



RESEARCH PAPER

Gravidity-Associated Shoaling Decisions in Three-Spined Sticklebacks (*Gasterosteus aculeatus*)

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Abstract

Group living has evolved in many animal species as an antipredator behavior, an evolutionary effect that might be augmented by grouping with similarly looking individuals. Consequently, groups are often composed according to species, size, or coloration. During egg ripening or embryo growth, the outer appearance of females often changes drastically within days, which makes them more prone to predation. Thus, a female's group preference should change according to her reproductive state, an issue that has seldom been investigated. To test this, we gave gravid and non-gravid three-spined sticklebacks (*Gasterosteus aculeatus*) the choice to shoal either with a gravid or a non-gravid conspecific. The results showed that shoaling preferences of gravid and non-gravid individuals differed significantly. Non-gravid females preferred gravid fish as shoaling partners, which might rely on the fact that gravid sticklebacks show reduced escape performance, which in turn might increase a non-gravid female's chance of survival. However, in contrast to our predictions, gravid fish did not show any significant preference. A reason for this pattern might be competition between gravid females for mating partners, which might overrule benefits of shoaling with similar looking individuals. Hence, gravidity influences social preferences in a shoaling fish, which might pose a largely overlooked form of the cost of reproduction.

Introduction

Most animal species live in social associations at least at some point of their lives. The reasons for this are multifarious (Pitcher & Parrish 1993; reviewed in Krause & Ruxton 2002). An individual might find food (reviewed in Clark & Mangel 1986) or a mating partner (e.g. Wedekind 1996; Hutter et al. 2010) faster when living in a group or benefit from reduced energetic costs (e.g. Weimerskirch et al. 2001). Maybe the most important factor facilitating group living is the reduction of predation risk (e.g. Brock & Riffenburgh 1960; Magurran 1990; Krause & Ruxton 2002), which can be explained by several, not mutually exclusive, reasons. First, the 'many eyes effect' suggests that groups detect approaching predators earlier than single individuals

(reviewed in Roberts 1996), which eventually lead to a reduced need of vigilance for a single individual. Second, the 'dilution effect' predicts that risk dilution leads to a reduced probability for an individual of being preyed upon (Hamilton 1971; Foster & Treherne 1981). A third reason for an individual to join a group is that predators become confused when attacking more than one individual. This 'confusion effect' increases with increasing group size (Krakauer 1995; Ruxton et al. 2007). For example, leopard geckos (*Eublepharis macularius*) and common marmosets (*Callithrix jacchus*) took longer to catch one out of several prey compared with one single prey (Schradin 2000). Humans also suffer from an inability to hit a target when group size and distraction increased (Milinski 1990). Similar results were found in hunting three-spined

sticklebacks (Milinski 1977, 1979; Ohguchi 1978). Furthermore, the confusion effect is expected to be strongest in similar looking individuals. Indeed, it has been observed that predators prefer to attack odd individuals within a group (Landeau & Terborgh 1986; Theodorakis 1989; Rutz 2012).

Pregnancy or egg ripening usually leads to phenotypic changes in many animal species, often increasing their risk of predation (Magnhagen 1991). For example, gravid broad-headed skinks (*Eumeces laticeps*) suffer from a reduced running speed (Cooper et al. 1990), while in northern death adders (*Acanthophis praelongus*) swimming performance is altered (Webb 2004). European starlings (*Sturnus vulgaris*) show a decrease in escape performance before and during egg deposition (Lee et al. 1996), presumably leading to a higher predation risk. Similar results were shown in wolf spiders (*Pardosa milvina*) that carry egg sacs (Colancecco et al. 2007). In fish, gravidity has been shown to impair females' swimming ability. In gravid shorthorn sculpins (*Myoxocephalus scorpius*) swimming performance and the contractile properties of fast muscle fibers are reduced (James & Johnston 1998). In guppies (*Poecilia reticulata*) velocity and distance travelled decline rapidly over the course of pregnancy (Ghalambor et al. 2004; Evans et al. 2007). Consequently, gravid females often show changes in their antipredator behavior. Bighorn sheep (*Ovis canadensis*), for example, avoid particular habitats to reduce risk of predation, even though this is associated with reduced foraging opportunities (Ruckstuhl & Festa-Bianchet 1998). Gravid prairie rattlesnakes (*Crotalus viridis*) reduce the risk of being detected by reducing their rattling behavior (Kissner et al. 1997). Furthermore, altered escape behaviors have been shown, for example, in gravid keelbacks (*Tropidonophis mairii*), which try to escape a possible predation threat earlier than non-gravid ones (e.g. Brown & Shine 2004), and Bougainville's skinks (*Lerista bougainvillii*), which add additional escape elements (Qualls & Shine 1998). In contrast, fright reactions of female crucian carp (*Carrasius carrasius*) are decreased during the later stages of sexual maturation, maybe allowing uninterrupted spawning (Lastein et al. 2008).

Additionally to these rather direct impairments of gravidity, gravid females might also be easier to detect in a group of non-gravid, relatively uniform conspecifics, for example, because of their conspicuous morphology (Theodorakis 1989). Thus, one would expect gravidity leading to changes in shoaling preferences. A preference of gravid females to shoal with other gravid conspecifics appears plausible for several reasons: first, in a group of non-gravid fish, a gravid

female is expected to be slower than the average shoal mate, thus facing a higher risk of being attacked by a predator. Second, in a homogeneous group of non-gravid conspecifics, a gravid female would be odd because of its different morphology induced by the developing eggs. As a consequence, the risk of being attacked would increase. On the other hand, gravid females might compete for mating partners, leading to an avoidance of females of comparable reproductive state. Also the expectations of the preferences of non-gravid females are not clear. As non-gravid females are faster than gravid females, they might prefer these females as shoaling partners and reduce the risk of being attacked by doing so (see Mathis & Chivers 2003 for a comparable argument). On the other hand, in a group of gravid females, a non-gravid one would be the odd fish and thus might avoid such a group.

The Model System

In this study, three-spined sticklebacks (*Gasterosteus aculeatus*) were used as a model species. Outside their breeding season, three-spined sticklebacks form loose shoals (Wootton 1984). Shoaling in this species is usually understood as a response to the threat of predation (e.g. Krause et al. 1998; Giesing et al. 2011). Indeed, fish from populations with low predation risk form less dense shoals (Kozak & Boughman 2012). Furthermore, shoals tighten when fish are attacked (Krause et al. 1998). Several studies have described a preference for shoals composed of fish that are more similar in size (e.g. Hoare et al. 2000; Barber 2003; Frommen et al. 2009a). During the breeding season, reproductive males leave the shoal and establish territories near the shore line, while non-reproductive males and females remain shoaling (Wootton 1984). Gravid females develop a distended abdomen caused by the comparatively large eggs (Fig. 1). A female's clutch might comprise more than 30 % of the total body mass (Wootton & Evans 1976; Wootton 1984; Mehlis 2007) leading to a reduction of swimming ability (Milinski & Bakker 1992; Rodewald & Foster 1998 for a detailed description). Accordingly, gravid three-spined sticklebacks show a variety of changes in their behavior, like modified habitat use and escape behavior (Rodewald & Foster 1998) or an increase in predator inspection (Frommen et al. 2009b). Furthermore, in the closely related nine-spined stickleback (*Pungitius pungitius*), gravid females show more risk-averse behavior (Webster & Laland 2011). Nevertheless, gravid three-spined sticklebacks show a reduced probability to escape from an artificial predator attack (Rodewald & Foster 1998).



Fig. 1: Picture of a non-gravid (a) and a gravid (b) three-spined stickleback female from the used population. Notice the swollen abdomen caused by the developed eggs. © Simon Vitt.

Aim of the current study was to investigate how gravidity would influence shoaling decisions of female three-spined sticklebacks. Therefore, we gave gravid and non-gravid females the choice to either shoal with another gravid or a non-gravid female.

Material and Methods

Experimental Subjects

About 400–500 sticklebacks were caught in the pond ‘Stadtweiher’ near Euskirchen, Germany (50°38’N/6°47’E) on Mar. 27, 2008, and brought to the Institute for Evolutionary Biology and Ecology, Bonn, Germany. Here, both sexes were kept together in three large outdoor tanks (750 l) with air ventilation. Water temperature depended on weather conditions, but never rose above 18 °C due to a constant supply of tap-water (3 l/min). All fish were fed with defrosted red mosquito larvae (*Chironomus* spp.) once a day in excess.

Experiments were carried out between April 15th and April 29th, 2008. Individuals used in the experiments were females. Males were identified by initial signs of nuptial coloration (Arnold et al. 2003; Frommen et al. 2009b) and were discarded. Gravid stickleback females can easily be detected by their swollen abdomen (see Fig. 1) and by eggs shining through the skin near the cloaca. Directly before starting one paired trial, two test females and two stimulus females were chosen haphazardly from the outdoor tanks. Thus, the experimental tank posed an unknown and potentially dangerous surrounding to all fish. Test females and stimulus females were always taken from different outdoor tanks to elimi-

nate familiarity effects (Frommen et al. 2007). As fish from the used population are known to include body size differences in their shoaling decisions (Frommen et al. 2009a), stimulus fish were matched in body length.

Experimental Design

To measure shoaling preferences, we used a binary choice test (Wright & Krause 2006). The test aquarium measured 80 × 40 × 40 cm (water depth 16 cm). It was divided into three compartments using sheets of transparent Plexiglas glued to the tank walls. As we aimed to test the influence of the outer appearance (gravid or not) on female’s shoaling behavior, there were no holes in the Plexiglas to exclude the influence of olfactory cues (e.g. Ward et al. 2004; Mehlis et al. 2008). By doing so, two stimulus sections measuring 16 × 40 cm each were obtained on the left and right end of the aquarium. The center compartment measured 48 × 40 cm. Choice zones of 12 cm (approx. three body length of the test fish, Pitcher & Parrish 1993) were marked on the back wall of the tank, next to each stimulus compartment. The setup was illuminated using a fluorescent tube (36 W) placed 40 cm above the aquarium. To prevent interactions with the environment, a black curtain surrounded the setup. Fish movements were recorded from aside through a small spy-hole cut into the curtain using a webcam (Logitech QuickCam Pro 9000; Fremont, CA, USA) positioned in 90 cm distance.

In total, 16 paired trials were conducted. For each paired trial, a gravid female was put in one stimulus compartment and a non-gravid one in the other, resulting in a total of 32 stimulus fish. The preference for the same stimulus pair was measured twice, once for a gravid (N = 16) and once for a non-gravid test fish (N = 16). To avoid sequence effects shoaling preferences of gravid females were recorded first in half of the paired trials, whereas in the other half, non-gravid females were tested first. Furthermore, to avoid side effects, the position of the stimulus fish alternated between the paired trials. After both stimulus fish had been placed into their compartments, the test female was put into a clear Plexiglas cylinder, which was placed in the middle of the aquarium. Hence, females had visual contact to both stimulus fish. After 5 min of acclimatization, the cylinder was lifted from outside the curtain using a pulley system and the test female was allowed to swim freely in the center compartment. The time the test female spent in each choice zone was recorded for 15 min after it had entered both choice zones once. When the test female had not

entered both choice zones within 10 min, the trial pair was discarded ($N = 2$). This ensured that all focal females were aware of both stimulus fish. To exclude olfactory cues of the previous test fish water was changed completely after the first part of a paired trial. Afterward, stimulus fish were reintroduced into the same compartment as before, and the second part of the paired trial started as described above. All fish used in a pair of trials (two test females and two stimulus females) were measured afterward to the nearest millimeter. Standard lengths of gravid and non-gravid stimulus fish did not differ significantly (Wilcoxon matched-pairs signed-ranks test, $N = 16$; $Z = -1.286$; $p = 0.198$). Used test females ($N = 32$) were placed in a separate tank and kept there until the end of the experiment to be sure not to use them again. In the evening after the last trial of the day, all stimulus fish were put back in the large outdoor tanks. Thus, we cannot exclude the possibility that we used stimulus fish more than once on different days. However, as we had a stock of 400–500 fish, it is unlikely that we used stimulus fish twice or in the same combination. One week after the last experiment, the test fish were again checked for developing breeding coloration. We found two male individuals with beginning breeding coloration that had not been visible at the time the experiments took place. As all test fish were kept in one single tank, we were not able to assign data to these two fish.

Data Analysis

The videos were analyzed after the last experiment was finished. The person analyzing the videos was unaware of the position of the gravid stimulus fish. Time test females spent in each choice zone was quantified. For analysis, we calculated a preference index by dividing the time the test fish spent in the choice zones next to a gravid stimulus female by the time spent next to a non-gravid female. Thus, a value larger than one reflects a preference for a gravid stimulus, while a value smaller than one indicates a preference for the non-gravid stimulus. To test whether preferences of gravid and non-gravid test fish differed from each other, we compared the preference indices using a Wilcoxon matched-pairs signed-rank test. To elucidate whether gravid and non-gravid test fish show a preference for one of the two stimulus fish, we compared the preference index against a null expectation of 1 using One-sample Wilcoxon signed-ranks tests. We tested for the possible influence of the two male test fish on the results of non-gravid females by running an additional analysis in which we removed the two data points,

which showed the strongest preference for the gravid stimulus fish. Finally, to compare total time gravid and non-gravid test females spent shoaling time spent in the two choice zones was added. As the sample size was rather low and most data failed normal distribution according to Kolmogorov–Smirnov tests with Lilliefors correction, non-parametric tests were used. Given p -values are two-tailed throughout. All tests were performed using SPSS 20.0 (SPSS Inc., Chicago, IL, USA).

Results

The preferences of gravid and non-gravid females differed significantly (Wilcoxon matched-pairs signed-ranks test, $N = 16$, $Z = -2.017$, $p = 0.044$, Fig. 2). While gravid test fish showed no significant preference for one of the two stimulus fish (One-sample Wilcoxon signed-ranks test, $N = 16$, $Z = 1.086$, $p = 0.379$, Fig. 2), non-gravid test fish spent significantly more time next to the gravid stimulus fish (One-sample Wilcoxon signed-ranks test, $N = 16$, $Z = 2.285$, $p = 0.01$, Fig. 2). Preference of non-gravid fish remained significant after excluding the two fish showing the strongest preference for the gravid stimuli (One-sample Wilcoxon signed-ranks test, $N = 14$, $Z = 2.166$, $p = 0.03$). The total time test females spent shoaling with both stimulus females combined did not differ significantly between gravid (median [s]: 586.5, 1st quartile: 525.25, 3rd quartile 618.5) and non-gravid (611, 590,

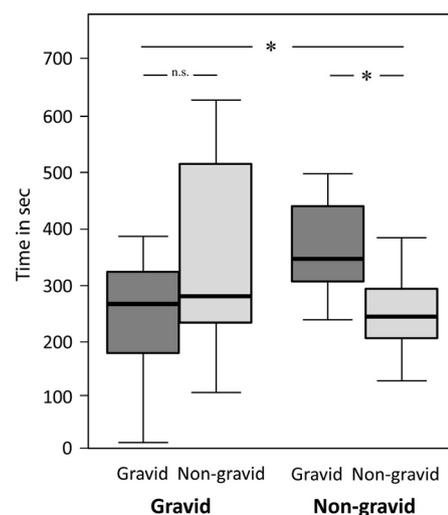


Fig. 2: Time gravid and non-gravid test females spent next to gravid (dark bars) and non-gravid (light bars) stimulus females. While gravid females showed no significant preferences non-gravid females preferred to swim next to gravid females. Given are medians, quartiles and ranges of the raw data. n.s.: non-significant, * $p < 0.05$.

639.25) females (Wilcoxon matched-pairs signed-ranks test, $N = 16$, $Z = -0.776$, $p = 0.438$).

Discussion

The results of the present study showed that reproductive state influences shoaling decisions of female three-spined sticklebacks. Other than theoretically predicted by oddity- and confusion effects, gravid females showed no significant preferences when given the choice between a gravid and a non-gravid fish, while non-gravid females preferred their gravid conspecifics. Thus, the benefits of being a member in a rather uniform group might have been overruled by other benefits. For example, it is possible that non-gravid females preferred fish that showed reduced escape abilities compared with themselves as shoaling partners. Gravid sticklebacks are known to face a higher risk of predation (Rodewald & Foster 1998), most likely because of a reduced maneuverability and lowered swimming ability (Milinski & Bakker 1992). Thus, in case of a predator attack, non-gravid females should have a higher chance to escape than their gravid conspecifics, making gravid fish a preferred shoaling partner. Mathis & Chivers (2003) described a similar effect. Here, the oddity effect was overruled by the advantages of joining a partner whose antipredator morphology was weak. Armored brook sticklebacks (*Culaea inconstans*) preferred to join non-armored minnows (*Pimephales promelas*) when confronted with predators, while minnows joined groups of similar looking conspecifics. Additionally, gravid females should also be slower competitors for food because of their reduced maneuverability. Food competition and nutritional state are known to influence shoaling decisions in sticklebacks (Peuhkuri 1997; Utne-Palm & Hart 2000; Frommen et al. 2007), making a preference for weaker competitors another possible explanation for the choice of non-gravid females. Furthermore, a recent study using fish from the same population showed an increase in predator inspection behavior in gravid females (Frommen et al. 2009b). Predator inspection is known to be costly, as the inspecting individual faces an increased risk of being attacked (Milinski et al. 1997). However, the knowledge of the predator's motivational state is thought to outweigh the costs of inspecting (Häberli et al. 2005). Still, an individual not inspecting on its own might gain this knowledge also by watching the outcome of the inspection behavior of others. Thus, joining a gravid female might bring further benefits for non-gravid fish. A final explanation for the preference of the non-gravid fish might be sexual attraction

between gravid females and other individuals. However, non-reproductive males are usually easy to detect in the used population, as they develop rudimentary signs of red coloration. Thus, we were able to exclude most male individuals. Still, two of the test fish appeared to be males after the experiments. As we were not able to allocate the respective data for these two fish, we could not exclude them from analyses. Instead, we removed the two values that indicated the strongest preference for the gravid stimulus females. The results were not qualitatively changed by this conservative procedure. Furthermore, male sticklebacks establish territories and build nests before courting females (Wootton 1984). Taken these arguments together, we can exclude sexual preference as an explanation for the preference of non-gravid fish.

As outlined above, joining a gravid female could have ample benefits. Thus, it should also be advantageous for other gravid females to join these fish, especially as in this case, the benefits of increased predator confusion through oddity effects might add on. Still, gravid females showed no clear preference for any of the stimulus fish at all. The most likely explanation for this finding is that in sticklebacks both sexes are choosy (Kraak & Bakker 1998; Frommen et al. 2009c). Consequently, ready-to-spawn females compete with each other for mating partners (Wootton et al. 1995). Thus, by choosing a female of the same reproductive state, a gravid female would decrease its predation risk, but at the same time would face competition for a mating partner, leading to a rather indifferent choice (see van Havre & FitzGerald 1988 for a comparable argument).

Fish in our experiment were not confronted with direct predatory cues. Thus, an alternative explanation for the finding that oddity did not influence social preferences could be that test fish did not perceive their environment as risky. However, test fish had no experience with small tanks before, making the experimental tank a new and potentially dangerous surrounding. Furthermore, the movement of the Plexiglas cylinder additionally served as a mild aerial threat. Indeed, fish spent on average more than 60 % of their time within the preference zones next to a conspecific, indicating that they were not swimming freely in the tank. Still, the lack of direct contact to a bird or fish predator might have influenced test fish's choice, which might especially explain the indifferent behavior of gravid females. Evidence for gravid females being less likely to escape an attack is fairly robust (e.g. Magnhagen 1991; Lee et al. 1996; Rodewald & Foster 1998; Colancecco et al. 2007). However, whether these findings are mostly based on

reduced maneuverability and a higher conspicuousness of gravid females or on active preferences of the predators is not well understood. Eventually both explanations will result in an increased risk of predation of gravid females. These issues should be clarified in future experiments.

The current results are partly in contrast to an earlier study of van Havre & FitzGerald (1988). They showed that gravid three-spined sticklebacks preferred non-gravid females as shoaling partners, of which we also saw an indication (but far from significant). However, in contrast to our findings, van Havre & FitzGerald (1988) did not find any preference of non-gravid females at all. This difference might be explained by differences in body shape of fish from the different populations (Bakker & Sevenster 1988). While fish used in van Havre & FitzGerald (1988) originated from a marine population that shows bony plates all along their body (fully plated, forma *trachura*), fish in our study were caught in a freshwater habitat. These fish have a low number of body plates (forma *leiura*) that are restricted to the anterior half of the body (Banbura & Bakker 1995). As these rather inflexible bony plates might limit the extent of the abdomen, the body shape of gravid females of the two forms often differ, with gravid *leiura* females showing more pronounced swellings compared with their body size (see also Mori 1987). Thus, differences in body shape of gravid and non-gravid females of van Havre & FitzGerald (1988) might have been not obvious enough to elicit different shoaling preferences of non-gravid fish.

Summarizing, this study shows that gravidity influences social preferences of a fish. While non-gravid test fish preferred gravid fish as shoaling partners and thus, most likely, increased their antipredator benefits, gravid females showed no clear preferences. These results add knowledge about a largely overlooked form of reproductive costs for females.

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