rank 1 vs. 3	1.1	-0.3	2.5	1.1	-0.2	2.5	-0.5	-1.9	1.0
	daily rank 1 vs. 4	0.1	-1.3	1.5	-0.4	-1.9	1.0	-0.7	-2.1	0.8

		Likelihood to eat novel food first					
		virgin microplastic			biofouled microplastic		
	parameter	estimate	2.5%	97.5%	mean	2.5%	97.5%
Group of 2	intercept	0.2	-1.6	1.9	0.3	-1.6	2.1
	daily rank 1 vs. 2	-0.5	-2.3	1.3	-0.6	-2.3	1.3
Group of 3	intercept	-1	-2.6	0.3	-0.5	-2	0.6
	daily rank 1 vs. 2	-0.1	-1.6	1.5	-1.3	-2.7	0.2
	daily rank 1 vs. 3	-0.3	-1.8	1.3	-0.2	-1.5	1.2
Group of 4	intercept	-0.6	-1.9	0.5	-1	-2.5	0.2
	daily rank 1 vs. 2	-1.1	-2.5	0.4	-0.5	-2	1.1
	daily rank 1 vs. 3	-0.4	-1.8	1	-0.5	-1.9	1.1
	daily rank 1 vs. 4	-1.4	-2.9	0.1	-0.8	-2.4	0.8

Table 3.3F. Median odds ratios of contrasts between ranks for each model of likelihood to eat novel food first, broken down by novel food type.

		Brine shrimp			Glass beads			Wood chips		
contrast between ranks		estimate	2.5%	97.5%	estimate	2.5%	97.5%	estimate	2.5%	97.5%
Group of 2	1 vs.2	1.33	0.22	7.3	2.4	0.44	11.3	2.44	0.38	12.2
Group of 3	1 vs.2	1.3	0.26	5.98	1.39	0.3	6.01	3.93	0.99	13.8
	1 vs.3	1.99	0.39	8.67	1.04	0.23	4.37	4.71	1.25	16.6
	2 vs.3	1.5	0.21	10.9	0.74	0.12	4.57	1.2	0.26	5.86
Group of 4	1 vs.2	0.97	0.24	4.46	0.61	0.15	2.61	1.45	0.31	6.19
	1 vs.3	0.31	0.08	1.37	0.32	0.09	1.24	1.66	0.35	6.9
	1 vs.4	0.89	0.23	3.57	1.47	0.36	6.4	1.99	0.44	8.17
	2 vs.3	0.33	0.05	2.04	0.52	0.09	2.73	1.14	0.17	7.72
	2 vs.4	0.92	0.15	5.15	2.4	0.39	14	1.38	0.2	9.23
	3 vs.4	2.81	0.5	15.7	4.61	0.88	25.5	1.2	0.19	7.47

		Virgin microplastics			Biofouled microplastics		
contrast between ranks		estimate	2.5%	97.5%	estimate	2.5%	97.5%
Group of 2	1 vs.2	1.76	0.28	9.65	1.82	0.27	9.72
Group of 3	1 vs.2	1.07	0.22	5.04	3.74	0.8	15.4
	1 vs.3	1.31	0.28	5.84	1.17	0.29	4.44
	2 vs.3	1.22	0.16	9.09	0.32	0.05	1.85
Group of 4	1 vs.2	2.85	0.65	12.7	1.61	0.34	7.37
	1 vs.3	1.5	0.35	5.87	1.6	0.35	6.96
	1 vs.4	4.18	0.92	18.6	2.29	0.47	10.5
	2 vs.3	0.52	0.08	3.2	0.99	0.14	6.68
	2 vs.4	1.45	0.22	9.56	1.43	0.2	10.3
	3 vs.4	2.81	0.43	18.3	1.44	0.2	9.93

Contrasts are calculated from posterior parameter estimate quantile intervals for each rank.