Department of Physics, Chemistry and Biology

Master Thesis

Personality of the three-spined stickleback in relation to *Glugea anomala* infection

Márton Kuti

LiTH-IFM- Ex--99/1111--SE

Supervisor: Hanne Løvlie, Linköping University

Examiner: Urban Friberg, Linköping University

Linköpings universitet

Department of Physics, Chemistry and Biology

Linköpings universitet

SE-581 83 Linköping, Sweden

Institutionen för fysik, kemi och biologi
Department of Physics, Chemistry and Biology

Avdelningen för biologi
Instutitionen för fysik och mätteknik

Rapporttyp
Masters thesis
Title:
Personality of the three-spined stickleback in relation to *Glugea anomala* infection
Author:
Márton Kuti

Abstract:

Parasite-host relationships can be important for a range of aspects in biology, due to a large number of parasitic species and the influence parasites can have on hosts. For example, parasites can influence the condition and behaviour of their hosts. It is also theoretically predicted that parasite infection can explain variation in animal personality (i.e. among-individual consistency in behavioural responses), although this is still scarcely empirically investigated. In this study, I have examined the relationship between the personality traits of wild-caught three-spined sticklebacks (*Gasterosteus aculeatus*), and the infection status and load by a microsporid parasite, *Glugea anomala*. Activity and exploratory behaviour were observed in a novel arena, social and aggressive behaviours in a mirror test, and boldness during a simulated predator attack. Consistent behavioural traits describing personality were identified and analysed for their relationship to infection status. Parasite infection explained variation in social behaviour, where the amount of time fish spent near the mirror correlated positively with parasite load, and in aggression, where attacks launched at the mirror correlated negatively with parasite load. Parasite infection did not explain variation in other personality traits. These results indicate that parasite infection and personality are connected, although future studies are needed to investigate the causality of this relationship.

ISBN
LITH-IFM-A-EX—99/1111—**SE**

ISRN

Title of series, numbering

Supervisor **Hanne Lovlie**

Location: Linköping
Keyword: Glugea, parasite, personality
Date:
2018-04-17
URL för elektronisk version

Table of contents:

1 Abstract

Parasite-host relationships can be important for a range of aspects in biology, due to a large number of parasitic species and the influence parasites can have on hosts. For example, parasites can influence the condition and behaviour of their hosts. It is also theoretically predicted that parasite infection can explain variation in animal personality (i.e. among-individual consistency in behavioural responses), although this is still scarcely empirically investigated. In this study, I have examined the relationship between the personality traits of wild-caught three-spined sticklebacks (*Gasterosteus aculeatus*), and the infection status and load by a microsporid parasite, *Glugea anomala*. Activity and exploratory behaviour were observed in a novel arena, social and aggressive behaviours in a mirror test, and boldness during a simulated predator attack. Consistent behavioural traits describing personality were identified and analysed for their relationship to infection status. Parasite infection explained variation in social behaviour, where the amount of time fish spent near the mirror correlated positively with parasite load, and in aggression, where attacks launched at the mirror correlated negatively with parasite load. Parasite infection did not explain variation in other personality traits. These results indicate that parasite infection and personality are connected, although future studies are needed to investigate the causality of this relationship.

2 Introduction

Personality is defined as among-individual consistency in behavioural variation (Dall et al. 2004; Stamps & Groothuis 2010; Sih et al. 2004; Reale et al. 2007). Personality variation has now been described in a broad range of species, ranging from insects to primates (Gosling 2001; Carere & Maestripieri 2013). This means that animals do not fully adjust their behaviour with perfect plasticity to match any given situation, but tend to follow patterns and respond to recurring situations in an individually predictable manner, even if that response is not always optimal (Dall et al. 2004; Stamps & Groothuis 2010). Personality can affect numerous aspects of animals' behavioural repertoire, from cognition and social abilities to exploration, aggression and foraging (e.g. Dingemanse & Réale 2005; Favati et al. 2014). How personality arises is not fully understood, but it is predicted to be linked to variation in neuroplasticity and the development of the neuroendocrine system

(Øverli & Sørensen 2016). Often, there is no single "best" personality type in a population, but variation seems to remain over time (Dall et al. 2004). It is thought that such variation is maintained because of a dynamically changing environment, and different approaches are successful at different time points or situations (Dall et al. 2004; Kolhaas et al. 2007). Exploring the factors that can explain why animals have personality is therefore important for improving our understanding of animal behaviour in general.

Parasites are organisms which live on, off, and at the expense of another organism (the host), very often in some form of physiological dependence (Esch & Fernández 2013). Several studies have noted that parasitic infection is concurrent with behavioural changes in the host, and in some cases, such changes are advantageous to the parasite and facilitate its survival or reproductive success to the detriment of the host (Poulin 1994). Parasitism is an influencing factor of behaviour is relevant since there is a large number of parasitic species on Earth (10%-50% of all known species, depending on the broadness of the definition, Esch & Fernández 2013). The mechanisms through which parasites affect host behaviour are poorly understood. Possible explanations include affecting nutritional status, immuno-modulation, or monoaminergic effects (e.g. Øverli et al. 2001; Hicks et al. 2018).

To improve our understanding of how parasite infection can explain variation in behaviour, in this study, I focus on the three-spined stickleback (*Gasterosteus aculeatus*) and its parasite *Glugea anomala*. The study aims to investigate possible differences in host personality, looking at behaviour describing variation in the five personality traits laid out by the seminal paper by Reale et al. (2007), namely activity, exploration, boldness, sociability and aggression. The three-spined stickleback is a well-studied fish species, being a popular model animal of behavioural research as well as for parasite-host relationships (Bell & Sih 2007; Dingemanse et al. 2007; Barber & Scharsack 2010). The relationship between the fish and its specific cestode parasite, the *Schistocephalus solidus* has been studied extensively, including the topic of behavioural manipulation. The current study focuses on another common, but a less studied parasite, the microsporid *Glugea anomala*. Microsporids are highly specialized intracellular parasites (Weiss et al. 2014). Species in the phylum most often infect fish (Rodriguez-Tovar et al. 2011). The infection spreads with free-floating spores which are ingested by the host. The spores normally germinate when the host is exposed to environmental stress and infiltrate the body, eventually forming distinct tumours, which contain a large number of parasites in various stages of development. The tumours (or xenomas) may form in most parts of the body and are usually highly visible. The life cycle of the organism is completed when tumours are ruptured by physical trauma and spores are released into the water (Cali & Takvorian 1999). This life cycle contrasts with that of the more widely studied *Schistocephalus solidus*, in which different life stages of the parasite develop in different host species. As such, studying it should offer insight into the parasite-host relationship in general. In sticklebacks infected by *Schistocephalus solidu*s, changes to foraging and antipredator behaviour, like near-surface swimming and decreased escape response have been observed (Poulin 2010), along with behavioural changes resulting in increased boldness (Giles 1983). Such changes increase the chance of transmission of the parasite to the definitive host (a bird) through predation. In sticklebacks infected by *Glugea anomala,* reduced swimming speed, and reduced antipredator behaviour have been observed (Mehlhorn 2015), as well as increased shoal sizes (Ward et al. 2005). A broader investigation of variation in personality traits and infection with *Glugea anomala*, however, has not been studied. Exploring personality changes regarding *Glugea anomala* infection would enable linking different behavioural effects previously observed in this parasite-host system and would also allow for comparison with effects seen in cases of *Schistocephalus solidu*s infection. Also, better understanding the parasite-host relationship in general means better understanding of a factor which can have a major impact on animal behaviour broadly and potentially also personality.

3 Material & methods

3.1 Collection of fish

Three-spined sticklebacks were collected near Oxelösund, Sweden (58°40′N 17°07′E, see Figure 1) using sink nets, on two occasions (01. 09. 2015, and 11. 11. 2015). The fish used in the study were collected at 3 different locations 1-3 kilometres from each other. In Sweden, the three-spined stickleback has a 2-year life-cycle. We collected fish smaller than 3.5 cm, which implies that they are in their first year of life and thus not sexually mature. The fish were transported from the location of collection and placed in one of 30, 27l, filtered, plastic aquaria with gravel bedding and plastic plants for enrichment back at the university. 2-5 fish were in the same aquarium. Aquaria were covered on all sides in order to minimize visual disturbance and approximately 50% on top to provide a shaded area. Lighting was produced by light tubes above the tanks running on a 16 hours day / 8 hours night cycle. The fish were fed on a daily basis with defrosted deep-frozen brine shrimps. During each feeding, enough food was given so that there were leftovers.

Figure 1. The sites in the province of Östergötland, Sweden, where three-spined sticklebacks were collected for the current study. The numbers indicate the order in which the sites were approached. (Google, 2018).

3.2 Study population

A total of 64 fish were used in the study, 22 from the fish collected on the first sampling (location 1) and 42 from the fish obtained during the second sampling (22 from location 2, and 20 from location 3). The fish collected during the first sampling were elastomer-tagged for identification (as they were uninfected by *Glugea anomala*). The fish from the second sampling were distributed among the aquaria in a way that made visual identification possible based on size differences and infection marks, without elastomer tags. Fish collected from location 1 were visually selected for being uninfected. Identifying infected fish was based on the lack of tumours caused by the parasite. Such tumours are often relatively large, causing a visible bulge, and produce a bright spot on the fish. In populations 2 and 3 there were in total 17 infected fish. Infection status (whether positive or negative) in all animals was later confirmed by dissection.

Prior to behavioural observations, one focal animal at a time was retrieved from its residential tank using a small hand net. This was done in a rotating pattern, taking one fish from each aquarium consecutively, to minimize the effect of disturbing the same tank repeatedly over a short period of time. Feeding always took place after behavioural observations were conducted.

3.3 Behavioural tests

Novel environment test

A 35l novel arena tank was used for a novel arena test. In trial 1, contained fine white sand, a small pile of stones for shelter in one end and round stones arranged to divide the lower half of the aquarium into 6 explorable segments for the fish (see Figure 2, left side). In trial 2, the tank contained coarse brown sand, and a similar stone pattern placed in a reversed layout, the hiding area being on the opposite side. The novel arena tank in both trials was divided into 12 regions, 6 lower, and 6 upper (using markings of the edges of the tank).

To investigate activity, exploration and boldness, the focal animal was placed in a novel environment tank, entering from the top over the middle of the area with shelter. The focal animal was allowed to do an immediate escape from the location where it was inserted (which was a very common first reaction) before the data collection started. Recordings of behavioural data started when the fish stopped for at least a second after insertion. Latency to make the first move (at least 1 body length) was measured and after this, behaviour was recorded every 20 seconds continuing for 15 minutes (behaviours detailed in Table 1). The data was grouped in 5-minute blocks for easier recording and was collated afterwards. Visually comparing distance to the body length of the focal animal is good for judging small distances in an aquarium with a swiftly moving animal. It is also better than a set length (say, 3 cm) to distinguish between movement and posture change in animals of different body sizes. The latency to reach any upper region, and to visit all 6 lower areas, and to visit all areas, were also recorded.

Table 1. Description of behaviours scored during testing of sticklebacks

Behaviour	Description
Swim	The fish is moving in a direction covering a distance of at least a body length over the course of a second (identified visually).
Still	The fish does not move in any direction fast enough to cover at least 1 body length distance over the course of a second.
Interact	The fish touches an object with its snout.
Cover	The fish is either in cover or is at the bottom of the tank with the entire body touching the bottom.

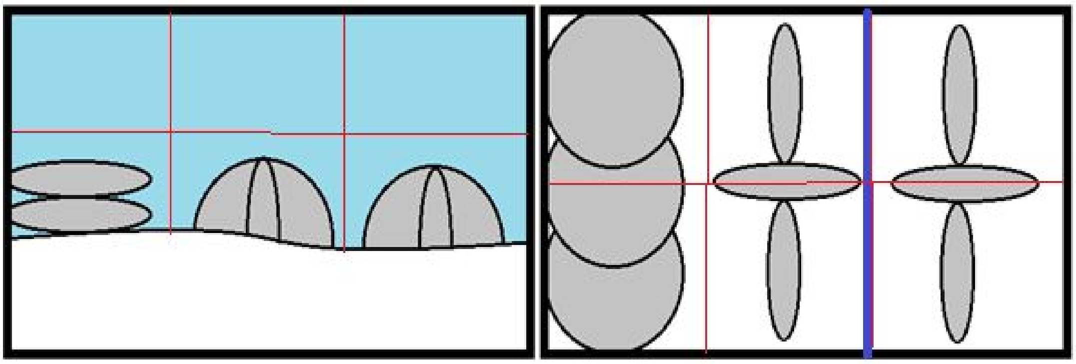

Figure 2. Novel environment and social behaviour setup used to score behaviour of stickleback (side and top-down view). White = sand, grey = stones, dark blue = mirror, red lines = zones.

Mirror test

To investigate aggression and social behaviour, a mirror was gently inserted into the test tank following the novel environment test. The mirror was positioned to contain the fish in the last 30% of the tank (see Figure 2, right side), away from the sheltered area. The focal animal was allowed to stop after the insertion of the mirror, with latency to move recorded. In the following 10 minutes, time spent in close vicinity of the mirror (equal to or less than one body length) and the number of attacks launched at the mirror were recorded. The data was recorded in 5-minute blocks. After the 10 minutes had passed the mirror was removed.

Simulated predator attack
In order to test boldness and antipredator behaviour, a simulated predator attack was launched at the fish after the social behaviour test, the next time the focal animal spontaneously reached the upper half of the tank. In the first population, the simulated attack was carried out by stabbing a metal stick into the water next to the fish by a helper. In subsequent populations, attacks were executed by dropping a small bag of stones into the water. After the attack, latency to move was recorded and behaviours were observed and recorded every 20 seconds for 5 minutes (Table 1). The data was grouped in 5-minute blocks for easier recording. At the end of the experiment, the focal animal was carefully retrieved using a net and was placed back in its residential tank. In order to be able to compare behaviours across time (which is necessary to describe personality traits) the process was repeated on the same individual, using a different novel environment, after waiting for at least 1 day.

After all individuals sampled from one location had been tested twice, the fish were decapitated, measured for length (head included, with 0.1 cm accuracy) and weight (0.00001 g accuracy), dissected to check for infection status, and parasites were also measured for weight after excess water has been removed by a paper towel (0.00001 g accuracy). The fish showed no sign of reproductive activity during the study.

3.4 Statistical analyses

Statistical analyses were conducted in SPSS 2.2. Data was non-normally distributed so non-parametric statistics were used. To explore which behaviours were consistent over time (and could thus be considered personality traits), Spearman's rank correlation was used between behaviours measured during the two different test periods. With consistent behaviours, a Kruskal-Wallis test was used to investigate if fish collected at different fishing spots within the collection area showed differences since such differences might indicate behavioural variation arising from differences in their environment, and not the factors in the focus of my study. If such difference was noticed in a behaviour, that behaviour was not analysed further. To investigate whether a *Glugea* infection (or not) explained variation in personality, a Mann-Whitney U test was used. To explore if any of the personality traits correlated with *Glugea* parasite load (i.e. the proportion of parasite weight to fish body weight), Spearman's rank correlations were used. A Kruskal-Wallis test was used to compare fish based on their infection status alone (infected vs. uninfected, without specific parasite load) to determine if being infected could be associated with behavioural differences.

The fish populations showed significant differences in latency to move. Consequently, latency to move in the social behaviour test was not analysed further. Attacks launched at the mirror were recorded in two consecutive 5-minute blocks for convenient tracking, but, unlike other behaviours, were not collated into a single total, due to a difference between them which was noticed during the observation; the initial interactions with the mirror were often vigorous and declined in intensity later. The fish seemed to become relatively accustomed to their mirror image over the course of 10 minutes, and so the 5-minute blocks were kept separate for analysis to make sure this detail was not ignored.

Individuals that were initially identified as uninfected were confirmed to be uninfected upon dissection and fish identified as parasitized were confirmed to be parasitized by *Glugea anomala*. Two individuals were excluded from the analysis in population 3 because dissection showed that they had *Schistocephalus solidus* infection in addition to *Glugea anomala* (bringing sample size to 62).

4 Results

4.4 Novel arena

Fish differed consistently in all behaviour recorded in the novel arena, and parasite load did not explain variation in these (Table 2).

Table 2. Behaviour of sticklebacks in a novel arena test, its consistency and link to parasite load

Novel Arena Test	Population	Consistency	Parasite load	Infection Status
latency to move	p=0.47	r=0.30, p=0.017	r= 0.09, p=0.48	p=0.45
first upper region visited	p=0.37	r=0.30, p=0.019	r= 0.11, p=0.40	p=0.28
all lower regions visited	p=0.51	r=0.30, p=0.016	r= 0.03, p=0.81	p=0.90
all regions visited	p=0.39	r=0.36, p<0.01	r=-0.06, p=0.66	p=0.80
swim	p=0.37	r=0.41, p<0.01	r= 0.20, p=0.12	p=0.20
still	p=0.73	r=0.40, p<0.01	r=-0.16, p=0.23	p=0.18
interact	p=0.03	-	-	-
cover	p=0.47	r=0.21, p=0.096	-	-

"latency to move" was the time a fish took to start moving after being placed in the setup. "first upper region visited" was the time a fish took before entering the upper half of the setup for the first time. "all lower regions visited" was the time a fish took before entering all areas in the lower half of the setup at least once. See Table 1 for details. Population refers to the results of the Kruskal-Wallis test comparing fish from the different collection areas. "Consistency" refers to the correlation between the first and the second test. Significant correlation means the behaviour was consistent over time within the sample. "Parasite load" refers to the correlation between parasite mass/body mass and behaviour. "Infection status" refers to the comparison of infected vs. uninfected fish. Blank spaces mean the previous test step yielded a result which made further tests on the given behaviour unnecessary.

4.5 Mirror test

Fish differed consistently in all behaviour recorded during the mirror test, and parasite load explained variation in the amount of time spent near the mirror, and the number of attacks launched at the mirror (first 5 minutes, Table 3).

The amount of time spent near the mirror showed a significant positive correlation with parasite load (Figure 3). The parasite load fish had correlated negatively with the number of attacks these fish launched at the mirror, but the effect was only present during the first 5 minute period of observation (Figure 4).

Table 3. Behaviour of sticklebacks in a mirror test, its consistency and link to parasite load

Mirror test	Population	Consistency	Parasite Load	Infection Status
latency to move	p=0.017	-	-	-
latency to approach mirror	p=0.28	r=0.31, p=0.015	r=-0.29, p=0.15	p=0.18
total time spent near the mirror	p=0.33	r=0.31, p=0.015	r=0.36, p<0.01	p<0.01
attacks at the mirror / 1st part	p=0.50	r=0.22, p=0.019	r=-0.30, p=0.017	p=0.031
attacks at the mirror / 2nd part	p=0.61	r=0.27, p=0.033	r=-0.16, p=0.20	p=0.23

"latency to move" was the time a fish took to start moving after the mirror was placed in the setup. "latency to approach mirror" was the time before the fish first approached the mirror within a body length distance. "total time spent near the mirror" was the total amount of time the fish spent within 1 body length of the mirror. "attacks at the mirror" mean the total number of attacks (forceful jabs with the mouth) launched at the mirror, during the first half and the second half (5 minutes each) of the observation, respectively. "Population" refers to the results of the Kruskal-Wallis test comparing fish from the different collection areas. "Consistency" refers to the correlation between the first and the second test. Significant correlation means the behaviour was consistent over time within the sample. "Parasite load" refers to the correlation between parasite mass/body mass and behaviour. "Infection status" refers to the comparison of infected vs. uninfected fish. Blank spaces mean the previous test step yielded a result which made further tests on the given behaviour unnecessary.

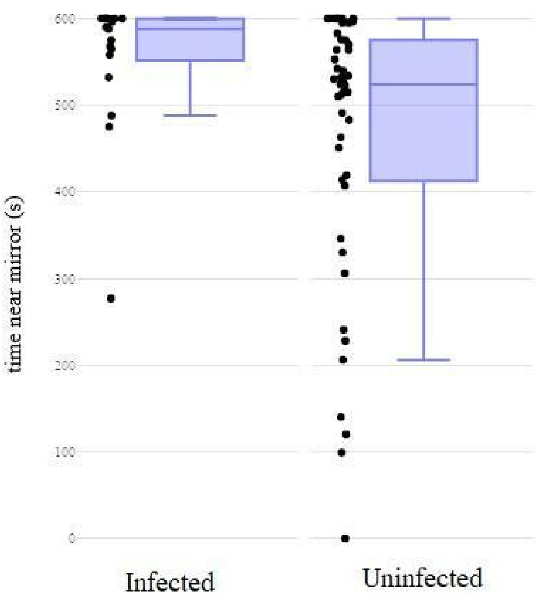

Figure 3. Total time spent near the mirror, for infected and uninfected sticklebacks. Y-axis shows the total amount of time a stickleback spent near a mirror (s). Whisker bars show upper and lower fences, individuals dots show data points, boxes show lower and upper quartiles, and the thick line within the box shows the median value.

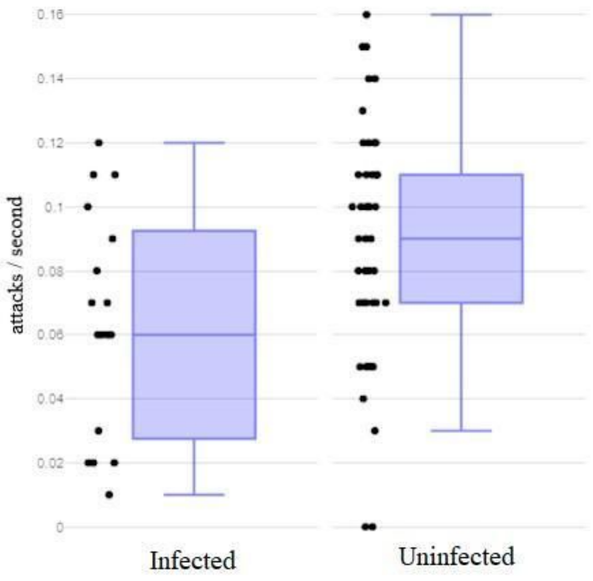

Figure 4. Attacks per second shown by infected and uninfected sticklebacks during the first period of observation (see text for details). Y-axis shows the number of attacks the fish have launched at the mirror, per second. Whisker bars show upper and lower fences, individuals dots show data points, boxes show lower and upper quartiles, and the thick line within the box shows the median value.

4.6 Simulated predator attack

After exposure to simulated predator attack, fish did not show consistency in the amount of time spent still, or in the time spent in cover (Table 4). Fish differed consistently in their latency to move after the stimulated attack, and the amount of time spent swimming and interacting with the environment. Parasite load did not explain variation in these (Table 4).

Table 4. Behaviour of sticklebacks after a simulated predator attack test, its consistency and link to parasite load

Simulated Predator Attack	Population	Consistency	Parasite Load	Infection Status
latency to move after attack	p=0.22	r=0.38, p<0.01	r=0.012, p=0.93	p=0.48
swim	p=0.50	r=0.46, p<0.01	r=0.17, p=0.18	p=0.74
still	p=0.39	r=0.25, p=0.05	-	-
interact	p=0.70	r=0.38, p<0.01	r=0.087, p=0.50	p=0.64
cover	p=0.21	r=0.05, p=0.68	-	-

"latency to move after attack" was the time a fish took to start moving after the simulated attack. See Table 1. for details. "Population" refers to the results of the Kruskal-Wallis test comparing fish from the different collection areas. "Consistency" refers to the correlation between the first and the second test. Significant correlation means the behaviour was consistent over time within the sample. "Parasite load" refers to the correlation between parasite mass/body mass and behaviour. "Infection status" refers to the comparison of infected vs. uninfected fish. Blank spaces mean the previous test step yielded a result which made further tests on the given behaviour unnecessary.

5 Discussion

In my study, I aimed to explore the *G. anomala* / *G. aculeatus* relationship from the perspective of personality, and parasite-host manipulation. I conducted a novel arena test, a mirror test, and a simulated predator attack test on the fish in my sample. I used these tests to first investigate whether three-spined sticklebacks displayed personality in these setups, and then to investigate how parasitized fish were different from healthy ones. I have here shown that three-spined sticklebacks display consistent behavioural variation (i.e. personality), in the context of exploratory behaviour, social behaviour, and antipredator behaviour. With regards to the three-spined stickleback-*Glugea anomala* system, I have here shown that infection status is associated with increased social behaviour and decreased aggressiveness, but personality was not affected in other contexts, that I observed

All measured behaviours were consistent over the time span between test periods, with the exception of time spent hiding in cover, and time spent still without any other activity. This confirms previous studies showing that the same or similar behavioural responses describe variation in personality in this species (Bell & Sih 2007; Dingemanse et al. 2007).

The observed link between sociality and parasite load of *Glugea* infection confirms a link between personality and parasitism. There are still not very many studies investigating *Glugea* infection and behaviour of the host. My study has turned up results that show minor differences from the results of existing studies. For example, *Glugea* infected fish have been observed to swim slower than uninfected fish (Kuhn et al. 2015). In my study, differences with regards to swimming, in general, were not observed between infected and uninfected fish. It should be noted, though, that my study focused on how much time the fish spent swimming, not on speed, so the results are not directly comparable. Still, increased periods of inactivity associated with parasite load could still have pointed to a similar effect (i.e. decreased physical activity associated with the energetic cost of carrying a parasite, Ward et al. 2005). It is worth noting that in both studies referenced by Kuhn et al. with regards to swimming speed, the feeding and activity regime of the fish were different from those in this study. Ward et al. (2005) studied the shoaling behaviour of sticklebacks using flow channels, which are more physically demanding than swimming in still water. Milinski (1985) studied the energy economy of sticklebacks under the threat of predation, which means the fish were motivated to get food and to keep away from feeding areas simultaneously. In my study, the fish received abundant food and were able to move at their own pace. It should also be noted that the few other studies that have investigated the relationship between *G. anomala* infection and host behaviour did not investigate personality, so their results may or may not have been individually consistent among their fish.

Some of my results reflect on the conclusions of earlier studies in a way that offers some additional context. Previously, it has been found, that the shoaling behaviour of infected fish is altered, and fish parasitized by *G. anomala* display a tendency to swim in larger shoals (Ward et al. 2005). The decreased aggressiveness of infected fish towards conspecifics, that I have observed, offers an explanation for that phenomenon. Large shoals are favourable for the transmission of the parasite, but they also offer protection from predators to the infected fish (which are very visually conspicuous), which makes it difficult to set the two factors apart (Ward et al. 2005). It is certainly possible that a behaviour, which is in the best interest of the infected fish, is also, incidentally, beneficial to the parasite. Fish infected by *G. anomala* have also been observed to display less vigorous antipredator behaviour (Kuhn et al. 2015). No such effects were observed in my study, which might be explained by the fish my study come from different source environment, and so may have experienced different predator threats. The threat of predation is known to be a contributing factor in explaining personality (Bell & Sih 2007). An obvious way to eliminate that uncertainty would be by using fish that were raised entirely in a controlled environment. The causality of the observed relationship between personality and parasite load this needs further investigation to be clarified. Preferentially, experimental infection of future hosts with known personality profiles should be done to determine this.

6 Conclusions

According to my findings, *G. anomala* infection can be linked to variation in the social personality of the host, and the effect is different from that observed in the stickleback – *S. solidus* system. For *G. anomala*, I have observed an effect on social behaviour which may facilitate the horizontal transfer of this parasite.

The observation of personality differences in sticklebacks infected with *Glugea anomala* means the *G. anomala* - three-spined stickleback relationship can also be used to study the relationship between parasites and host personality. That is important because the complex, multi-species life cycle of *S. solidus* makes it rather resource-intensive and complicated to conduct artificial infections in a controlled environment (Smyth 1954). *G. anomala* spores, on the other hand, can be obtained from dead sticklebacks, and are much more easily introduced into an aquarium. Artificially infecting healthy sticklebacks may help decide conclusively whether the parasite causes the emergence of a certain personality in the host or certain personalities are merely more likely to become infected.

7 Acknowledgement

I would like to express my thanks to Hanne Løvlie, my supervisor, for her guidance and help through my thesis project as well as Urban Friberg for his work as my thesis examiner. Additionally, I would like to thank José Pereira and Emelie Jansson, both of whom offered practical help during my project.

8 References

Barber, I., Scharsack, J. P. (2010). The three-spined stickleback-Schistocephalus solidus system: an experimental model for investigating host-parasite interactions in fish. *Parasitology*, *137*(03), 411-424.

Bell, A. M., Sih, A. (2007). Exposure to predation generates personality in three-spined sticklebacks (Gasterosteus aculeatus). *Ecology Letters*, *10*(9), 828-834.

Cali, A., Takvorian, P. M. (1999). Developmental morphology and life cycles of the microsporidia. *The microsporidia and microsporidiosis*, 85-128, 86. American Society of Microbiology.

Carere, C., Maestripieri, D. (2013). Animal Personalities: behavior, physiology, and evolution. Chicago, 589 USA, University of Chicago Press.

Dingemanse, N. J., Réale, D. (2005). Natural selection and animal personality. *Behaviour*, *142*(9-10), 1159-1184.

Dingemanse, N. J., Wright, J., Kazem, A. J., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three‐spined stickleback. *Journal of Animal Ecology*, *76*(6), 1128-1138.

Esch, G. W., Fernández, J. C. (Eds.). (2013). A functional biology of parasitism: Ecological and evolutionary implications. Springer Science & Business Media.

Favati, A., Leimar, O., Radesäter, T., Løvlie, H. (2014). Social status and personality: stability in social state can promote consistency of behavioural responses. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*(1774), 20132531.

Giles, N. (1983). Behavioural effects of the parasite Schistocephalus solidus (Cestoda) on an intermediate host, the three-spined stickleback, Gasterosteus aculeatus L. *Animal Behaviour*, *31*(4), 1192-1194.

Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research?. *Psychological bulletin*, *127*(1), 45.

Hicks, O., Burthe, S. J., Daunt, F., Newell, M., Butler, A., Ito, M., Sato, K, Green, J. A. (2018). The energetic cost of parasitism in a wild population. *Proceedings of the Royal Society of London B: Biological Sciences*, *285*(1879), 20180489.

Koolhaas, J. M., De Boer, S. F., Buwalda, B., Van Reenen, K. (2007). Individual variation in coping with stress: a multidimensional approach of ultimate and proximate mechanisms. *Brain, Behavior and Evolution*, *70*(4), 218-226.

Kuhn, T., Klapper, R., Münster, J., Dörge, D. D., Kochmann, J., Klimpel, S. (2015). Remote Control: Parasite Induced Phenotypic Changes in Fish. In *Host Manipulations by Parasites and Viruses* (pp. 117-148). Springer, Cham.

Milinski, M. (1985). Risk of predation of parasitized sticklebacks (Gasterosteus aculeatus L.) under competition for food. *Behaviour*, *93*(1), 203-216.

Øverli, Ø., Pall, M., Borg, B., Jobling, M., Winberg, S. (2001). Effects of Schistocephalus solidus infection on brain monoaminergic activity in female three-spined sticklebacks Gasterosteus aculeatus. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*(1474), 1411-1415.

Poulin, R. (1994). The evolution of parasite manipulation of host behaviour: a theoretical analysis. *Parasitology*, *109*(S1), S109-S118.

Poulin, R. (2010). Parasite manipulation of host behavior: an update and frequently asked questions. *Advances in the Study of Behavior*, *41*, 151-186.

Rodriguez-Tovar, L. E., Speare, D. J., Markham, R. F. (2011). Fish microsporidia: immune response, immunomodulation and vaccination. *Fish & shellfish immunology*, *30*(4-5), 999-1006.

Smyth, J. D. (1954). Studies on tapeworm physiology. VII. Fertilization of Schistocephalus solidus in vitro. *Experimental Parasitology*, *3*(1), 64-71.

Stamps, J., Groothuis, T. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, *85*(2), 301-325.

Ward, A. J., Duff, A. J., Krause, J., Barber, I. (2005). Shoaling behaviour of sticklebacks infected with the microsporidian parasite, Glugea anomala. *Environmental Biology of Fishes*, *72*(2), 155-160.

Weiss, L. M., James, J. B. (2014). Microsporidia: pathogens of opportunity. John Wiley & Sons.