Parasitism, personality and cognition in fish

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21 **Abstract**

22 It is well established that parasites can have profound effects on the behaviour of host
23 organisms, and that individual differences in behaviour can influence susceptibility to
24 parasite infections. Recently, two major themes of research have developed. First,
25 there has been a growing interest in the proximate, mechanistic processes
26 underpinning parasite-associated behaviour change, and the interactive roles of the
27 neuro-, immune, and other physiological systems in determining relationships
28 between behaviour and infection susceptibility. Secondly, as the study of behaviour
29 has shifted away from one-off measurements of single behaviours and towards a
30 behavioural syndromes / personality framework, research is starting to focus on the
31 consequences of parasite infection for temporal and contextual consistency of
32 behaviour, and on the implications of different personality types for infection
33 susceptibility. In addition, there is increasing interest in the potential for relationships
34 between cognition and personality to also have implications for host-parasite
35 interactions. As models well-suited to both the laboratory study of behaviour and
36 experimental parasitology, teleost fish have been used as hosts in many of these
37 studies. In this review we provide a broad overview of the range of mechanisms that
38 potentially generate links between fish behaviour, personality, and parasitism, and
39 illustrate these using examples drawn from the recent literature. In addition, we
40 examine the potential interactions between cognition, personality and parasitism, and
41 identify questions that may be usefully investigated with fish models.

1. Introduction: Behaviour, personality and parasite infections in fish

Interest in the relationships between host behaviour and parasite infections has persisted for decades (Moore 2002; Barnard and Behnke 1990; Sukhdeo 1994; Moore 2013, 2012), and has intensified over recent years as new experimental approaches and tools have become available to address tantalizing questions, such as how parasites manipulate the behaviour of their hosts through neuromodulation (Adamo 2013; Adamo and Webster 2013; Thomas, Adamo, and Moore 2005; Hébert and Aubin-Horth 2014). Importantly, the behaviour of animals and their parasite infections may be linked at a range of phenotypic, ecological and evolutionary levels, and through a wide range of mechanisms, including those by which pre-existing behavioural variation influences infection susceptibility (Hart 1990, 1997).

Identifying the drivers of correlations between behaviour and infection, disentangling cause from effect, as well as identifying the neurophysiological mechanisms that underpin infection-associated behavioural variation among hosts (Demas, Adamo, and French 2011; Beckage 1997; McCusker and Kelley 2013; Adamo 2012), remain centrally important topics in this rapidly developing field (Poulin 2010; Poulin 1994).

Teleost fish are frequently used in studies investigating these relationships, as they are behaviourally well-characterized (Pitcher 1993; Godin 1999; Reebs 2001; Magnhagen et al. 2008) and are well-studied subjects in both lab and field parasitology (Buchmann 2007; Woo and Buchmann 2011). Furthermore, various small-bodied fish species – including sticklebacks, killifish, zebrafish, and guppies – are ideally suited to study under controlled laboratory conditions, and have been developed as excellent models for behaviour and / or experimental parasitology (Scott 1985; Lafferty and Morris 1996; Barber 2013), facilitating their use in studies aimed at understanding linking mechanisms. As a consequence, a significant body of work has emerged

examining the interactions between parasite infections and patterns of fish behaviour. Another benefit is that steroid hormones can be measured repeatedly and non-invasively, as they leak across the gills (Ellis, Sanders, and Scott 2013; Scott et al. 2008), meaning that relationships between behaviour, infection and (for example) cortisol can be studied experimentally. The recent development of fish as models for the experimental study of animal cognition (Brown, Laland, and Krause 2011), personality and behavioural syndromes (Conrad et al. 2011; Toms, Echevarria, and Jouandot 2010), means fish are ideally placed to give further insights into the mechanisms underlying relationships between individual differences in behaviour and parasitism.

Our aim in this review is to give a broad overview of the range of mechanisms that potentially generate links between fish behaviour and parasitism, and illustrate these using examples drawn from the recent literature. In addition, we examine the potential mechanisms linking cognition, personality and parasitism that may be usefully investigated using fish.

1.1 Infection-associated variation in fish behaviour: cause, effect or corollary?

While it is well established that patterns of behaviour among individual fish frequently co-vary with their level of infection with parasites (Barber, Hoare, and Krause 2000), very often these associations are based on correlational data, arising from behavioural studies carried out on wild-caught fish that vary naturally in infection intensity. Whilst these types of studies can generate interest and stimulate the development of testable hypotheses about underpinning mechanisms, they may give only weak insights into the likely ecological consequences or evolutionary basis

91 of relationships. There are a number of reasons to be cautious when interpreting such
92 correlations. First, as well as varying in the load of the focal parasite, wild-caught
93 organisms often harbor mixed infections with a variety of parasite and pathogen
94 species, making it difficult to attribute behavioural differences to any particular
95 infecting agent (e.g. Hammond-Tooke, Nakagawa, and Poulin 2012; Petney and
96 Andrews 1998). These problems may be exacerbated if infection by one parasite leads
97 to an increased (or decreased) probability of infection by another (e.g. Seppälä et al.
98 2009), a mechanism that can contribute to the generation of diverse parasite
99 communities among individual hosts (Rynkiewicz, Pedersen, and Fenton 2015).

100 Second, parasites are acquired through a wide diversity of routes, many of which are
101 ecological (including those acquired through feeding or social contact, or when
102 inhabiting specific habitats), so pre-existing behavioural differences among wild-
103 sampled fish may have influenced levels of exposure to parasites, potentially driving
104 infection-behaviour correlations. Third, the age, nutritional and growth history,
105 immune challenge and previous experiences of individual fishes sampled in this
106 manner are unknown, leading to – at best – noisy data, and also potentially affecting
107 their likelihood of reliable performance in experimental behavioural trials.

108 Recognizing these difficulties associated with using naturally infected fish to test
109 hypotheses about the ecological consequences, evolutionary implications or
110 mechanistic bases of infection-associated behavioural variation, researchers have
111 adopted a range of approaches to link behavioural differences among individuals
112 more clearly to parasite infections. Experimental infections of lab bred fish that are
113 free from co-infections – and can be standardized in terms of their genetic
114 background, age, nutritional background and growth history – have been used to
115 demonstrate causal links between infection and behaviour change in some cases.

More recently, there has been a shift toward using post-genomic tools to examine the effects of parasites on host behavior and underlying physiology, and this appears to offer a promising approach in the search for underpinning mechanisms (Hughes 2013; Biron and Loxdale 2013; Hébert and Aubin-Horth 2014).

1.2 Personality studies versus ‘simple’ behavioural studies

Over the past decade the fields of animal behaviour and behavioural ecology have experienced a paradigm shift in the way in which behaviour is studied, quantified and considered, with a move away from examining individual behaviours in isolation and toward investigating behaviour within an ‘animal personality’ or ‘behavioural syndromes’ framework (Sih and Bell 2008; Sih, Bell, and Johnson 2004; Reale et al. 2007). The major conceptual difference between these two approaches is that while ‘simple’ behavioural studies tend to examine single dimensions (antipredator behaviour, social behaviour, aggression, etc.) at one point in time, personality studies typically attempt to consider longer-term consistency of behavioural differences among individuals and the extent to which this generates a predictable syndrome of behaviours across contexts. As a consequence, the concept of animal personality incorporates notions of temporal consistency in behaviour, and of the cross-contextual nature of individual behavioural differences, both of which have far-reaching implications for interactions with parasites (Barber and Dingemanse 2010; Kortet, Hedrick, and Vainikka 2010; Poulin 2010; Poulin 2013).

An example may serve to outline the distinction between the simple ‘behavioural’ and the ‘personality’ paradigms, in the context of the current review. Hungry fish may need to investigate risky foraging environments and as a consequence expose

themselves to infective parasites that may be prevalent in such environments. A study in which we hold some fish without food for a period of time and then study their propensity to explore a risky foraging habitat would give insight into how a particular behaviour (in this case exploration) might affect parasite exposure. Similar approaches could be taken to investigate the risk of promiscuous behaviour on susceptibility to sexually-transmitted infections (STIs), or shoal membership on acquiring socially-transmitted parasites. However, while documenting how specific behaviours affect parasite exposure provides an important first step, this might be less insightful at an ecological or evolutionary level, since most (or even all) fish will be hungry, reproductively active or sociable at some points in their lives, and so spend a proportion of their time exposed to elevated infection risk. However, if some individual fish are *consistently* more likely to forage in risky habitat, engage in sexual activity or join shoals – as a consequence of ‘personality’, underpinned by physiological or genetic differences – then this would be expected to have a far greater ecological or evolutionary relevance, not least in terms of the distribution of parasites among and within host populations. Furthermore, if behavioural differences between individuals are consistent over time, this might also promote behavioural syndromes – relationships between contextually different behaviours within individual fish (Conrad et al. 2011; Sih, Bell, and Johnson 2004) – that may also have implications for interactions with parasites (Barber and Dingemanse 2010; Kortet, Hedrick, and Vainikka 2010; Poulin 2013).

The previous example exemplifies the notion that behavior and personality affect an individual’s probability of exposure, but other stages exist in the host-parasite interaction (Figure 1). Indeed, behaviour and personality can also connect – via various physiological mechanisms – with the probability of infection given a

particular level of exposure (Hawley et al. 2011; McCusker and Kelley 2013). Infected hosts often display a distinct phenotype from uninfected conspecifics, a phenotype that of course includes behaviour and personality (Adamo 2012; Adamo 2013; Adamo and Webster 2013). Thus, as both individual behaviours and personality can affect the host-parasite interaction, a consideration of both types of studies is appropriate, and included in this review relevant to the different stages of the interaction.

[FIGURE 1 HERE]

2. Behaviour, personality and infection susceptibility

There is growing evidence, from a wide range of taxa including fish, that pre-existing differences in behaviour can influence the interactions of host organisms with parasites, potentially driving correlations between host behaviour and infection (Koprivnikar, Gibson, and Redfern 2012; Stumbo et al. 2012; James et al. 2008; Wisenden, Goater, and James 2009; Dizney and Dearing 2016; Aalvik et al. 2015; Boyer et al. 2010). Most intuitively, a correlation may arise if behaviour alters the likelihood of exposure (Daly and Johnson 2011; Dizney and Dearing 2013). However, other mechanisms may also play a role. Individual immuno-physiological differences often have implications for both behaviour or personality and the probability of an encountered infective parasite establishing (Kittilsen et al. 2012; Øverli, Kotzian, and Winberg 2002; Øverli et al. 2002; Øverli, Winberg, and Pottinger 2005; Hawley et al. 2011). Furthermore, pre-existing behaviour / personality differences may have implications for infections post-establishment if, for example, individuals with different personalities are more (or less) likely to engage in infection-reduction

behaviours (Zylberberg, Klasing, and Hahn 2014; Zylberberg, Klasing, and Hahn 2013), or provide environments that are differently suitable for parasite growth, development or proliferation. Here we consider each of these mechanisms separately, detailing examples from fish where they exist, highlighting knowledge gaps and identifying areas for future study.

2.1 Probability of exposure influenced by behaviour or personality

Parasites exhibit a broad range of life cycles and transmission strategies, and fish become infected through many different routes. Consequently, whether – and the extent to which – particular behaviours are likely to influence parasite exposure will depend on the nature of transmission of parasite species.

Most studies examining the impact of behaviour on parasitism have focused on social behaviour. Associating with conspecifics could potentially increase or decrease exposure to parasites, depending on the specific nature of parasite transmission (Rifkin, Nunn, and Garamszegi 2012; Patterson and Ruckstuhl 2013; Côté and Poulin 1995). For directly-transmitted parasites that rely on close inter-individual distances for transfer between hosts, and which are often capable of rapid proliferation on the skin of the host, increased tendency to aggregate (i.e. join groups) or shoal more tightly is likely to lead to enhanced rates of transmission. For example, shoaling behaviour drives higher rates of monogenean (*Gyrodactylus* spp.) transmission in guppies *Poecilia reticulata*. Among shoals of fish held under lab conditions, and ‘seeded’ with controlled numbers of infected fish, parasite transmission was increased when shoal members showed more frequent and more prolonged contact (Richards, van Oosterhout, and Cable 2010). In that study, females shoaled more than males and

213 as a result had a four-fold increased risk of becoming parasitized; however, in a
214 subsequent study males exhibited greater numbers of intra-specific interactions and
215 had correspondingly high transmission rates (Richards, van Oosterhout, and Cable
216 2012). It therefore appears that shoaling *per se*, rather than any inherent differences
217 between the sexes, is responsible for increased transmission rates in this system.
218 Consistent with this, Richards (2010) found that shy individuals, which formed tighter
219 shoals, showed both higher levels of infection and greater increases in infection load
220 (Richards 2010); however, whether increased susceptibility arose solely from
221 increased transmission opportunity, or was influenced by lower resistance of shy fish
222 to infections (see section 2.2) is unclear.

223 In contrast, for parasite transmission strategies that rely on individual, free-swimming
224 infective stages targeting individual hosts – i.e. host-seeking behaviour similar to the
225 attack strategies of predators – aggregated fish may benefit from ‘dilution’ or
226 ‘swamping’ effects akin to those that provide antipredator benefits (Ims 1990; Pitcher
227 and Parrish 1993), with the *per capita* risk of infection being reduced in larger groups
228 (Mooring and Hart 1992; Poulin and Fitzgerald 1989; Côté and Gross 1993).
229 However, more complex relationships have also been demonstrated; for example,
230 among coral reef fish, fish in intermediate-sized shoals appear to gain the most
231 protection against ectoparasite infections (Sasal 2003).

232 Shoal members may also benefit from an increased ability to detect infective
233 parasites, and can adopt other group behaviours that can reduce the likelihood of
234 infection. Mikheev et al. (2013) found that rainbow trout *Oncorhynchus mykiss* held
235 in groups of five were better able to detect (and avoid) compartments of an
236 experimental tank harboring snails shedding infective cercariae of the
237 trematode *Diplostomum pseudospathaceum* than fish housed individually. Fathead

238 minnows *Pimephales promelas* held in groups were better protected against infective
239 trematode cercariae than singly-held fish; in the presence of parasites groups became
240 more cohesive and compact, with antiparasite benefits being greatest among
241 individuals occupying central positions (Stumbo et al. 2012).

242 Few studies have examined the implications of variation in non-social behaviors for
243 infection exposure in fish, yet variation in any of the major axes of personality might
244 reasonably be expected to be associated with altered susceptibility to infection by
245 parasites. For example, individual variation in aggression might be expected to
246 influence damage to skin and fins arising from encounters, rendering more aggressive
247 individuals that engage more frequently in fights more susceptible to acquiring
248 secondary infections by water-borne pathogens (e.g. in caged salmonids: Turnbull et
249 al. 1998; Abbott and Dill 1985). Variation in exploration tendency or general activity
250 levels might also be important; more active or more exploratory individuals may be
251 exposed to a greater number or a greater diversity of parasites if they have greater
252 home range size, or sample a greater diversity of habitat types. However, while
253 correlations between boldness and parasite loads have been reported among wild
254 caught fish (Wilson et al. 1993), we are not aware of any studies that have examined
255 these links experimentally. While such relationships may appear intuitive, studies of
256 wild-sampled mammal populations have not supported the hypothesis (Bordes et al.
257 2009; Nunn et al. 2003; Ezenwa et al. 2006). These studies are typically
258 compromised, however, by potentially important confounding factors, such as
259 relationships between individual quality (including immunocompetence) and home
260 range size. Fish may offer ideal subjects for future experimental tests of these
261 hypotheses. Individual differences in sexual behaviour might also predispose certain
262 individuals to sexually transmitted infections. Interspecific differences in promiscuity

can be substantial even among closely related species (Fitzpatrick et al. 2009), and in species that exhibit active mate choice, individuals vary in the extent to which they sample mates (Lindström and Lehtonen 2013). While we know of no studies that have examined how individual differences in promiscuity influence parasite exposure in fish, more promiscuous honey bees (*Apis mellifera*) have a higher risk of infection with *Nosema* microsporidians (Roberts et al. 2015). Such mechanisms have potential implications for the transmission of ectoparasites among externally-fertilizing fish, and microparasites of internal fertilizers

Inter-individual variation in energy metabolism and ‘pace of life’ has been suggested as a possible explanation for maintenance of personality differences within and between populations (Careau et al. 2008; Reale et al. 2010). Variation in the basal or resting metabolic rate, which is expected to co-vary with personality in fish (but see White, Kells, and Wilson 2016) may also have implications for the likelihood of parasite encounter. For example, fish with higher metabolic rates may emit stronger odour plumes that can be tracked by free-swimming parasites such as ectoparasitic lice or trematode cercariae (Mikheev, Pasternak, and Valtonen 2004), or have higher opercular beat frequencies, which increases the number of infective stages that are ‘filtered through the gills (Mikheev et al. 2014).

2.2 Influence of physiological correlates of personality on the probability of infection following exposure

Another mechanism that could generate links between pre-existing behavioural variation and parasite infection is the underpinning role of the neuroendocrine and immuno-physiological systems in behaviour and immune functioning (Winberg et al.

1997; Dufour et al. 2010; Øverli, Pottinger, et al. 2001). Individual differences in these systems have the potential to co-affect both individual personality and the probability of infection given a fixed level of exposure. For example, cortisol – the key hormone in the stress response of fish – has significant effects for energy metabolism, the innate immune response and the behaviour (including the aggression and locomotor activity) of rainbow trout (Øverli, Kotzian, and Winberg 2002; Cortés et al. 2013). As a consequence, trout selected for stress responsiveness develop highly divergent behavioural and neuroendocrine phenotypes (Øverli et al. 2002; Øverli, Winberg, and Pottinger 2005), with likely implications for their interactions with infective parasites. Cortisol, and the expression of a number of genes involved in the stress response, are also correlated with personality among wild-caught sticklebacks (Aubin-Horth, Deschênes, and Cloutier 2012). In salmonids, cortisol is also associated with skin melanin pigmentation (Kittilsen et al. 2009), which itself is known to be associated with variability to infection with ectoparasitic sea lice *Lepeophtheirus salmonis*. Taken together these studies suggest an underlying role of steroid hormones such as cortisol in determining phenotypic syndromes spanning behaviour, pigmentation, neuroendocrine and immune function in fish (Kittilsen et al. 2012).

2.3 Variation in host infection phenotype, dependent on personality

Infection phenotype is a concept that combines information on both the intensity or severity of infection with the host responses to infection – including its behaviour, physiology and immune function. Infection phenotype can therefore be considered as the way in which a particular infection manifests itself in a specific host individual, and presents as a disease. We propose that pre-existing variation in behaviour or personality might alter the infection phenotype of individuals though two non-

312 exclusive mechanisms.

313 First, individual variation in personality might alter the probability that infected fish
314 exhibit infection reduction behaviours. Many animals have evolved specific
315 behaviours – ranging in complexity from prey choice and grooming through to self-
316 medication – to avoid parasites, or reduce their levels of infection once parasitized
317 (Hart 1990, 1997). Fish engage in a wide range of such behaviours, including simple
318 behaviours such as flashing and jumping that dislodge ectoparasites, to more complex
319 social behaviours, including highly ritualized interactions with cleaner fish.

320 Personality may influence the likelihood of individuals engaging successfully in these
321 types of infection-limiting behaviours, especially in the case of cleaner-client
322 interactions, in which the behavior of client fish at cleaning stations can significantly
323 impact the likelihood of being cleaned (Côté, Arnal, and Reynolds 1998). However,
324 while it is known that variation in the personality of cleaner wrasse *Labroides*
325 *dimidiatus* in a non-cleaning context carries over to their cleaning behaviour (Wilson
326 et al. 2014), we are not aware of any studies linking individual personality among
327 client fish to the likelihood of seeking out cleaners or being cleaned. Given the level
328 of interest in cleaner-client systems in fish, we suggest this might prove a fruitful
329 avenue for future research.

330 Second, physiological mechanisms that underpin behavioural variation might
331 influence the progression of infection, following establishment. For example, if
332 personality variation is linked to energy metabolism (Careau et al. 2008), immunity
333 (Koolhaas 2008) or other component of ‘pace-of-life’ (Reale et al. 2010), or if it
334 affects competitive foraging ability, then this is likely to have implications for food
335 intake, or otherwise affect the availability of nutrients to growing or developing
336 parasites. While no studies have directly tested this hypothesis in fish, it is known that

parasite performance can be related to patterns of host growth and alimentation. For example, host growth rate co-varies with parasite growth in sticklebacks infected with *Schistocephalus solidus* (Barber 2005), suggesting that any physiological factors underpinning behavioural differences that affect host energetics are also likely to affect parasite performance in infected fish. In lab trials, sticklebacks that consistently exhibited more 'bold' behavior in experimental screenings in a non-foraging context also exhibited increased voluntary food intake under a no-competition scenario (Jolles, Manica, and Boogert 2016), supporting predictions of the 'pace-of-life' theory, and suggesting that pre-existing personality differences are likely to influence certain infection phenotypes.

2.4 Do population differences in personality relate to the threat of infection?

A number of influential studies have examined how inter-population variation in predation threat impact the personality of fish populations, demonstrating that fish populations facing high predation risk typically exhibit stronger behavioural syndromes than those from lower predation risk regimes (Dingemanse et al. 2007; Bell 2005). Since populations of host organisms can also vary consistently in the level of threat they face from parasites (Poulin and Morand 1999; Wilson 1998) any link between individual personality and infection risk could also lead to the evolution of populations that differ in personality, or in the strength or direction of behavioural syndromes. Such mechanisms, for example, have been implicated as causal factors underpinning observed correlations between parasite infection risk and average personality in different human societies (Fincher and Thornhill 2014). Furthermore, as discussed in 2.3 above, if infections have dramatically different consequences for the reproductive success or survival of hosts with divergent pre-existing personality, they

could select for differential personality types, or different behavioural syndromes, among populations that vary in the level or type of parasite exposure they normally experience (Barber and Dingemanse 2010).

Experimental studies examining such relationships in fish are now beginning to emerge. Kortet et al. (2015) compared personalities in two European minnow *Phoxinus phoxinus* populations that differed in both their intrinsic risk of parasite infection and in their predation risk, and identified population-level differences in personality; however, since infection and predation risk were confounded in these populations, it was not possible to test the hypothesis that parasitism could drive selection of personality. As a first step to determining the potential for parasites to shape the evolution of personality in host populations, experimental studies are needed that quantify the parasite susceptibility and infection phenotypes of fish that vary in their pre-exposure personality. Most recently, Jacquin et al. (2016) quantified behavioural variation among wild-caught and lab-bred guppy *Poecilia reticulata* populations that varied in both predation and parasitism risk, to determine the importance of each factor for behavioural phenotypes. Both factors were associated with behavioural variation between the populations, but while behavioural variation associated with predation differences had a strong genetic component and was retained in lab-bred fish, this was not the case for differences associated with differences in infection risk. The study suggests that population differences in behaviour associated with parasitism are more likely to reflect behavioural plasticity, and that parasites have a more transitory effect on behaviour than predators.

3. Parasite infections that change host behaviour

In contrast to the relative lack of studies that have investigated the consequences of individual differences in behaviour and personality for exposure and susceptibility to infection, the post-infection behaviour of fish has been extensively studied. Providing an encyclopedic coverage of all examples of infection-associated behavioural variation in fish is beyond the scope of this review, so we refer the reader to the selected examples presented in Table 1 (chosen to illustrate the diversity of behaviours, host and parasite taxa that have been investigated), and also to published reviews that focus on fish host-parasite systems (Barber, Hoare, and Krause 2000; Barber and Rushbrook 2008; Barber and Wright 2006).

In this section we instead focus on two key aspects of parasite-mediated behaviour change that have been advanced by studies employing fish host-parasite models. First, we look at how experimental fish-parasite systems are informing our understanding of the neurophysiological mechanisms underpinning parasite mediated behaviour change. Second, we examine how model fish-parasite systems are being used to investigate parasite-mediated host behaviour change within the animal personality and behavioural syndromes frameworks.

3.1 Neurophysiological mechanisms underpinning behaviour change in fish

In a landmark paper, Poulin (1994) discussed how an improved mechanistic understanding could give insight into the evolutionary basis of parasite-mediated host behaviour change, arguing that the discovery of direct neuro-manipulation mechanisms would provide strong evidence in favour of adaptive manipulation. Since then, neurobiologists and evolutionary behavioural biologists alike have become increasingly motivated to uncover these mechanisms, which may also shed light on

fundamental aspects of the control of animal behaviour (Demas, Adamo, and French 2011; Beckage 1997; McCusker and Kelley 2013; Adamo 2012). Alongside invertebrate models, fish have been featured significantly as hosts in these studies, with much of the effort focused on a small number of experimental systems. Here we discuss the insights from two of these study systems.

3.1.1 Case study I: Mechanisms of behaviour change in *Schistocephalus* infected sticklebacks

Three-spined sticklebacks *Gasterosteus aculeatus* are frequently infected with plerocercoids of the diphylobothriidean cestode *Schistocephalus solidus*, with infections being associated with a wide range of behavioural and physiological changes (Barber 2007, 2013; Milinski 1990; Barber and Scharsack 2010). The widespread distribution of the host and parasite in Europe, North America and beyond (Wootton 1976), the suitability of sticklebacks for lab and field studies of behaviour (Huntingford and Ruiz-Gomez 2009) and the dramatic effects of infection on host phenotype have meant that behaviour change in this system has been well studied. Early studies of naturally-infected fish documented a myriad of effects on antipredator behaviour (Giles 1983; Milinski 1984, 1985; Tierney, Huntingford, and Crompton 1993), shoaling behaviour (Barber, Huntingford, and Crompton 1995; Barber, Downey, and Braithwaite 1998), position in the water column (Lobue and Bell 1993; Lester 1971), and on respiration (Meakins and Walkey 1975), host energetics (Arme and Owen 1967) and sexual development (Heins and Baker 2008). The adoption of experimental *in vitro* parasite culture techniques originally developed to study parasite biochemistry (Smyth 1990) opened up the stickleback-*Schistocephalus* model for use as an experimental host-parasite system for the study

435 of experimentally-infected fish under controlled laboratory conditions (Barber and
436 Scharsack 2010). Subsequent studies have demonstrated that many of the effects
437 associated with infection – including effects on antipredator behaviour, escape
438 responses, habitat use and reproductive behaviours – are indeed caused by the parasite
439 (Barber 2007, 2013). Attention is now turning to using the experimental model to
440 examine the neurophysiological mechanisms underpinning the behavioural changes
441 caused by infection. *Schistocephalus* plerocercoids attain a very large size relative to
442 their hosts, and their growth – which is fuelled by host-derived nutrients – places host
443 fish under severe energetic stress under normal, food limited conditions (Barber,
444 Arnott, and Wootton 2008), which could have significant consequences for behaviour
445 even in the absence of direct neurochemical manipulation by the parasite. A key
446 question is therefore whether host behaviour changes constitute true ‘manipulation’ –
447 in other words, if they arise as a result of direct, adaptive manipulation of host
448 behaviour by parasites – or whether they represent unavoidable side effects of
449 energetic drain caused by the growing worms.

450 Altered behaviour of infected sticklebacks is associated with altered monoamine
451 neurotransmitters signatures in lobes of the brain. Among a wild-sampled population
452 of sticklebacks, *Schistocephalus* infection was associated with significantly elevated
453 HIAA:5-HT ratio in both the hypothalamus and brainstem, and a reduced
454 concentration of 5-HT and NE in the telencephalon compared to controls (Øverli,
455 Páll, et al. 2001). While tempting to speculate that these patterns might imply direct
456 manipulation of host neurochemistry by the parasite – perhaps by secreting
457 biologically-active substances such as neurotransmitter analogues, receptor
458 antagonists or other substances that alter biosynthetic pathways or the epigenetic
459 control of neurotransmission that interact directly with the host’s neuroendocrine

system – these results are also consistent with a chronic stress response. Alternatively, they might arise as a side effect of cryptic interplay between immune and neuroendocrine systems.

One potentially insightful approach is to examine transcriptomic changes in plerocercoids before and after the 50mg point – at which they attain infectivity to final avian hosts (Tierney and Crompton 1992) and change the behaviour of host sticklebacks (Tierney, Huntingford, and Crompton 1993; Barber, Walker, and Svensson 2004) – to identify candidate parasite-synthesized molecules that could be involved in host-parasite molecular ‘cross-talk’ (Hébert and Aubin-Horth 2014). The development of a large transcriptomic dataset, spanning the pre-infective, post-infective and adult stages of *Schistocephalus* worms, now provides a solid foundation for such studies (Hébert et al. 2016). Hébert et al. (2015) identified 94 proteins, with four of them being either secreted or membrane proteins from *Schistocephalus* that showed high local sequence homology with stickleback proteins, which could potentially act as signaling molecules to modulate host physiological pathways involved in the control of behavioral phenotypes. These candidate proteins include a member of the *Wnt* family of signaling molecules, which play an important role in cell-to-cell interactions, and others that are involved in ion transport and post-translational protein modification. Using a differential gene expression analysis, Hébert et al. (submitted) were able to identify a large module of 407 co-expressed genes that were significantly up-regulated in infective, compared to non-infective, plerocercoids. The majority of the enriched genes with GO-annotations had functions involved in cellular responses to drugs and neuromodulators, and secretion and transport of various molecules through the cell membrane; however, this module was also notable because the majority of these differentially expressed genes were un-

485 annotated. For example, the top 15 most highly differentiated genes between pre-
486 infective and infective plerocercoids were all completely unknown, and all were
487 *Schistocephalus*-specific, with no homology match to any known database except the
488 *S. solidus* genome. These results provide tantalizing glimpses into how future studies
489 may utilize genomic and post-genomic techniques to examine the molecular
490 (epi)genetic basis of behaviour change; they also highlight the level of work still
491 needed, for example, to assign functions to parasite genes.

492 An alternative to studying the proximate mechanisms directly is to examine the
493 ultimate patterns of behaviour observed, to determine whether they are best explained
494 by the adaptive or non-adaptive side effects hypotheses, and the utility of the
495 stickleback-*Schistocephalus* system facilitates this approach. Recent studies have used
496 elegant experimental infection approaches to generate a ‘conflict’ between co-
497 infecting *Schistocephalus* plerocercoids, and have studied the behaviour of infected
498 stickleback hosts to gain insight into the likely mechanisms. Hafer and Milinski
499 (2016) used temporally-separated infections to generate stickleback hosts that
500 harboured two parasites, such that only the older co-infecting worm had attained a
501 mass greater than the 50mg infectivity threshold. The behaviour of these host fish was
502 compared with the behaviour of fish harbouring a single, infective worm. The
503 prediction was, that if parasites manipulated behaviour directly, then the smaller
504 worm would either counteract – or at least, not augment – the manipulative action of
505 larger worms such that behaviour of doubly-infected ‘conflict’ fish should be
506 manipulated no more than singly infected fish. However, behaviour was altered more
507 severely in the ‘conflict’ fish. While this appears to provide evidence against adaptive
508 parasite induced host ‘manipulation’, and supports the ‘nutritional side effect’
509 hypothesis, at least one alternative explanation exists. It is possible that plerocercoids

in co-infections, which grow more slowly than in single infections (Heins, Baker, and Martin 2002), may switch to an alternative developmental strategy that permits successful transmission at a smaller body size. Future studies will need to measure the reproductive potential of single and co-infecting plerocercoids in order to relate the consequences of host behaviour change more clearly to parasite fitness.

While a consensus has yet to be reached on the nature of the mechanism(s) underpinning the behavioural changes in three-spined sticklebacks infected with *Schistocephalus solidus*, this system is uniquely well-suited to such investigations, and further studies are underway. The greatest insights seem likely to come from studies that combine both the proximate and ultimate approaches, studying both the mechanistic basis of behaviour change and the fitness implications for hosts and parasites under naturalistic environmental conditions.

3.1.2 Case study II: Digenean infections in the eyes and brains of teleost fish

Parasites that locate in, or close to, sensory and neural tissues including the brain have particular capacity to influence behaviour; indeed, the preferences of parasites for these locations may have evolved at least in part because of the potential to manipulate hosts.

Diplostomatid trematodes are parasites that infect birds as adults, and commonly utilize fish as 2nd intermediate hosts in their life cycle. Fish become infected when free-swimming cercariae released from snails penetrate their skin, and the parasites migrate to target locations through host blood vessels (Haas et al. 2007; Matisz and Goater 2010; Matisz, Goater, and Bray 2010; Sandland and Goater 2000), before undergoing development to the metacercarial stage of development, which is infective

534 to predatory birds. Some of these parasites (e.g. the *Diplostomum* spp. complex) target
535 various tissues of the fish eye, including the lens, vitreous humor and retina and
536 infections with these parasites are associated with reduced visual acuity in feeding
537 trials (Owen, Barber, and Hart 1993), most likely as a result of physical damage to
538 sensitive optical tissues. For example, dace (*Leuciscus leuciscus*) infected by
539 increasing numbers of *Diplostomum spathaceum* are less efficient foragers, and need
540 to spend more time foraging to compensate (Crowden and Broom 1980). Infected
541 trout are also more easily caught by humans with dip-nets (Seppälä, Karvonen, and
542 Valtonen 2005), and form smaller, less cohesive shoals than non-infected conspecifics
543 (Seppälä, Karvonen, and Valtonen 2008). Taken together, the effects on host visual
544 performance and behavior imply a higher susceptibility of host fish to predation by
545 surface-feeding birds, though this has yet to be conclusively demonstrated (Seppälä,
546 Karvonen, and Valtonen 2006). Cataract formation is commonly associated with
547 *Diplostomum* infection, and is likely the mechanism through which visual acuity is
548 reduced (Karvonen, Seppälä, and Valtonen 2004; Seppälä, Karvonen, and Valtonen
549 2011). Alternatively, trematodes residing in the eye could reduce visual acuity
550 directly by occluding the visual field. For example, *Tylodelphys* trematodes in the
551 eyes of common bully (*Gobiomorphus cotidianus*) remain unencysted and move in
552 front of the fish's visual field during the day, but not at night (Stumbo and Poulin
553 2016). Daytime obstruction of the common bully's visual field is believed to make
554 host fish more susceptible to predatory birds that forage during the day, while
555 allowing the fish to maintain vigilance against nighttime-foraging predatory fish
556 which are not suitable definitive predators for the parasite (Stumbo and Poulin 2016),
557 but additional studies are necessary to explore this hypothesis.

558 Other species – including *Diplostomum phoxini*, *Orinthodiplostomum ptychocheilus*,

559 and *Euhaplorchis californensis* – target the brain, where they accumulate over the life
560 of the fish and can achieve high densities on the surface and in various brain lobes
561 (Matisz and Goater 2010; Matisz, Goater, and Bray 2010; Barber and Crompton 1997,
562 1997; Sandland and Goater 2000; Shaw et al. 2010). While *Euhaplorchis* species
563 reside on the brain surface, species in the genera *Diplostomum* and
564 *Ornithodiplostomum* tend to reside within their host's brain tissue; for example,
565 *Diplostomum phoxini* infecting European minnows (*Phoxinus phoxinus*) tend to
566 aggregate in the cerebellum, medulla oblongata, and optic lobes (Barber and
567 Crompton 1997). Behavioral changes are likely associated with pathology, as the
568 parasites appear to consume the host's brain tissue directly, compounds secreted by
569 the parasite appear to degrade surrounding brain tissue, and the presence of host-
570 derived rodlet cells suggests a neuroinflammatory response to infection (Dezfuli,
571 Giari, and Shinn 2007; Dezfuli et al. 2007). Metacercariae of *Ornithodiplostomum*
572 *ptychocheilus* infecting fathead minnows (*Pimephales promelas*) also initially
573 aggregate in the cerebellum and optic lobes (Hendrickson 1979), and for about 28
574 days post-infection project microvilli that presumably are used to feed on host brain
575 tissue (Goater, Bray, and Conn 2005). After 28 days post-infection, the trematodes
576 migrate to the meninges, encyst, and stimulate the production of rodlet cells indicative
577 of a host neuro-inflammatory response (Matisz, Goater, and Bray 2010). No changes
578 in social behavior or antipredator behavior were noted in naturally infected fathead
579 minnows (Wisenden et al. 2012). However, reduced optomotor responses in fathead
580 minnows infected by *O. ptycholcheilus* have been observed (Shirakashi and Goater
581 2002). These behavioral changes likely reflect pathology as they are observable while
582 the parasite is maturing but not when the parasite has matured and is competent to
583 infect definitive hosts (Shirakashi and Goater 2005).

California killifish are infected by metacercariae of a trematode parasite, *Euhaplorchis californiensis*, which reside on the surface of the killifish brain. Infection reaches near 100% prevalence in the adult population (Shaw et al. 2010), and infected killifish exhibit “conspicuous behaviors”, including darting to the surface of the water and performing rapid body contortions, far more frequently than uninfected killifish (Lafferty and Morris 1996). The frequency of conspicuous behaviors increases with *E. californiensis* infection intensity, and infected fish are 10-30 times more likely to be consumed by predatory birds, which are the definitive hosts of *E. californiensis* (Lafferty and Morris 1996). In both wild-caught and naturally infected killifish, *E. californiensis* infection is associated with parasite density-dependent decreases in serotonergic activity in the hippocampus (Shaw et al. 2009; Shaw and Øverli 2012). Additionally, while teleost fish frequently exhibit an increase in serotonergic metabolism in the raphe nuclei in response to stress, infection appears to dampen this response (Shaw et al. 2009). In fish, serotonin is associated with reduced aggression and locomotor activity (Winberg and Nilsson 1993). While direct links between serotonergic activity and conspicuous behaviors have yet to be established, these results suggest that *E. californiensis* may induce conspicuous behaviors (which are largely locomotory) through suppression of the host serotonergic system.

3.2 Host behaviour change in the context of animal personalities and behavioural syndromes

Since the adoption of the animal personality paradigm by ethologists and behavioural ecologists, a small number of studies have attempted to investigate the effects of parasite infections on fish behaviour using these approaches. These studies have

addressed two major themes; the effects of parasite infections on the temporal consistency of host behaviour, and on the relationships between behaviours among infected, compared to non-infected, sub-populations of fish. Parasites have been suggested to increase or decrease temporal consistency of host behaviour following infection, as a result of damage or manipulation of sensory or motor systems that could either generate more erratic behaviour, or channelize host responses to be less variable; similarly, it has been suggested that parasites could either generate / strengthen or weaken / decouple existing behavioural syndromes, if this gives them a selective benefit, for example in terms of enhancing transmission to susceptible predators (Barber and Dingemanse 2010; Poulin 2010; Poulin 2013).

Hammond-Tooke et al. (2012) studied the activity, aggression and boldness of wild-caught common bullies (*Gobiomorphus cotidianus*) that varied naturally in their infection levels with four different trematode parasites. Behaviour was tested in the presence and absence of a predator cue, and the repeatability of – and correlations among – behaviours were quantified. Multiple uncontrolled co-infections made it difficult to interpret the results of the study, but one interesting result was that temporal consistency of activity tended to be related negatively to infection levels. As the study used naturally infected fish, it was not possible to determine whether fish showing greater consistency in their activity levels were less susceptible to infection, or whether higher levels of infection generate greater within-individual variation in activity; either appear possible, and experimental studies would be required to gain further insights.

Recognizing the potential for experimental infection studies to provide detail on mechanisms, Kekäläinen et al. (2014) compared the boldness, activity and exploration behaviour of European minnows *Phoxinus phoxinus* that had been experimentally

infected with the brain-dwelling trematode *Diplostomum phoxini* with that of sham-exposed controls. Their results showed that while there were no differences in mean behavioural values, infected fish showed higher repeatability in boldness and activity, and lower repeatability in exploration than controls, and there was some evidence that – among fish harboring the highest levels of infections – that the boldness-exploration syndrome exhibited by non-infected fish might break down. However, the documented effects of infection on host personality are not consistent between study systems. In a similar study involving rainbow trout being exposed to controlled doses of *Diplostomum pseudospathaceum*, which develops in the eye rather than the brain of the host fish, infected fish were found to be less bold than controls – suggesting a single-axis effect on behaviour – but there was no difference between parasitized and control fish in terms of the temporal consistency of, or relationships between, individual behaviours (Klemme, Kortet, and Karvonen 2016). Further experimental studies are now needed to test the generality of the finding that parasite infections can have implications for the temporal and cross-contextual consistency of behaviour, to gain greater insights into wider implications of infection for the ecology and evolution of behaviour.

4. Personality, cognition and the potential for interaction with parasites

Cognition has been defined as the acquisition, processing, storage and use of information (Shettleworth 2010). In recent years, there has been a surge of interest in relationships between personality and cognition in non-human animals (Griffin, Guillette, and Healy 2015; Sih and del Giudice 2012). A long established idea is that the proactive-reactive axis is associated with both personality traits and learning tendencies (Coppens, de Boer, and Koolhaas 2010). Proactive animals tend to be

bolder and more aggressive, but less sensitive to and thus slower to learn about changes in their environment. Sih & Del Giudice (2012) built on this idea to outline a series of hypotheses on relationships between behavioural types and cognitive styles. They first noted, as have others, that behavioural types fall along a 'fast-slow', risk-reward continuum where fast behavioural types (bolder, more active, more aggressive, more exploratory) take greater risks to gain greater rewards (compared to slow behavioural types). They then added that cognitive styles can also be arrayed along a fast-slow continuum based on a speed-accuracy tradeoff where rapid decisions, based perhaps on less information collection, and faster, less careful processing would tend to be less accurate. Putting these two simple generalities together yielded the prediction that proactive, fast-exploring, bold, aggressive animals would tend to be more impulsive, less choosy, and more risk prone. With regard to learning, predictions on personality and learning depend on the type of task. Sih and Del Giudice (2012) predicted that fast, high risk, high reward personality types would learn new activity-based tasks more quickly, but would be slower to learn avoidance tasks and slower at reversal learning.

Since 2012, numerous studies have tested these predictions, including studies on fish (Mamuneas et al. 2015; DePasquale et al. 2014; Kotrschal et al. 2014; Trompf and Brown 2014), and have found mixed results. Griffin et al. (2015) noted, however, the logistical challenges associated with conducting a proper test of relationships between personality and cognition, and concluded that to their knowledge, no studies have yet fulfilled their criteria for testing Sih and Del Giudice (2012)'s hypotheses.

Although the 'jury is still out' on whether we are making progress towards a general theory on individual differences in personality and cognition, here we outline two major areas in which cognitive science might be linked to host-parasite interactions.

First, we suggest that pre-existing individual variation in cognitive ability, potentially linked to variation in personality or behavioural ‘type’, may have implications for infection susceptibility. Second, we examine the possibility for infections to interfere with host cognitive function.

4.1 Avoiding infections

Here we explore a number of different routes through which variation in cognition might influence parasitism. Fish can use visual and other cues to detect parasite infections and use the information to make avoidance decisions. For example, sticklebacks can detect ectoparasitic *Argulus* spp. lice and actively avoid vegetation infested with the parasites; furthermore, these fish also avoid habitat types associated with increased risk of *Argulus* infection, even in the absence of the parasites themselves (Poulin and Fitzgerald 1989). For parasites that infect fish hosts by penetrating the skin, chemicals released from the damaged epithelium can be used by fish to identify and avoid risky habitats (Chivers et al. 2007). Given their clear potential to significantly impact fitness, many of the cognitive mechanisms by which fish identify and avoid predators and/or high predation risk habitats, including the use of social cues (Brown and Laland 2003), are also expected to be used in parasite detection.

Following the Sih and Del Giudice (2012) hypothesis on relationships between risk-reward tradeoffs, fast-slow behavioural types and speed-accuracy cognitive styles, we hypothesize that bolder, more aggressive, more exploratory animals might not only tend to encounter more parasites (e.g., by using a broader range of habitats including those with more parasites), they might also be slower to learn to avoid situations

associated with high parasite risk. That is, they might be less attentive to cues associated with parasites, and slower to learn cues or habitats associated with higher parasite risk.

Interestingly, an alternative framework suggests the opposite conclusion: that faster behavioural types should be quicker to learn to avoid parasites. If faster behavioural types are more likely (than slow ones) to encounter parasites and if parasites can be very costly, then these bold, exploratory animals should have had stronger selection favoring the evolution or development of a stronger tendency to learn cues that would help them avoid parasites. Or, even if personalities do not differ in their tendency to learn from experience with parasites, if faster behavioural types simply have more experience with parasites, they should have a higher likelihood of learning to avoid situations with high parasite risk. Recent experimental evidence in support of this hypothesis has been provided by Klemme and Karvonen (2016) who demonstrated that bolder sea trout *Salmo trutta* performed better in learning tests than shy individuals, suggesting that an increased investment in cognitive ability may be an adaptive compensatory response of individuals with ‘faster’ behavioural types that are more likely to encounter infective parasites.

An interesting ‘special case’ involves socially-transmitted parasites. Animals, including fish, frequently differ in sociability (e.g. Cote et al. 2010). More social animals are more likely to be found in larger schools where they might be exposed to more parasites; however, if sociality is associated with higher parasite risk, social individuals should also be more attuned to, and faster to learn to avoid specific situations associated with risk of parasite transmission.

To date, few studies have tested these contrasting predictions, but we suggest that fish may provide ideal models for the subsequent development of this field. Intriguingly,

because host-parasite interactions are dynamic, predictions on associations between personality, cognition and parasites might depend not just on how personality and cognition relate to host responses to parasites, but vice versa on how parasites affect personality and cognition. We earlier discussed how parasites influence host personalities; we next discuss how they might also affect host cognition.

4.2 Impacts of infections on cognitive processes: Does infection affect learning and memory in fish?

The effects of parasite infections, or their associated consequences for immune stimulation, on cognitive processes have been widely studied in mammals, including humans (Sternberg et al. 1997), and some invertebrate model systems. For example, honeybees (*Apis mellifera*) that receive a non-pathogenic stimulant to the immune system have a reduced ability to associate an odour with a sugar reward (Mallon *et al.*, 2003) and bumblebees (*Bombus terrestris*) whose immune systems are experimentally challenged perform worse in memory tests than healthy bees (Riddell and Mallon, 2006). This suggests a trade-off between high functioning immune systems and increased learning and memory. Kavaliers and Colwell (1995) found mice (*Mus spp.*) infected with the nematode *Heligmosomoides polygyrus* had reduced spatial learning ability, and mice infected with *T. gondii* are also shown to have impaired learning (Hodkova *et al.*, 2007), though it is unclear whether this is due to an impaired ability to recognise the learning stimuli, or learning ability *per se*.

Fish exhibit the full range of cognitive abilities, as discussed extensively in this volume and elsewhere (Brown, Laland, and Krause 2011), and are particularly well studied in the context of social learning, cooperation and spatial learning (Bshary and

Brown 2014). Despite this, we are aware of no published studies that have yet examined the implications of parasite infections for the cognitive abilities of fish. Again, we suggest that many of the experimentally-amenable, laboratory fish-parasite systems that exist offer ideal opportunities to investigate the implications of infections for cognitive function, both at a mechanistic basis and also in terms of the ecological consequences of parasite-induced changes. Zebrafish (*Danio rerio*), which are well-established as models for experimental cognitive neuroscience (Oliveira 2013; Spence, Magurran, and Smith 2011), have been used to examine the mechanistic basis and functional aspects of personality (Kern et al. 2016; Martins and Bhat 2014; Norton et al. 2011), and are frequently infected in laboratory facilities with parasites that have reported effects on behaviour (Spagnoli, Sanders, and Kent 2016; Spagnoli, Xue, and Kent 2015), might be especially well suited for the future development of this exciting research direction.

4.3 Parasites, cognition and environmental heterogeneity

As well as conferring potential fitness benefits (Dukas and Bernays 2000), cognitive function also incurs costs, including energetic costs associated with forming and retrieving information (Dukas 1999) and opportunity costs (Sih 1992). As a consequence, behaviours that rely on advanced cognitive abilities are expected to evolve only in environments in which they provide adaptive value (Niemelä et al. 2013). In the context of our review, in environments that offer a uniform, persistent threat of parasite infection, the costs of cognitively-demanding behaviours may not be sufficiently covered by the associated benefits. Similarly, in environments where the risk of infection is highly unpredictable over temporal or spatial scales, there may be little selection for cognitively-demanding behaviours. On the other hand, selection for

such behaviours might be expected to be strong in environments where the threat of infection is moderate and intermediately variable. Furthermore, following arguments proposed by Niemelä et al. (2013), such environmental differences may also have implications for individual flexibility *versus* consistency of cognitively-demanding behaviours. While these hypotheses remain untested in the context of host-parasite interactions, we suggest that fish may prove excellent models for testing these ideas within an experimental framework.

5. Conclusions

The overarching aim of our review has been to examine the range of mechanisms that may engender links between fish behavior and parasite infections, specifically by exploring the different stages of the host-parasite interaction: exposure, infection probability given exposure, and phenotypic changes post-infection. Within these, we consider the roles played by neuro-, immune, and physiological systems, as well as their interplay. It is clear that we are only beginning to uncover the details of the extent of mechanisms that are involved, and that there is still a dearth of knowledge about how fish personalities and parasitism interact, even in well-studied model systems. While post-infection effects on host phenotypes have been relatively well studied, how pre-infection behaviour (and personality) affects infection susceptibility – and how this influences post-infection changes – remains largely unknown. Similarly, how changes affect personality, rather than simply behavior, is also only now starting to be investigated.

The suitability of many fish species both as model hosts for experimental parasitology and for behavioural research means they are well positioned for studying the

806 proximate mechanisms underlying the many links between host behaviour and
807 infection status, potentially allowing cause, consequence, and corollary to be
808 separated in controlled laboratory studies. Such studies will increase our
809 understanding of interactions between the endocrine, immune, and neuronal systems
810 and pave the way toward a more integrated understanding of the mechanistic basis of
811 personality variation. Mechanistic studies of behaviour manipulating parasites may
812 prove particularly insightful in this regard, by potentially revealing the mechanistic
813 basis of personality. In particular, new genomic and post-genomic tools offer exciting
814 opportunities to delve far more deeply into the proximate mechanisms underpinning
815 behavioural manipulation by parasites. Despite the availability of well-suited fish
816 model systems, the role of cognition has been studied little in the context of
817 parasitism, and almost not at all in combination with personality; we suggest this as
818 an area that could rapidly expand and offer considerable opportunities for productive
819 research.

820 As model species, fish provide many benefits regarding accomplishing these research
821 goals. Their behaviours in the lab are well characterized, many species have published
822 genomes, their physiology, endocrinology and immunology is readily studied and
823 well characterized, and a number of useful, ecologically-relevant experimental host-
824 parasite systems have been developed to facilitate controlled lab studies. Taken
825 together, this means that fish-parasite models may require little “overhead” work
826 before targeted experiments can be used to gain information on these aforementioned
827 topics. To conclude, fishes appear to be good model organisms for studying the role
828 of behaviour, personality and cognition at all stages of the host-parasite interaction. In
829 the process we are likely to learn more about the mechanistic bases underpinning not
830 only parasite-host interactions, but the fundamental proximate mechanisms

831 underlying behavior and personality.

832

833

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842

Figure legend

Figure 1 Schematic diagram illustrating the major conceptual relationships linking individual differences in fish behaviour and / or personality to parasite infection. (1) Pre-existing differences in behaviour or personality influence exposure to infective parasites [Section 2.1]. (2) Pre-existing differences in behaviour or personality influence the probability of infection independently of any effect on exposure, as a result of (e.g.) underpinning immuno-physiological variation among hosts [Section 2.2]. (3) Pre-existing differences in behaviour or personality influence the growth, development or proliferation of parasites, or of host responses to established parasites, affecting the ‘infection phenotype’ of fish [Section 2.3]. (4) Infection *per se* alters host behaviour or personality [Section 3]. (5) Infection phenotype influences host behaviour or personality [Section 3].

857 **Table 1.** Selected examples of fish behaviour change associated with parasite infection, chosen to highlight the diversity of behaviours affected,
858 the range of infections studied and the mechanisms proposed.

Behaviour category	Host	Parasite	Behavioural change observed	Proposed physiological mechanism of behavioural change	Experimental or natural infection	Reference(s)
Aggression	Rainbow trout (<i>Oncorhynchus mykiss</i>)	<i>Diplostomum spathaceum</i> (Trematoda)	Reduced aggression when parasites pre-infective, increased aggression when parasites became infective	Not tested (parasite encysts in eye lens, inducing cataract formation and vision loss)	Experimental	(Mikheev et al. 2010)
Aggression	Common bullies (<i>Gobiomorphus cotidianus</i>)	<i>Apatemon</i> sp. (Trematoda)	Infection loads positively associated with aggression	Not tested	Natural	(Hammond-Tooke, Nakagawa, and Poulin 2012)
Antipredator behaviour	Rainbow trout (<i>Oncorhynchus mykiss</i>)	<i>Diplostomum pseudospathaceum</i> (Trematoda)	Reduced escape response, impaired crypsis, decreased shoaling	Not tested (parasite encysts in eye lens, inducing cataract formation and vision loss)	Experimental	(Seppälä, Karvonen, and Valtonen 2005, 2006; Seppälä, Karvonen, and Valtonen 2008)

Antipredator behaviour	Rainbow trout (<i>Oncorhynchus mykiss</i>)	<i>Diplostomum pseudospathaceum</i> (Trematoda)	Fish harboring pre-infective parasites less vulnerable to simulated predation and were less active, supporting the predation suppression hypothesis	Not tested (parasite encysts in eye lens, inducing cataract formation and vision loss)	Experimental	(Gopko, Mikheev, and Taskinen 2015)
Habitat selection	Longnose killifish (<i>Fundulus similis</i>)	<i>Euhaplorchis</i> sp. A (Trematoda)	Infected fish spent more time at the water surface; infection intensity correlated positively with time-at-surface	Not tested	Natural	(Fredensborg and Longoria 2012)
Sociality	European minnow (<i>Phoxinus phoxinus</i>)	<i>Ligula intestinalis</i> (Cestoda)	Infected fish exhibit higher nearest neighbor distances, more likely to occupy periphery of schools, occupy spatially inappropriate positions following a predatory attack compared with uninfected fish	Not tested (parasite grows to a large size in body cavity, possibly disrupting lateral line function)	Natural	(Barber, Huntingford, and Crompton 1995)
Boldness	European minnow (<i>Phoxinus phoxinus</i>)	<i>Diplostomum phoxini</i> (Trematoda)	Infected minnows showed higher repeatability in boldness and activity, reduced	Not tested	Experimental	(Kekäläinen et al. 2014)

			repeatability in exploration behavior			
Boldness	Rainbow trout (<i>Oncorhynchus mykiss</i>)	<i>Diplostomum pseudospathaceum</i> (Trematoda)	Infected trout were less bold than control fish	Not tested	Experimental	(Klemme, Kortet, and Karvonen 2016)
Antipredator behaviour	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	<i>Schistocephalus solidus</i> (Cestoda)	Infected fish exhibited increased surfacing, reduced antipredator behaviors	Elevated 5-HT activity in brainstems of infected fish	Experimental	(Øverli, Páll, et al. 2001; Lobue and Bell 1993; Giles 1983; Milinski 1985, 1984; Barber, Walker, and Svensson 2004)
Antipredator behaviour	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	<i>Schistocephalus solidus</i> (Cestoda)	Infected fish returned to food patches more quickly than uninfected conspecifics following a simulated predator attack	Not tested	Natural	Giles 1983
Sociality	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	<i>Schistocephalus solidus</i> (Cestoda)	Infected fish more likely to leave shoals to forage than uninfected fish	Not tested	Natural	(Barber, Huntingford, and Crompton 1995)

Antipredator behaviour	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	<i>Schistocephalus solidus</i> (Cestoda)	Infected fish feed in closer proximity to a live cichlid predator compared with uninfected fish	Not tested	Natural	(Milinski 1985)
Foraging	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	<i>Diplostomum pseudospathaceum</i> (Trematoda)	Infected fish experience reduced visual acuity, shorter reactive distance to prey	Not tested (parasite encysts in eye lens, inducing cataract formation and vision loss)	Natural	(Owen, Barber, and Hart 1993)
Competition	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	<i>Schistocephalus solidus</i> (Cestoda)	Infected fish display lower competitive ability compared with uninfected conspecific	Not tested (parasite encysts in eye lens, inducing cataract formation and vision loss)	Natural	(Barber and Ruxton 1998)
Antipredator behaviour	California killifish (<i>Fundulus parvipinnis</i>)	<i>Euhaplorchis californiensis</i> (Trematoda)	Fish with higher infection intensities perform more conspicuous swimming behaviors than fish with fewer parasites	Reduced 5-HT and increased DA activity in brainstems of infected fish	Natural and Experimental	(Lafferty and Morris 1996; Shaw et al. 2010; Shaw et al. 2009)

Antipredator behaviour	Roach (<i>Rutilus rutilus</i>)	<i>Ligula intestinalis</i> (Cestoda)	Compared with uninfected fish, infected fish preferred upper water layer and surfaced more readily following simulated predatory stimulus	Not tested	Natural	(Loot et al. 2001)
Reproductive behaviour	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	<i>Schistocephalus solidus</i> (Cestoda)	Infected males less likely to build nests and court females	Reduced levels of circulating 11-KT in infected makes	Natural / Experimental	(Macnab et al. 2011; Macnab, Katsiadaki, and Barber 2009; Candolin and Voigt 2001)
Reproductive behaviour	Two-spotted goby (<i>Gobiusculus flavescens</i>)	<i>Kabatana</i> spp. (Microsporidia)	Infected males courted females less intensely	Not tested (parasite encysts and destroys musculature)	Natural	(Pélabon et al. 2005)
Migratory behaviour	Gudgeon (<i>Gobio gobio</i>)	<i>Ligula intestinalis</i> (Cestoda)	Infected fish delayed migrations to deeper water at end of summer	Not tested	Natural	(Bean and Winfield 1989)
Migratory behaviour	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	<i>Schistocephalus solidus</i> (Cestoda)	Infected fish did not show same diel vertical movement as non-infected fish; overrepresented in trawl	Not tested	Natural	(Quinn et al. 2012)

			samples taken from the surface during the day			
Thermal choice	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	<i>Schistocephalus solidus</i> (Cestoda)	Fish infected with infective parasites preferred warmer temperatures than non-infected controls	Not tested (Parasites grow faster at warmer temperatures, suggesting parasite manipulation)	Natural / experimental	(Macnab and Barber 2012)
Thermal choice	Guppy (<i>Poecilia reticulata</i>)	<i>Gyrodactylus turnbulli</i> (Monogenea)	Infected fish preferred warmer temperatures than non-infected controls	Not tested (Parasite infection level decreased at warmer temperatures, suggesting self-medication by hosts)	Experimental	(Bean and Winfield 1989; Macnab and Barber 2012; Mohammed et al. 2016)

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