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Animal behaviour

Rational choice of social group size in mosquitofish

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Choice of social group can affect the likelihood of survivorship and reproduction for social species. By joining larger social groups—shoals—small freshwater fish like the mosquitofish *Gambusia affinis* can reduce predation risk and forage more efficiently. We tested shoal choice in mosquitofish to determine whether such choices are economically rational, i.e. consistent and optimal. Although many studies of decision-making assume rational choice, irrational decision-making is common and occurs across contexts. We tested rationality of shoaling decisions by testing the constant ratio rule, which states that the relative preference for two options should not change in the presence of a third option. Female mosquitofish upheld this rule when tested for shoal preference based on group size. Our results contrast with other studies showing violations of the constant ratio rule in foraging and mate choice decision-making contexts. These results suggest that decisions that immediately influence survivorship or decision-making along a single dimension may favour rational decision-making.

1. Introduction

An animal's choice of social group can affect its likelihood of survivorship and reproduction. Choosing the wrong social group can mean exposing yourself to greater risk of predation [1,2], using more energy to move through the environment [3] or taking longer to forage [4]. Behaviourists typically assume that these choices are economically rational or optimal, meaning that choices are consistent and options can be mapped onto some univariate scale (e.g. utility in economics), just as numbers can be mapped to the number line [5–7]. Rationality is a key assumption in expected utility theory in economics, and as Richard Thaler explains, 'expected utility is the right way to make decisions' [8, p. 29]. Do animals choose social groups in 'the right way'?

While rational decision-making processes have been investigated in the context of mate choice [9–12] and foraging [6,13,14] decisions, determining whether animals make rational choices in the context of an anti-predatory response has not yet been investigated. In order to understand whether fish choose social groups in a rational and thus optimal way, we tested the constant ratio rule in the western mosquitofish *Gambusia affinis*. The constant ratio rule mandates that a rational chooser's relative preferences for two options does not change in the presence of a third option (sometimes referred to as a decoy), and is often studied in the context of the decoy effect [7,15]. Freshwater fish are a common model for studying social group choice as they form aggregations called shoals. Shoal choice can be easily studied in the laboratory and laboratory findings often mirror findings from the wild [16]. Fish near-universally prefer shoals with more members as joining a larger group lowers predation by a variety of mechanisms, but it also comes at some cost, like increased competition for food [2]. We first test female mosquitofish preference for a shoal of four fish when paired with a shoal of two fish. We then ask whether their relative preference for the larger shoal is altered in the presence of a third shoal.

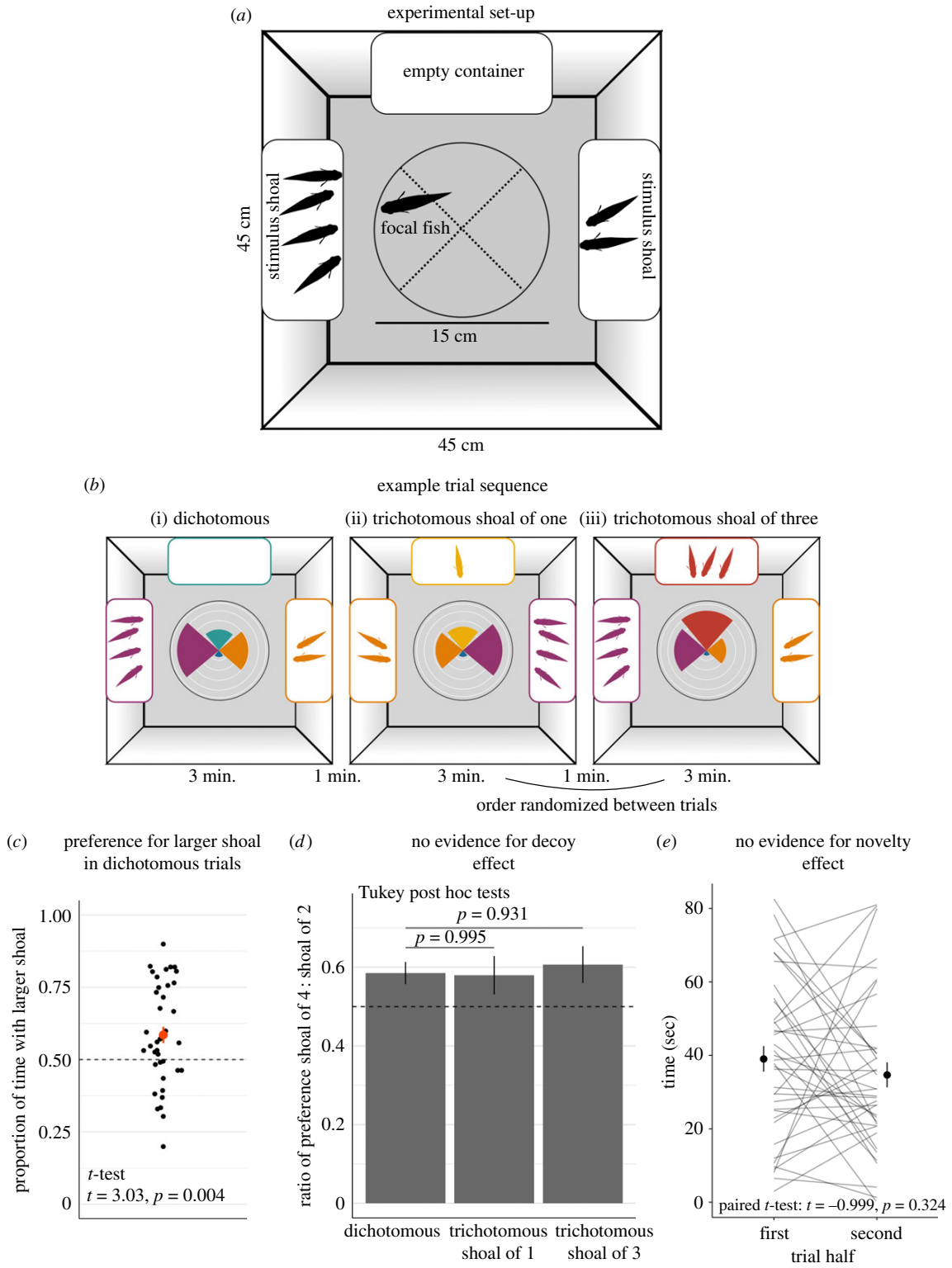

Figure 1. (*a*) Schematic of experimental tank with positions of shoals in the dichotomous trials. (*b*) Example trial sequence. Plots in the middle of each tank show the average amount of time spent in each tank region. (*c*) Preference for the larger shoal in the dichotomous choice trials; individual data are jittered with mean ± standard error in red. (*d*) Ratio of preferences for the shoal of 4 compared to the shoal of 2 in each trial. Fences are standard errors. (*e*) Time spent with the shoal of 3 in the first and second half of the dichotomous choice trial. Lines show individual data points; means ± standard error are given by the points and fences. (Online version in colour.)

2. Methods

The full methods are given in the electronic supplementary material. Briefly, female *G. affinis* were collected from mixed species pools (including the predator *Lepomis macrochirus*) at Brackenridge Field Laboratory and housed according to IACUC AUP 2016–00246 at the University of Texas at Austin. Each of the $n = 39$ focal fish was tested in three conditions: a dichotomous choice between shoals of two and four fish, then two trichotomous choices where a shoal of one or three was added (figure 1*a*,*b*). Each choice lasted 3 min. Mosquitofish have been shown to discriminate between shoals of four, three, two and one [17]. Focal

fish were confined to a circular glass cylinder as in [18], which results in fast, repeatable shoaling preferences. We recorded the fish's movement from above with a webcam and tracked the fish using tracking software [19]. We defined four zones in the circular tank and recorded the amount of time the fish spent in each of these zones.

We first ensured the fish showed a population-level preference for the larger shoal in the binary trials. Our metric of preference is always the proportion of time the fish spent in the zone adjacent to the shoal of four relative to the total time spent near the shoal of four and two. We used a *t*-test to test whether this proportion differed from chance. Additional control tests were done to ensure preferences did not decay over the course of the trial and that the stimulus shoal did not affect preferences (see the electronic supplementary material). To test the constant ratio rule, we calculated the preference for the shoal of four compared to the shoal of two, excluding time spent with the third shoal, because we were only interested in changes in relative preference between the initial two options (as in [10]). We used Tukey post hoc tests from a linear mixed model to determine whether this ratio changed between the dichotomous and trichotomous trials. Preference for the shoal of four over the shoal of two should be unchanged if fish are choosing rationally. Because we found that individuals spent similar amounts of time with the shoals of three and four fish, we tested for a novelty effect by comparing the amount of time fish spent with the shoal of three in the two halves of the trial with a paired *t*-test. All statistics and analyses were done in R [20].

3. Results

We first tested female mosquitofish preference for a shoal of four when paired with a shoal of two in a dichotomous test (figure 1*a*,*b*(i)). As expected, there was a statistically significant preference for the larger shoal (figure 1*c*, *t*-test, $t_{38} = 3.03$, $p = 0.004$; for all tests, $n = 39$). The average preference for the larger shoal was 0.59, similar to previous studies of shoaling preferences in a congeneric mosquitofish (0.62; [17]). We next tested whether this relative preference could be altered by adding a third shoal to the tank. Neither a shoal of one (figure 1*b*(ii)) nor a shoal of three (figure 1*b*(iii)) significantly changed the relative preference for the larger shoal in the original two versus four comparison (figure 1*d*; Tukey post hoc tests; $z = -0.092$, $p = 0.995$ and $z = 0.359$, $p = 0.931$, respectively), suggesting that fish choose shoals rationally.

Figure 1*b* shows the average proportion of time fish spent in each of the four zones of the tank. When presented with a third shoal of three fish, focal fish spent equivalent amounts of time with three- and four-member shoals (average difference: 13.3 s, $t = 1.2821$, $p = 0.208$). To test whether this was potentially owing to the novelty of a new shoal, we compared the amount of time focal individuals spent near the shoal of three in the first and second halves of this trial. The amount of time did not approach statistical significance (figure 1*e*; paired *t*-test, $t = -0.999$, $p = 0.324$), providing little evidence for a novelty effect.

4. Discussion

Although choice of social groups can have numerous consequences, group choice has never before been studied through the lens of rationality. Here, we tested rational decision-making in a small freshwater fish. We found that female mosquitofish upheld the constant ratio rule, a hallmark of rational decision-making, suggesting they are able to make consistent, optimal decisions in terms of selecting a shoal based on group size.

We found that mosquitofish females maintained the same relative preference for a large shoal compared with a smaller shoal, independently of the presence of a third shoal. Evidence for violating the constant ratio rule (in the form of the decoy effect) is widespread and often occurs in mate choice and foraging contexts (summarized in [21]). For example, nearly all tests of the constant ratio rule in a mate choice context have found violations of rationality [9–12], while evidence is more mixed for foraging decisions [6,13,21,22]. Why did the fish in our experiment obey rational expectations?

One possibility is that rational decision-making is easier when options vary along a single dimension. The options available to the focal individuals in our experiment only differed along a single dimension—number of fish. Notably, the constant ratio rule is usually tested in the context of the decoy effect, where options differ in two dimensions [23]. Bateson *et al*. [6], for example, manipulated the amount and concentration of nectar available to hummingbirds in artificial flowers. They found that the presence of a third option (the decoy) changed the relative preference for the initial two options, violating rational expectations. In a subsequent experiment, Morgan *et al*. [14] manipulated the flowers so that they varied only along a single dimension (e.g. flowers only varied in nectar volume). Under these conditions, hummingbirds adhered to the constant ratio rule in some (but not all) cases, suggesting that reducing the dimensionality of the options can increase the probability of rational decision-making.

A second possibility is that predation pressures are stronger than those associated with mate choice or foraging. We focused on a decision task that may have fatal consequences if an error occurs, as shoal group size affects survivorship [1]. Other contexts, like mate choice or foraging, clearly affect survivorship and fecundity but are not necessarily life or death decisions, as shoal choice can be. While it is an intriguing idea that the type of decision affects the decision rules animals use to choose, we are unaware of any studies that test rationality of decision-making across contexts in a single species.

High levels of predation have been associated with changes in male ornamentation [24], male mating tactics [25] and body shape [26] in poeciliid fishes. Shoaling tendencies have also been shown to be influenced by predation pressures [27]. Is it possible that predation pressure shaped rational responses in this species? A future test of this hypothesis would require testing rational decision-making tendencies for shoaling decisions across populations that vary in predation intensity.

We found that the fish in our experiment showed no statistically significant preference for a shoal of four fish compared with a shoal of three. We showed that this lack of preference for the larger shoal was unlikely owing to a novelty effect, though the short assays we used here may be too brief to show clear evidence for a novelty effect. It is possible that the fish in this experiment were unable to detect a difference in size between these two shoals, in contrast to a study that used *G. affinis*' sister species *Gambusia holbrooki* [17]. This would suggest that perceptual constraints should be considered when studying optimality of decision-making and that perceptual constraints can impose limits on the optimality of choice. The lack of a strong preference for the shoal of four in this experiment suggests that more general tests of rationality,

like regularity [7], might show some violation in this species. More generally, our understanding of the basic choice rules that animals use to choose among options might be improved if we probe rationality in different ways for the same choice.

Here, we studied how mosquitofish choose social groups and showed that they were rational in their choice of groups, in contrast with studies of rationality in other contexts. Future studies should aim to understand how the type of decision and the attributes of the options available to the chooser affect whether choice is rational. Choosing your social group can be a life or death decision, and in mosquitofish, it appears that selection has optimized mosquitofish to make rational decisions.

Ethics. All experiments were conducted in accordance with IACUC AUP 2016-00246.

Data accessibility. Data and R code are available as electronic supplementary material.

Authors' contributions. L.R. and M.E.C. designed the experiment. L.R. conducted the experiment, analysed the data and wrote the manuscript with contributions from M.E.C. Both authors approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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