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Four's a crowd: social preferences for larger groups in golden mantella (*Mantella aurantiaca*) tadpoles

Daniel Wright¹ · Jade Newton-Youens¹ · Joachim G. Frommen¹

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Abstract

Group living results in various benefits and costs, which often depend on group size and ontogenetic state of the individual. Therefore, certain group sizes are favourable over others, often depending on individual age or intrinsic state. Under natural conditions many amphibians can be found in aggregations, especially during the larval stage. Yet, whether these aggregations are the result of active social preferences or are driven by environmental factors has only been tested in a limited number of taxa. This study explores social preferences and group size discrimination in golden mantella (*Mantella aurantiaca*) tadpoles. We gave tadpoles the choice between different numbers of conspecifics using a two-choice design. To test for general social tendency, tadpoles could either join a group of three or remain solitary (3 vs. 0). To test for group size preferences, we tested tadpoles in two different ratios: 2 vs. 1 and 4 vs. 2 conspecifics. We repeated the trials weekly until metamorphosis to determine potential shifts in preference through ontogeny. Tadpoles preferred being with a group over being alone, and the strength of this preference declined with increasing age. Furthermore, tadpoles preferred to be close to the larger of two groups. This preference was stronger in the 2 vs. 1 treatment. *Mantella aurantiaca* tadpoles, therefore, show clear social tendencies and possess the ability to spontaneously discriminate between group sizes. The lower preference at higher group sizes might indicate cognitive limitations or lower benefits of choosing the larger of two groups when overall group size is high. These findings are one of the few showing social preferences depending on group size in tadpoles and contribute to our understanding of social behaviour in amphibians in general.

Keywords Shoaling decisions · Aggregation · Activity · Amphibian · Anuran larvae · Ontogenetic shift

✉ Joachim G. Frommen
j.frommen@mmu.ac.uk

¹ Ecology and Environment Research Centre, Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK

Introduction

Group living has evolved independently in many animal species as a result of a range of selection pressures (Ward and Webster 2016). It offers a variety of benefits, such as increased vigilance and predator detection (Roberts 1996; Michelena and Deneubourg 2011), dilution of predation risk (Wrona and Dixon 1991; Lehtonen and Jaatinen 2016) and increased foraging efficiency (Kurvers et al. 2010). However, there are also associated costs, such as intra-group competition (Krause and Ruxton 2002; Shrader et al. 2007; Sheppard et al. 2018), increased conspicuousness (Botham and Krause 2005; Ioannou et al. 2009), and an increase in pathogen susceptibility (Côté and Poulin 1995; but see Ezenwa et al. 2016 for an argument how group living may lead to increased pathogen resistance). These benefits and costs are often dependant on group size (Ward and Webster 2016). They might furthermore change through ontogeny, especially when they are linked to body size, leading to ontogenetic shifts in social preferences (Ward and Webster 2016). For example, some fish species group when they are young, but live solitary as they age and increase in size (Ryer and Olla 1991; Macpherson 1998). This may be due to an increase in intraspecific competition at larger sizes (Despland and Hamzeh 2004). Alternatively, the opposite has also been observed, where initially solitary animals become gregarious as they grow to reduce predation risk (Fobert et al. 2020).

Social aggregations have been described in several amphibians, especially during the larval stage. Here, environmental factors like food distribution (Sontag et al. 2006), time of day (Beiswenger 1977; Branch 1983) or weather (Espinoza and Quinteros 2008), and intrinsic factors like body size (Leu et al. 2013; Hase and Kutsukake 2019) or kinship (Blaustein and O'Hara 1986; Blaustein and Waldman 1992; Pizzatto et al. 2016) have been shown to mediate group formation. Thus far, these studies focus on a limited range of taxa, with a strong focus on Ranidae (e.g., Blaustein and O'Hara 1987; Balestrieri et al. 2019) and Bufonidae (e.g., Beiswenger 1977; Breden et al. 1982; Balestrieri et al. 2019).

With a multitude of factors affecting group size and social preference, individuals need to be able to assess the costs and benefits of joining or dispersing from a group. The ability to discriminate between group sizes can be invaluable to this. Several amphibian species possess the ability to discriminate between different numerosity, especially when foraging. Green-and-black poison dart frogs (*Dendrobates auratus*), European fire-bellied toads (*Bombina orientalis*) and red-backed salamanders (*Plethodon cinereus*), for example, prefer the larger of two food quantities, with some species-dependent differences in how derived these preferences are (Uller et al. 2003; Stancher et al. 2015; Khatiwada and Burmeister 2022). Studies testing for numerosity discrimination in amphibians in a social context are scarce so far (but see Balestrieri et al. 2019).

Ontogenetic shifts have been described for various tadpole behaviours including anti-predator responses (Gazzola et al. 2017) and activity. While spiny toad (*Bufo spinosus*), American toad (*Bufo americanus*), and clawed frog (*Xenopus leavis*) tadpoles show an increase in activity with increasing age (Golden et al. 2000; Smith et al. 2008; Cheron et al. 2021), activity decreases with age in green frog (*Rana clamitans*) and common toad (*Bufo bufo*) tadpoles (Smith et al. 2008; Kurali et al. 2018). These differences in direction might be explained, for example, as outcomes of different anti-predator strategies. Comparable ontogenetic changes of social preferences have been described for only a few amphibians, with Japanese mountain brown frogs (*Rana ornativentris*) tadpoles preferring to group with

smaller individuals with increasing age (Hase and Kutsukake 2019). Other amphibian larvae preferentially associate with individuals of similar size, including Southern leopard frogs (*Rana utricularia*; Alford and Crump 1982), Woodhouse's toads (*Anaxyrus woodhousii*; Breden et al. 1982), and white-lined leaf frogs (*Phyllomedusa vaillanti*; Branch 1983). This has been suggested to be a result of size-dependent habitat preference and swimming capabilities.

In the present study we aimed at broadening our understanding of larval anuran social preferences by testing a member of the *Mantella* radiation, endemic to Madagascar. We used tadpoles of the endangered golden mantella (*Mantella aurantiaca*) as model organisms (IUCN SSC Amphibian Specialist Group; 2020). The golden mantella is a small-bodied terrestrial species that only occurs in fragmented, humid forests close to the town of Moramanga in east-central Madagascar (Randrianelona et al. 2010). Adults can be found sheltering closely together during cool winter months (Edmonds et al. 2020), implying some kind of social preferences. Breeding occurs nearby seasonal, ephemeral ponds, with females laying egg-masses of on average 60–80 eggs on land (Edmonds et al. 2015). After approximately seven days the tadpoles hatch and are washed into the ponds, either due to their own movement, or aided by heavy rains. Tadpoles take approximately 6–8 weeks to metamorphose, at which time the froglets assume the terrestrial habits of the adults (Edmonds et al. 2015). This species is herbivorous in its larval stages and does not cannibalise, unlike some other amphibian larvae (e.g., Caldwell and de Araújo 1998; Summers 1999).

Through repeated testing at seven-day intervals we wanted to elucidate general social preferences as well as potential ontogenetic shifts in preference in *M. aurantiaca*. We first tested whether there is a general preference to be social over being alone (group size of 3 vs. 0, experiment one). Second, we assessed preference strengths in different group size combinations (2 vs. 1, 4 vs. 2, experiments two and three, respectively). As (larger) groups are thought of as being beneficial, we hypothesise that *M. aurantiaca* tadpoles prefer being with a group, and that they will discriminate between the two quantities at this low numerosity and ratio. Third, we tested for changes in social preferences during ontogeny. As larger size enhances individual conspicuousness and, consequently, detectability by visually oriented predators, we predict an increase in social preferences during ontogeny. Finally, we aimed at elucidating how activity of tadpoles changes during ontogeny. As there are examples for increases as well as decreases in activity in other anuran species, we predicted that activity would change with increasing size.

Materials and methods

Subjects

We kept adult golden mantellas in naturalistic set-ups at the amphibian facility of Manchester Metropolitan University (Newton-Youens et al. 2022), where we obtained two egg-masses spawned by different males and females. Tadpoles of the first egg-mass hatched on the 28th of March 2022 (n=42 tadpoles), while tadpoles of the second egg-mass hatched on the 30th of March 2022 (n=56 tadpoles). To keep track of the tadpoles' pedigree, the two different egg-masses were housed separate from each other in two tanks (Exo-Terra mini faunariums, 230×155×170 mm) until 5 weeks of age, when they were moved to two separate larger

tanks (Exo-Terra large faunariums, 370×220×250 mm). These holding tanks were filled with tannin-enriched water, (3.5 l in the smaller tanks, 5.0 l in the larger ones) made by soaking Indian almond leaves (*Terminalia catappa*) in aged tap water for a minimum of 24 hours. We provided Java moss (*Taxiphyllum barbieri*) and additional almond leaves for shelter. Tanks were kept in a climate-controlled unit, maintained on a 12:12 photo- and thermoperiod of 23°C during the day and 19°C at night. Lighting was provided by a standard ‘daylight’ lamp (30 W T8 ‘warm white’ 36” fluorescent tube, GE Lighting, Hungary). Tadpoles were fed the same diet for the duration of the experiment, which consisted of a 2:2:1 uniform ground mixture of fish flakes (Tetramin Tropical Food, Tetra, Germany), pellets (AmphibiGold, Arcadia Reptile, UK) and spirulina (Naturya, Netherlands). Ten grams of this dry mixture were added to 20 ml of water to create a thick paste before being frozen. Food was available *ad libitum*. It was replaced twice per week following routine cleaning, consisting of 20–30% water changes and the removal of excess food and waste material.

Experimental set-up

We started the experiments during the second week after hatching, with test animals being 14 and 11 days old, respectively. We repeated the trials every seven days for seven weeks, at which point the first tadpoles completed metamorphosis. Before each trial, we measured the used tadpoles to the nearest 0.5 mm on lined graph paper, which we placed underneath the tanks. Tadpoles measured on average 4 mm snout-vent length (SVL) at the beginning of the study and 8.6 mm SVL at metamorphosis stage.

We used eight identical test tanks throughout the experiment (Fig. 1), which were visually isolated from each other using light green, opaque foam wrapped around the outside of each tank. Test tanks were clear plastic containers measuring 180×110×125 mm (l×w×h) for trials in weeks 2–5. We used larger tanks (370×220×250 mm) for weeks 6–8 to account for tadpoles’ larger size. Tanks were filled to a height of 50 mm with aged tap water treated with Indian almond leaves. Water was changed after every trial. Test tanks were maintained under the same light and temperature regime as the housing tanks. We divided each test tank into three compartments using clear, perforated plastic slides, allowing the exchange of visual and olfactory cues between the compartments (Fig. 1). The compartments on the left and right side served as stimulus compartments to hold the tadpole groups. For weeks 2–5 each of these stimulus compartments measured 40 mm in length. The compartment in the middle served as a test chamber that contained the respective test tadpole. For weeks 2–5 the test chamber measured 100 mm. The test chamber was visually divided into three zones, indicated on lined graph paper placed underneath the test tank. The zones in front of the left and right stimulus compartment measured 20 mm each and served as choice zones. The remaining 60 mm wide area between the choice zones served as a neutral zone (Fig. 1). As the test tanks were double the size during week 6–8, the dimensions of all compartments and zones were doubled as well. The eight test tanks were arranged in a 4×2 grid. A camera (Axis companion cube L, f=2.0, fish-eye lens) was placed above every two tanks allowing video recordings of two trials simultaneously.

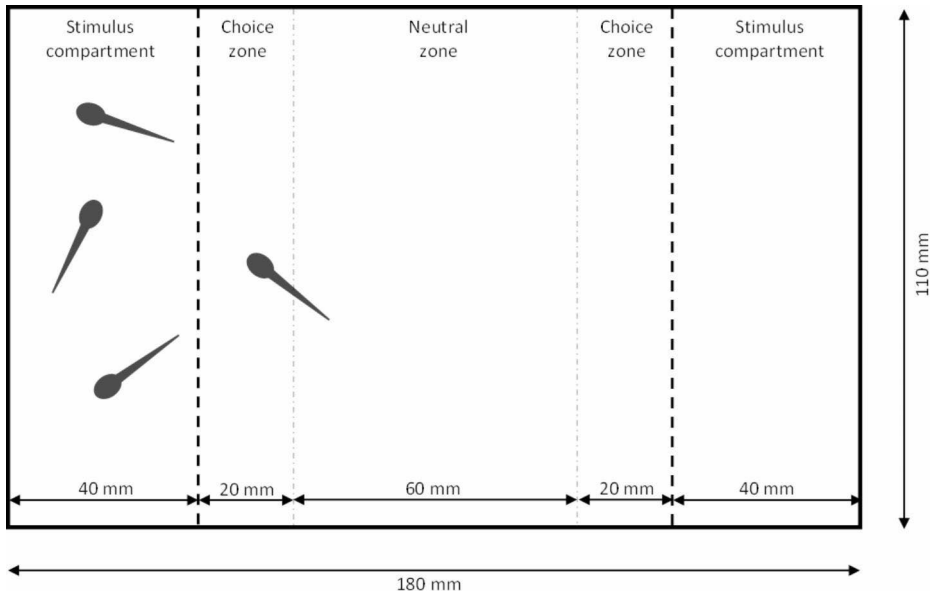


Fig. 1 Top view of the test tank, here showing a 3 vs. 0 trial. Dashed lines represent the clear, perforated barriers used to create stimulus compartments; grey dash-dotted lines represent the markings on the bottom of the tank indicating the division of the middle compartment into a neutral zone and two choice zones

Experimental procedure

We chose tadpoles haphazardly for each trial. All individuals in a given trial were within 0.5 mm SVL, to allow for minimal impact of size differences on test tadpoles' preferences. At the start of the trial the stimulus tadpoles were carefully placed in the outer compartments and a test tadpole was placed in a small, cylindrical vial made of clear plastic (35 mm diameter) placed in the centre of the neutral zone for a five-minute acclimation period (Dadda et al. 2003). After the acclimation period, we removed the plastic vial, and remotely started the video recordings, using the Axis companion app on the researcher's laptop to avoid interfering with the study. Video recordings lasted for a total of 20 min per trial. Afterwards, tadpoles were returned to their original tanks.

The first aim of the study was to test for overall social tendencies of the tadpoles. To that aim, we inserted a stimulus group of three tadpoles into one stimulus compartment, while the other stimulus compartment remained empty (experiment one). The second aim of the study was to test for group size preferences. To that aim we ran trials with two different group size combinations. Stimulus groups either consisted of one and two tadpoles respectively (absolute difference=1, ratio=0.5, experiment two), or of two and four tadpoles, respectively (absolute difference=2, ratio=0.5, experiment three). All tadpoles within a given trial were familiar full sibs in order to exclude potential influences of different levels of familiarity, relatedness or age on individuals' choice (Blaustein and O'Hara 1987; Blaustein and Waldman 1992). Within each run, four of the tanks had the larger stimulus group on the left-hand side and four had the larger group on the right-hand side to control for potential side biases.

All three experiments were repeated weekly for seven weeks. We ran 8 trials per egg-mass for each of the three separate experiments every week, resulting in 16 trials per experiment in each week and 112 trials in total for each of the experiments. All test tadpoles were only used once per week; stimulus tadpoles were used more than once, but never in the same group combination during a given week. Hence, each test tadpole could have been involved in a minimum of 0 and a maximum of 7 trials in total (that is if it was chosen every single week). However, given that we chose the tadpoles haphazardly it is unlikely that such extreme values occurred frequently. Furthermore, each experiment was repeated 112 times (that is 16 trials x 7 weeks), reducing the impact of an individual test animal, even if it would have been tested the maximum of 7 times. Details on the repeats of the different experiments in each week can be found in Table S1.

Data analysis

We analysed all video recordings using the Axis companion app video software. We recorded the time in seconds the subject tadpole spent in each choice zone. As a measure of general activity, we counted how often tadpoles crossed the lines indicating both choice zones (that is entering and leaving the choice zone). We considered a test tadpole to be in a given zone if at least its head crossed the lines indicated on the bottom of the test chamber (Fig. 1). Individual differences in activity might lead to less active tadpoles spending generally less time in the choice zones close to both stimulus groups. Hence, differences in time spent close to the larger of two shoals might indicate differences in preference strength or differences in general activity. To allow a meaningful comparison of preferences between different treatments and different weeks, we therefore calculated a preference index by dividing the time (s) the tadpole spent in the choice zone close to the larger shoal by the time it spent in both choice zones combined (cf. Raveh et al. 2019; Durrer et al. 2020):

$$\text{Preference index} = t[\text{large shoal}] / (t[\text{large shoal}] + t[\text{small shoal}])$$

An index larger than 0.5 thus indicates a preference for the larger stimulus group and an index below 0.5 indicates a preference for the smaller stimulus group, with values closer to 1 or 0 indicating a stronger preference or avoidance, respectively. As the intercept in our models on the preference index shows if the estimates are different from zero, we subtracted 0.5 from the index and used this variable for further analyses. Note that Fig. 2 shows the index before subtracting 0.5.

To analyse the overall social tendencies of the tadpoles (experiment one) a generalised linear model (GLM) was fitted, with preference index as the dependent variable and age in weeks as a fixed effect, testing for ontogenetic shifts in social preference.

To test for a difference in preference strength between different group sizes (experiments two and three), we fitted a generalised linear mixed effects model (GLMM), with preference index as the dependent variable, experiment as a fixed effect and age in weeks as a random effect to account for using the same individuals in different weeks. As this GLMM revealed a difference in preference indices between the two experiments, we continued by analysing the data of experiment two and three separately. A GLM was fitted for each experiment, with preference index as the dependent variable and week as a fixed effect to test for an ontogenetic shift in social preference. As this was not the case (see results), we changed the

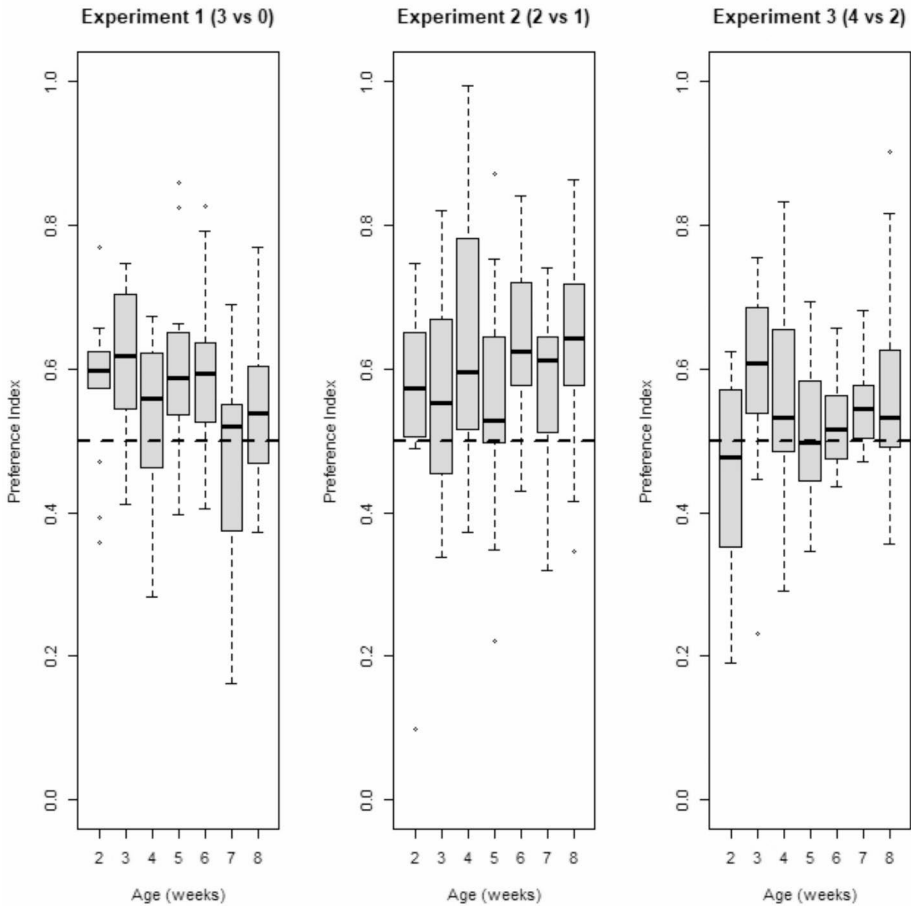


Fig. 2 Preference indices of the tadpoles at different ontogenetic stages in the three different experiments. In experiment one, tadpoles preferred to be with the group of 3 over being alone, and this preference declined with increasing age. In experiment two and three, tadpoles preferred the larger of the two groups. This preference was more pronounced in experiment two. Bold lines indicate medians, boxes interquartile ranges, whiskers 95% CI and circles outliers. The dashed line indicates a preference index of 0.5, values above the line indicate a preference for the larger shoal

week term to become a random effect to account for the repeated use of individuals between weeks and ran GLMMs. Here, a significant intercept would indicate a general preference for one of the stimulus group sizes.

As a measure of overall tadpole activity, we used the number of movements in and out of the preference zones as a proxy. A separate linear model (LM) was fitted to test for differences in tadpole total activity in each experiment with total number of movements between choice zones as the dependent variable and age in weeks as fixed effect. All data were tested for collinearity and multiple collinearity (Zuur et al. 2010) and no violations were detected. Gaussian error distributions and identity link functions were adopted for the models. Week was considered as a continuous predictor as it follows a set pattern. All statistical tests were run using R (version 4.1.2).

Results

In experiment one (3 vs. 0) tadpoles significantly preferred to be with the group over being alone (GLM: $\beta=0.056\pm 0.012$ (SD), $t=4.99$, $df=111$, $P<0.001$, Fig. 2). The strength of this preference declined with increasing age ($\beta = -0.012\pm 0.006$, $t = -2.07$, $df=111$, $P=0.04$, Fig. 2).

Preference indices of experiment two (2 vs. 1) and three (4 vs. 2) differed significantly (GLMM, $\beta = -0.058\pm 0.017$, $t = -3.32$, $df=207$, $P=0.001$), with tadpoles in experiment two showing stronger preferences for the larger group than in experiment three (Fig. 2). Analysing both experiments separated revealed a preference for the larger shoal in both experiments (GLM, 2 vs. 1: $\beta=0.095\pm 0.014$, $t=6.871$, $df=107$, $P<0.001$; 4 vs. 2: $\beta=0.037\pm 0.011$, $t=1.086$, $df=107$, $P<0.001$). In both experiments age at testing had no significant effect on preferences: Experiment two: ($\beta=0.009\pm 0.007$, $t=1.33$, $df=107$, $P=0.19$), experiment three: ($\beta=0.006\pm 0.006$, $t=1.09$, $df=107$, $P=0.28$; Fig. 2).

Test animals in all three experiments showed a considerable amount of activity, measured as the total number of movements in and out of each of the choice zones (Fig. 3). Activity decreased with increasing age in all three experiments (experiment one: LM, $\beta = -1.75\pm 0.595$, $t = -2.95$, $df=110$, $P=0.004$; experiment two: $\beta = -0.358\pm 0.66$, $t = -2.06$, $df=106$, $P=0.04$), though this trend failed statistical significance in experiment three ($\beta = -1.033\pm 0.587$, $t = -1.76$, $df=106$, $P=0.08$, Fig. 3).

Discussion

Amphibian species are often considered to be solitary-living animals. Still, while this often holds true for post-metamorphic individuals (but see Edmonds et al. (2020) for an exception in adult golden mantellas), larvae are frequently found in dense aggregations, and the mechanisms shaping these groups often remain elusive. Living in groups comes with various costs and benefits, which often depend on group size. The ability to discriminate between group sizes can therefore improve an individual's fitness as it will allow evaluating the costs and benefits of joining a particular group. Here, we show that *Mantella aurantiaca* tadpoles prefer being in a group over being alone (experiment one). Furthermore, tadpoles in our study discriminated between group sizes and preferred being with the larger of two groups, especially in experiment two, where stimulus group sizes were smaller.

Tadpoles in this study showed a preference for the larger shoals, conforming to previous studies on amphibians (Leu et al. 2013; Balestrieri et al. 2019) and fishes (e.g., Gómez-Laplaza and Gerlai 2011; Mehliis et al. 2015; Durrer et al. 2020). The preference for a larger group indicates the potential ability of *M. aurantiaca* to discriminate between low numerical quantities, however it is unclear what their capabilities at larger numerosity or larger shoal ratios would be. For example, tadpoles of green toads (*Bufo balearicus*) and edible frogs (*Pelophylax esculentus*) differed in acuity when discriminating between small numbers, with *B. balearicus* only discerning between groups of a ratio of 4 vs. 1 while *P. esculentus* also differentiated 4 vs. 3 (Balestrieri et al. 2019). Two distinct mechanisms for discriminating numerosity have been shown to occur in animals. The object tracking system is used for tracking small precise quantities, normally up to the value of four (Trick and Pylyshyn 1994). The approximate number system is less precise and useful for tracking

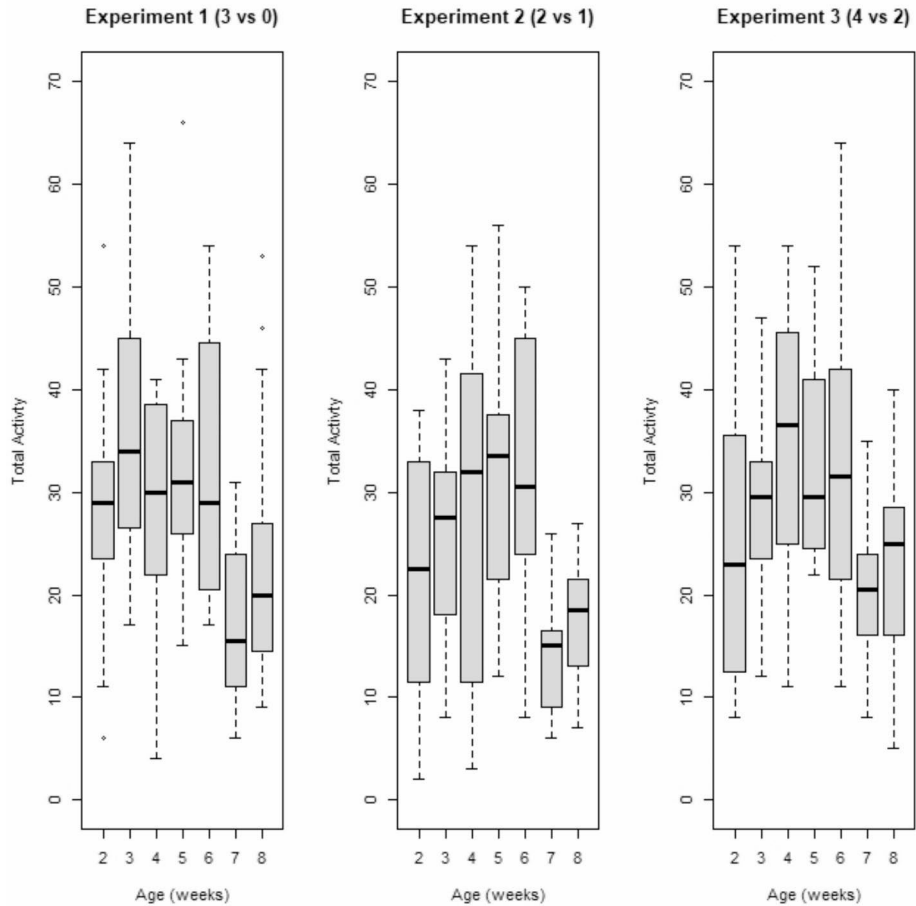


Fig. 3 Activity of the tadpoles at different ontogenetic stages, measured as the total number of movements in and out of each prescribed choice zone. In experiment one and two, activity significantly declined with increasing age, and there was a similar trend also in experiment three. Bold lines indicate medians, boxes interquartile ranges, whiskers 95% CI and circles outliers

larger quantities (Gallistel and Gelman 2000). In our study, the maximum stimulus group size was four, and hence fell within the boundaries of the object tracking system. Still, preferences were more pronounced in experiment two, where the total difference in group size was smaller, but at the same time also the total number of stimulus individuals was low. Whether these results are based on limited numerical capacities or variation in motivation to join a certain group cannot be discerned in our study. For example, it is plausible to assume that the benefits of joining a larger group is diminished by its costs, e.g., due to increased competition. Hence, tadpoles' motivation to join a group might be mediated by weighing the costs against the benefits, and this balance might be different in the 2 vs. 1 scenario than in the 4 vs. 2 scenario. Furthermore, it remains to be determined whether our result is evidence of true number discrimination capabilities, as seen in other amphibians (Uller et al. 2003; Balestrieri et al. 2019; Khatiwada and Burmeister 2022) and some fishes (Stancher et

al. 2013), or if it may be attributed to physical variables, such as the increased space use or higher individual density in larger shoals (Frommen et al. 2009; Stancher et al. 2015; Xiong et al. 2018).

As the clear partitions between the stimulus and test compartment were perforated, test tadpoles had visual and chemical contact to the stimulus groups. While quantity discrimination is usually tested based on visual cues, chemical information of conspecifics has been repeatedly shown to be involved in social decisions of aquatic animals (e.g., Thünken et al. 2010; Ward and Currie 2013; Raveh et al. 2019). Indeed, some fish species use chemical cues to differentiate between groups containing different numbers of conspecifics (Ward et al. 2002; Santacà et al. 2021). Using our setup, we cannot differentiate between the cues tadpoles use when choosing between groups.

The ontogenetic stage has the potential to play a considerable role in group association in amphibians. This can be due to increases in cognitive capabilities changing kin-recognition abilities (Gramapurohit et al. 2006), changes in diet (Hase and Kutsukake 2019) or increased swimming capabilities and therefore an increased ability to avoid predators (Brown and Taylor 1995; Balestrieri et al. 2019), all of which will play a role in the benefits associated with group living. For example, a switch from an herbivorous to an omnivorous diet in Japanese mountain brown frogs (*Rana ornativentris*) can result in increased competition and thus reduced group association (Hase and Kutsukake 2019). Number discrimination capabilities have also been shown to change during ontogeny (Stancher et al. 2013; Vallortigara 2017; Balestrieri et al. 2019). In the present study tadpoles show some ontogenetic shift in general social tendencies (experiment one, 3 vs. 0), with a decline in preference for the group during the later stages of development. The propensity to socialise less at later developmental stages may be a result of increased conspecific competition or a change in predator avoidance strategies at larger sizes (Brown and Taylor 1995; Relyea 2003). However, even though preferences decreased in experiment one as the larvae aged, they remained above the 0.5 threshold throughout the study. Additionally, experiments two and three showed no clear relationship between age and preference strength, suggesting that ontogenetic shifts may not be a general driver of tadpole sociality but might be situation dependent.

In our study, tadpoles showed decreased levels of activity with increasing size, and this decrease was comparable in all three experiments. These decreased activity levels might be caused by an ontogenetic shift in antipredator behaviour from fleeing or shoaling to hiding (Smith et al. 2008), or by an increase in foraging efficiency with increasing size (Kurali et al. 2018). Such changes in activity have the potential to influence the outcome of social preference tests, as a reduced activity might decrease sample rates, lowering the chance to detect existing preferences (cf. Fischer and Frommen 2013). Whether the shown reduction in preference in our study can be explained by reduced activity would be an interesting topic for future research.

In all three experiments, tadpoles were allowed to choose between groups composed of related individuals only. Earlier studies in anuran larvae have shown that tadpoles reared in kin groups showed more even growth rates (Pakkasmaa and Aikio 2003), lower aggressiveness (Fouilloux et al. 2022) and higher activity (Hokit and Blaustein 1995), and that tadpoles prefer to shoal with kin over non-kin (e.g., Blaustein and O'Hara 1986; Blaustein and Waldman 1992; Hase and Kutsukake 2019). However, when competition is high, related individuals in some species show lower mass at metamorphosis (Hokit and Blaustein 1994) and increased amounts of kin-directed cannibalism (Pfennig et al. 1993; Gray et

al. 2009). In such scenarios, individuals might prefer to group with unrelated individuals or with smaller groups (cf. Krause 1993; Frommen et al. 2007, for comparable results in fishes). How such potentially detrimental effects of relatedness interact with preferences for certain group sizes will be a worthwhile question for future studies.

In conclusion, by preference testing for different shoal sizes we show that golden mantella tadpoles actively form social aggregations. They furthermore possess the ability to discern between different group sizes, although the mechanisms underpinning this need further exploration. These findings provide valuable insight into mechanisms driving social aggregations in amphibians and deepen our understanding of the ecology of the endangered golden mantella and other members of the Mantellidae. Finally, our results can inform husbandry guidelines for this commonly kept, endangered species, supporting the idea that group housing may be preferable at the tadpole stage.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10682-023-10276-y>.

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Author contributions D.W., J.N.-Y. and J.G.F. conceived of the study; D.W., J.N.-Y. and J.G.F. planned the experiment; D.W. and J.N.-Y. bred and cared for the animals; J.G.F. supervised the research; D.W., J.N.-Y. and J.G.F. established the set-up; D.W. ran the experiments and analysed the videos; D.W. conducted the statistical analyses and was supported by J.G.F.; D.W., J.N.-Y. and J.G.F. worked on the manuscript drafts; all authors approved the final version.

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Data Availability Data will be made available upon acceptance of the manuscript.

Code Availability Not applicable.

Declarations

Competing interests The authors declare no competing interests.

Ethics approval The experiment followed the ASAB/ABS guidelines for the treatment of animals in behavioural research and teaching. The experiments were approved by Manchester Metropolitan University (Project ID 35889) and are in accordance with good scientific practice guidelines and national legislation.

Consent to participate Not applicable.

Consent for publication All authors agreed on publication of the final draft of the manuscript.

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