

Relative host body condition and food availability influence epidemic dynamics: a *Poecilia reticulata*-*Gyrodactylus turnbulli* host-parasite model

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(Received 28 June 2012; revised 23 August 2012; accepted 10 September 2012; first published online 5 November 2012)

SUMMARY

Understanding disease transmission is important to species management and human health. Host body condition, nutrition and disease susceptibility interact in a complex manner, and while the individual effects of these variables are well known, our understanding of how they interact and translate to population dynamics is limited. Our objective was to determine whether host relative body condition influences epidemic dynamics, and how this relationship is affected by food availability. *Poecilia reticulata* (guppies) of roughly similar size were selected and assembled randomly into populations of 10 guppies assigned to 3 different food availability treatments, and the relative condition index (K_n) of each fish was calculated. We infected 1 individual per group ('source' fish) with *Gyrodactylus turnbulli* and counted parasites on each fish every other day for 10 days. Epidemic parameters for each population were analysed using generalized linear models. High host K_n —particularly that of the 'source' fish—exerted a positive effect on incidence, peak parasite burden, and the degree of parasite aggregation. Low food availability increased the strength of the associations with peak burden and aggregation. Our findings suggest that host K_n and food availability interact to influence epidemic dynamics, and that the condition of the individual that brings the parasite into the host population has a profound impact on the spread of infection.

Key words: guppy, relative condition index, ectoparasites, transmission, aggregation, *Gyrodactylus*, population dynamics, epidemic spread.

INTRODUCTION

Infectious disease is a major cause of death for managed species and human populations (Murray and Lopez, 1997; Smith *et al.* 2009), and the relationship between nutrition and disease susceptibility is complex. The effects of nutrition and food availability have been well studied in vertebrates where limited access to food has been shown to have negative impacts on a host's ability to fight infections (Hughes and Kelly, 2006; Schmid-Hempel, 2011). Overcoming infection requires energy, so a host without sufficient caloric intake is likely to be more susceptible to parasite establishment and incur greater costs over the course of the infection, due to a weakened resistance that leads to higher infection intensity and/or a longer recovery period (Ilmonen *et al.* 1999; Lall, 2000; Gasparini *et al.* 2006; Brzek and Konarzewski, 2007). On the other hand, over-nutrition can also impair immune responses and may directly or indirectly optimize conditions for

the parasite (Woo, 2006). Host food acquisition, which serves as a proxy for nutrition, and disease defence are both also related to host body condition. An individual's condition is largely determined by food intake, and may also greatly contribute to an individual's ability to defend itself against disease; likewise, the energetic costs of fighting disease may diminish host condition (Møller *et al.* 1998). Therefore, host condition is generally used as a metric for an individual's health and well-being. Among the variety of metrics for measuring body condition in ecological and epidemiological studies, this study focused on relative condition index (K_n), as it takes into account an individual's weight-length ratio relative to that of others within the general population (Peig and Green, 2010).

These basic relationships have been shown to hold true with respect to the immune system of teleost fish (Landolt, 1989). For example, in isolated guppies (*Poecilia reticulata*) infected with the ectoparasitic monogenean *Gyrodactylus turnbulli*, low food-intake was shown to correlate with high parasite burden early after infection, presumably due to impaired innate immunity. However, intensity over the entire course of infection was higher in fish on a high-food diet, possibly because those individuals on the

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high-food diet had higher energy reserves to support larger parasite populations (Poulin and Rohde, 1997; Kolluru *et al.* 2006).

Guppies are live-bearing tropical teleost fish, commonly used as a laboratory model. Their diet largely consists of unicellular algae, benthic invertebrates and zooplankton (Dussault and Kramer, 1981). In the wild, guppies are infected by 2 gyrodactylid species, *Gyrodactylus bullatarudis* and *Gyrodactylus turnbulli* (see Harris and Lyles, 1992), that attach to the epidermis of their host via specialized hooks and feed on epithelial cells and mucus (Bakke *et al.* 2007). Although these ectoparasites are helminths, the guppy-gyrodactylid system provides an excellent model of microparasite epidemiology from a population dynamics perspective (Bakke *et al.* 2007). The parasites rapidly reproduce on individual guppies, their infection usually induces some host immunity (Scott, 1985a), they spread quickly through the host population by jumping to a new host during direct host-host contact or indirect contact with dislodged parasites at the surface of the water (Cable *et al.* 2002). Their external location on the fish allows infection to be monitored in a non-invasive manner (Scott and Anderson, 1984; Kearn, 1994), and parasite population dynamics on isolated guppies have been characterized under controlled conditions (Scott, 1982, 1985a), at different temperatures (Scott and Nokes, 1984) and under different feeding regimes (Kolluru *et al.* 2006). Furthermore, the epidemic dynamics have been studied in laboratory guppy populations (Scott, 1982; Scott and Anderson, 1984; Scott, 1985a,b, 1987; Richards and Chubb, 1998; Richards *et al.* 2010) and in mesocosms (Perez-Jvostov *et al.* 2012), but the impact of host condition and food availability on epidemic dynamics has not been examined.

The purpose of this study was to determine whether epidemic dynamics were influenced by pre-infection relative body condition (an indicator of health which compares individuals to the rest of the population rather than a simple weight-length ratio) and/or food availability, using the guppy-*Gyrodactylus turnbulli* host-parasite model. Given previous literature on condition and food intake on individual disease outcome, we predicted that both of these variables would influence epidemic dynamics.

MATERIALS AND METHODS

Fish, parasite and diet

Animal Care Approval was obtained according to McGill University Ethics Guidelines (AUP number 5759). Guppies were housed in the McGill University Department of Biology greenhouse at 26 °C ± 1 °C and a 12-h light-dark cycle. Feeder guppies obtained from a pet store in Montréal were bred in the laboratory for several generations without

parasites and were therefore naïve to *G. turnbulli* infection and presumed to be genetically similar. *Gyrodactylus turnbulli* obtained initially from a Montréal pet store and identified following Harris (1986) was maintained at high intensity in a laboratory population of feeder guppies by adding naïve fish on a regular basis according to Scott and Anderson (1984). For each experimental population, 10 adult guppies (5 males and 5 females) were placed in a 6 L tank (21 × 6 × 14 cm, water-level 12 cm) within a flow-through Aquaneering Inc. system (San Diego, CA, USA) designed to eliminate waste accumulation and maintain a steady flow of treated, filtered water through the system, thus homogenizing environmental conditions (except for food availability) in all treatments.

Experimental design

In order to test the effect of both excessive and insufficient food availability, 3 food availability treatments (high, low, and medium as a control) were replicated 7 times, for a total of 21 populations (each of 10 fish). Fish were fed TetraMin® (Tetra Werke, Melle, Germany) Tropical Food Flakes ground into a paste and distributed through a precision syringe (Hamilton Company, Reno, NV, USA) once daily. Based on preliminary observations that individual guppies of similar size to those used in our experiment consume 10 µl of flake paste before satiation, low food availability populations received 50 µl of flake paste/day, medium food availability populations received 100 µl of flake paste/day and high food availability populations received 200 µl of flake paste/day. Food availability levels were assigned to populations at random within each replicate. Our dependent variables included population level measures of infection. Our independent variables were initial relative host condition and food availability.

Experimental protocol

Fish were anaesthetized in 0.02% tricaine methanesulfonate (Finquel MS-222, Argent Laboratories, Redmond, WA, USA), buffered to a neutral pH with sodium bicarbonate. Excess water was removed with a KimWipe (Kimberly-Clark, Dallas, TX, USA) and fish were weighed to 0.001 g, and their standard length (tip of snout to end of caudal peduncle) was measured to 0.01 mm. Fish were then injected subdermally and away from major organs with visible implant elastomer dye (Northwest Marine Technologies Inc., Shaw Island, WA, USA) according to a unique marking scheme for individual identification. This marking technique does not affect fish behaviour and has low impact on mortality (Croft *et al.* 2003; Van Oosterhout *et al.* 2007;

Gordon *et al.* 2009). A total of 210 fish, with an average initial weight of 67.8 ± 1.4 mg and average SL of 14.7 ± 0.09 mm were used for this experiment. After weighing, measuring and marking, fish were randomly assigned to populations of 10 fish that were provided with their respective diets for a week prior to introduction of infection. All fish survived this period. Given that the length and weight of a mature guppy is unlikely to change significantly over a 17-day period, we only took these measurements prior to treatment/experimentation. While this is a limitation of our study, previous work in our laboratory has indicated no significant changes in these measurements for infected individuals over the course of 10 days, nor in uninfected fish after 1 week of altered diets (F. Dargent, *unpublished data*).

After 1 week, 1 female fish (the 'source' fish) was selected at random from each tank, anaesthetized in MS-222 and infected with 5 *G. turnbulli* by transferring 1 parasite at a time on a scale removed from a heavily-infected donor fish obtained from our *G. turnbulli* colony (Scott and Anderson, 1984). Within each replicate, the same donor fish was used to infect a female from the 3 food availability treatments.

Infections were then monitored every other day for 10 days. While *G. turnbulli* may persist in a population for much longer time scales (Richards and Chubb, 1998), our goal was to capture only the initial spread of infection throughout the population (and therefore parasite establishment within the population), and previous literature indicated that this time frame was sufficient to reach both peak prevalence and population peak parasite burden (Scott, 1985b). Each anaesthetized fish was examined using a Leica 18X dissecting microscope (Leica Microsystems GmbH, Wetzlar, Germany) and cold light source. Parasites were counted by scanning both sides of the fish beginning at the caudal fin and working towards the head and opening the fins. If a fish died, it was left in the tank for 1 day (Gheorghiu *et al.* 2007) so that parasites had the opportunity to transfer to a live host (Scott and Anderson, 1984). Rather than replacing an infected (dead) fish with a naïve one, which would change not only the proportion of naïve fish but also possibly the average population Kn , we calculated the average population density for each tank (total of fish alive in a population on each day of experiment divided by 10 days of experiment) in order to account for possible differences in transmission due to lower population density. However, so few fish died during this experiment (see Results section) that there were no significant differences in this variable among populations, and this variable was not used in the final analysis. The volume of food provided to the population was adjusted according to fish density by reducing the original volume by one tenth. After recording parasite loads on the tenth day, all fish were

treated with Clout® (Aquarium Products, Glen Burnie, MD, USA) and retired to a recovery aquarium.

Definition and calculation of dependent variables

Population parasite burden (the total number of *G. turnbulli* found in a fish population) was calculated for each sample day, and peak parasite burden (the maximum of this variable over the course of the experiment) was also recorded. Prevalence (the percentage of the population infected with *G. turnbulli*) was also calculated for each sample day, and its maximum over the course of the experiment was recorded. Incidence was defined as the number of initially uninfected fish within the population that became infected over the course of the 10-day experiment (Last, 2001). We defined infection establishment on a fish as parasites observed on 2 consecutive sample days on that fish. The degree of parasite aggregation within each guppy population was calculated as the variance to mean ratio of individual parasite burdens on the day of peak population burden. We noted whether or not the originally infected fish ('source' fish) was the most heavily infected fish on the day of peak parasite burden as an index of whether the 'source' fish continued to influence the epidemic dynamics after transmission had occurred. We refer to this binary variable as 'source burden'.

Definition and calculation of independent variables

For each fish, relative condition index (Kn) was used to assess host condition at the beginning of the experiment based on the initial (pre-food availability treatment) weight (W) and standard length (SL) of all hosts in the experiment. For each sex, a least squares regression of $\text{Log}(SL)$ and $\text{Log}(W)$ of all of the guppies used for the entire experiment was performed, and the slope (n) and intercept ($\log(a)$) for the line of best fit were obtained. Relative condition index (Kn) was then calculated for each individual fish using the formula: $Kn = W / (a * SL^n)$ (Le Cren, 1951). Kn , SL and initial weight of all fish were compared using one-way ANOVA and Tukey-Kramer post-hoc analysis to test for homogeneity of initial fish size and body condition among the 3 food availability treatments and across all 7 replicates. Individual initial Kn differed among replicates ($P < 0.0001$), but not among food availability treatments, indicating that initial Kn was homogenous among experimental treatments. A similar pattern was found for fish size: neither SL nor initial weight differed significantly among food availability treatments, but significant differences among replicates were observed ($P < 0.05$ for both). 'Source' Kn did not differ significantly among food availability

treatments. Average \bar{Kn} was then calculated for each population by calculating the mean Kn of all individuals in each population, and the Kn of the 'source' fish in each population was also noted.

Statistical analysis

All analyses were done using R Language and Environment for Statistical Computing version 2.14.2 (R Development Core Team, 2011). Generalized Linear Models (GLMs) were constructed to determine the effect of host relative body condition and food availability on population peak parasite burden, incidence, aggregation and 'source' burden. The distribution of each response variable was measured and then models fitting that distribution were generated using all independent variables ('source' Kn , the average \bar{Kn} of the population and food availability) and the interactions thereof. These models were tested using bi-directional stepwise model selection (stepAIC, MASS package) in order to find the combination of factors which yielded the lowest AIC value to produce the final model. In all cases, the level of significance was set at $P < 0.05$.

RESULTS

Gyrodactylus turnbulli infection established in all 21 populations and spread from the 'source' fish to at least 1 other fish. The prevalence reached 50% or more in 15 of the 21 tanks during the 10 days of the experiment. The total number of parasites also increased over time; peak parasite burden ranged from 5 to 222 and the day of maximum burden varied by tank, ranging from Day 2 to Day 10, although the day of peak did not vary significantly by food availability. In 12 of the 21 tanks, parasite burden reached a peak before day 10. The average population density did not differ among populations. Of the 11 fish that died (5.2%), 5 had been infected (2 of 6 fish from the low-food treatment, 1 of 3 fish from the medium-food treatment and 2 of 2 fish from the high-food treatment).

A summary of GLM outputs of the final models for population level disease outcomes can be found in Table 1.

Peak parasite burden

A significant interaction between 'source' \bar{Kn} and food availability was detected. The effect of 'source' Kn on peak parasite burden was lower at the medium ($P < 0.001$) and high ($P = 0.011$) food availabilities compared with the low food availability. 'Source' Kn had a highly significant ($P < 0.001$) positive impact on peak parasite burden ((Table 1a; Fig. 1).

Incidence

The number of non-source fish that became infected was positively related to the average \bar{Kn} of the population ($P = 0.028$) (Table 1b; Fig. 2). No other terms were significant in the final model.

Aggregation at peak burden

The degree of aggregation of parasites (variance to mean ratio) within a population was negatively affected by the average \bar{Kn} of the population ($P = 0.044$) whereas 'source' Kn had a positive impact ($P = 0.0001$) on the degree of aggregation (Table 1c). However, this relationship between 'source' Kn and aggregation was dampened at high food availability levels, as the interaction of 'source' Kn with medium ($P = 0.0006$) and high ($P = 0.001$) food availability was negative (Fig. 3).

Source burden

The Kn of the 'source' fish influenced whether it was the most heavily infected fish at the time of peak population parasite burden (Table 1d). When the average \bar{Kn} of the population was less than 1, the parasite load was more likely to be highest on the 'source' fish whereas when the average \bar{Kn} of the population was greater than 1, one of the other fish was more likely to have the highest parasite numbers at the time of population peak burden (Fig. 4). Food availability did not enter this model.

DISCUSSION

Our results demonstrate a consistent positive relationship between body condition of the initially infected 'source' host and major epidemic variables, indicating that the body condition of the individual through whom the infection was introduced to the population influences population-level infection outcomes. When the body condition of the 'source' fish was high relative to other fish in the population, the population peak parasite burden, the degree of parasite aggregation within the population and the likelihood that the 'source' fish was the most heavily infected at the time of peak parasite burden were higher. This indicates that parasites not only thrive on hosts of high condition, but specifically remain on hosts of high condition, particularly when relatively fewer hosts of high condition are available. This is consistent with our observation that incidence was positively associated with average \bar{Kn} but not 'source' Kn , implying that parasites were more likely to transfer to a new host when the surrounding fish had higher body condition. These relationships, however, were tempered by our environmental factor (food availability), as we observed lower parasite

Table 1. Summary of generalized linear model outputs for measures of epidemic dynamics

(a) Outcome: peak parasite burden (distribution: negative binomial)

Variable	Estimate (\pm s.e.)	z-value	P-value
Source $\bar{K}n$	12.0 (2.4)	4.94	<0.0001
Average $\bar{K}n$	2.1 (3.4)	0.61	0.54
Medium Food Availability	3.9 (4.7)	0.83	0.40
High Food Availability	6.3 (4.6)	1.37	0.17
Source $\bar{K}n$:Medium Food Availability	-12.9 (3)	-4.31	0.0001
Source $\bar{K}n$:High Food Availability	-7.7(3)	-2.52	0.011
Average $\bar{K}n$:Medium Food Availability	9.4 (4.8)	1.95	0.051
Average $\bar{K}n$:High Food Availability	2.1 (4.3)	0.48	0.63

(b) Outcome: incidence (distribution: normal)

Variable	Estimate (\pm s.e.)	z-value	P-value
Source $\bar{K}n$	1.3 (6.2)	0.22	0.83
Average $\bar{K}n$	20.5(8.2)	2.48	0.028
Medium Food Availability	1.0 (10.3)	0.09	0.92
High Food Availability	4.1 (10.3)	0.39	0.70
Source $\bar{K}n$:Medium Food Availability	-3.3 (7.6)	-0.44	0.66
Source $\bar{K}n$:High Food Availability	9.5 (7.8)	1.21	0.24
Average $\bar{K}n$:Medium Food Availability	2.8 (11.5)	0.24	0.81
Average $\bar{K}n$:High Food Availability	-13.6(10.7)	-1.27	0.22

(c) Outcome: degree of parasite aggregation at peak population burden (distribution: negative binomial)

Variable	Estimate (\pm s.e.)	z-value	P-value
Source $\bar{K}n$	602(106)	5.68	0.0001
Average $\bar{K}n$	-318(142)	-2.24	0.044
Medium Food Availability	242(177)	1.37	0.19
High Food Availability	275(178)	1.54	0.14
Source $\bar{K}n$:Medium Food Availability	-598(131)	-4.55	0.0006
Source $\bar{K}n$:High Food Availability	-578(135)	-4.28	0.001
Average $\bar{K}n$:Medium Food Availability	365(197)	1.85	0.088
Average $\bar{K}n$:High Food Availability	312(184)	1.69	0.11

(d) Outcome: highest parasite load at population peak on 'source' host (distribution: binary)

Variable	Estimate (\pm s.e.)	z-value	P-value
Source $\bar{K}n$	27.8 (11.3)	2.46	0.024
Average $\bar{K}n$	21.6 (10.6)	2.04	0.057
Source $\bar{K}n$:Average $\bar{K}n$	-26.7 (11.0)	-2.44	0.025

burdens at intermediate and high levels of food availability.

Introduction of an infected fish into a naïve population allows gyrodactylids to spread through the population. Whether infection reaches all fish in a population, and whether infection is sustained within a population is known to be a function of host population size and density, as well as host history of infection, and other characteristics of the host and parasite (Reno, 1998). In this study we were able to isolate effects of host relative condition from these other variables as all fish were naïve and we standardized host population size and density. To our knowledge, a measure of the 'quality' of the host that brings an infection into a population has not been examined, nor has this been considered relative to the

average 'quality' of other hosts. The effects of these 'qualities' on *Gyrodactylus sp.* behaviour have not been previously studied. However, such patterns of behaviour have been discussed in ecological theories in other systems. For example, optimal foraging theory suggests that successful foragers are those who assess the quality of the present foraging patch relative to their perception of the average patch (Pyke, 1984). Our data are consistent with the hypothesis that gyrodactylid parasites may also compare quality of 'patches' – in this case, potential guppy hosts. When arriving on a 'quality' host, it is to their advantage to stay on this host if the host has higher 'quality' than the average of other fish in the population. On the other hand, it makes sense for the parasite to move if the average quality is higher than

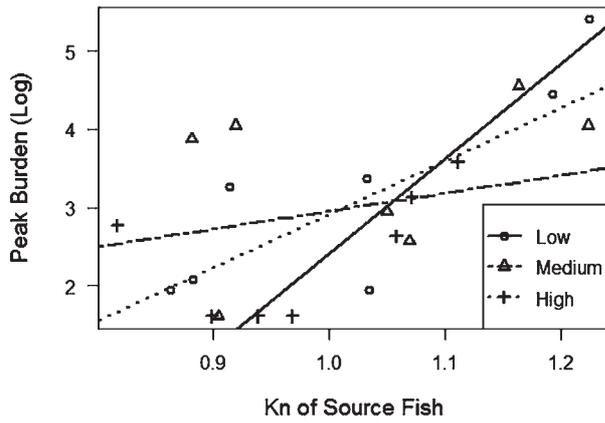


Fig. 1. Impact of interaction between relative body condition (Kn) of the 'source' guppy (*Poecilia reticulata*) and food availability on peak *Gyrodactylus turnbilli* burden in experimental epidemics, as demonstrated by best fit linear regression lines for low, medium and high food availability treatments ($n=7$ populations per treatment). Low food availability slope: 12.16, intercept: -9.76 ; medium food availability slope: 2.28, intercept: 0.67; high food availability slope: 6.82, intercept: -3.92 . Note: data were not log-transformed for statistical analysis but are shown transformed here for ease of viewing.

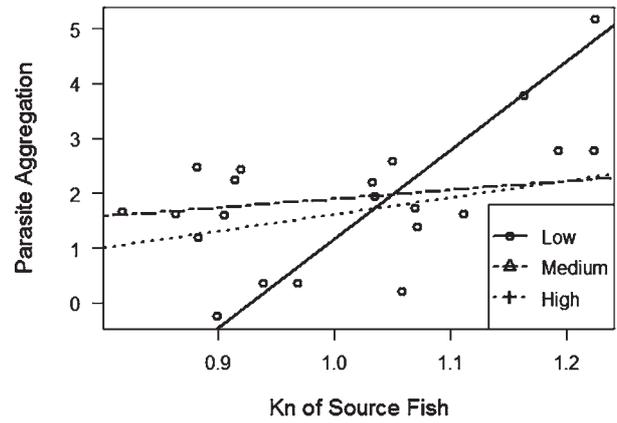


Fig. 3. Impact of interaction between relative body condition (Kn) of the 'source' guppy (*Poecilia reticulata*) and food availability on aggregation of *Gyrodactylus turnbilli* (variance to mean ratio on day of peak burden) in experimental epidemics as demonstrated by best fit linear regression lines for low, medium and high food availability treatments ($n=7$ populations per treatment). Low food availability slope: 16.23, intercept: -15.07 ; medium food availability slope: 1.63, intercept: 0.27; high food availability slope: 3.07, intercept: -1.46 . Note: data were not log-transformed for statistical analysis but are shown transformed here for ease of viewing.

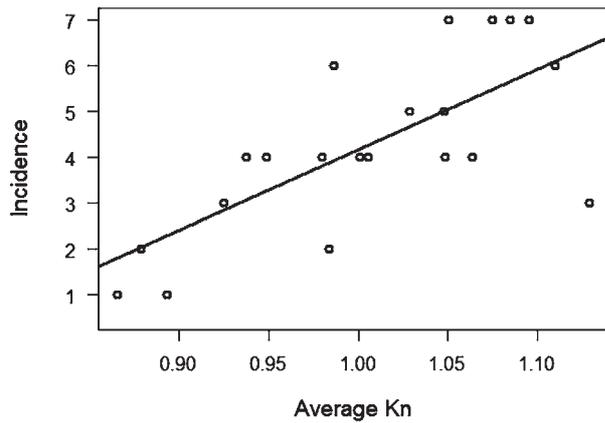


Fig. 2. Simple linear regression between incidence (total number of naïve fish in a population that became infected during the experiment) of *Gyrodactylus turnbilli* and average body condition (Kn) of guppies (*Poecilia reticulata*) during a 10-day experimental epidemic in 21 host populations. (Slope: 17.54, intercept: -13.37).

that of the 'source' fish. Such a line of logic is consistent with our findings, as we observed that parasites were aggregated on a 'source' host of high Kn , but were more dispersed on other hosts when the average Kn of the population was high. Future research into the impact of 'source' host condition on epidemic dynamics and mapping parasite transmission according to host relative condition may help to further illustrate the applicability of optimal foraging theory to host-parasite models.

Our observed positive relationship between 'source' fish size and high population parasite burden

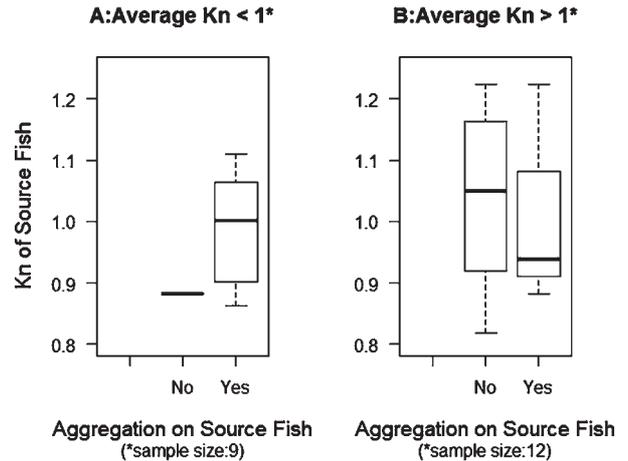


Fig. 4. Relationship between guppies (*Poecilia reticulata*) harbouring the majority of *Gyrodactylus turnbilli* on the day of population peak burden, average relative body condition of the fish population (average Kn) and relative body condition (Kn) of the 'source' fish. (A) When the average Kn was low (less than 1), the parasites tend to be aggregated on the 'source' fish. (B) When the average Kn was high (greater than 1), the parasites are less aggregated on the 'source' fish.

is consistent with the findings of Cable and van Oosterhout (2007) where parasite burdens were shown to increase with fish size, though their metric for fish body size was standard length and their infections were run on individual fish. Presumably, this relationship was observed because larger fish (with higher relative condition index) are able to offer more living space for ectoparasites (Poulin and

Rohde, 1997). Our results, however, indicate that initial relative condition of the 'source' fish, and not simply its length, not only played a large role in determining the course of infection on this individual (as seen by 'source burden') but also on the course of the epidemic as a whole. The positive relationship found between condition and parasite burden is counterintuitive in many aspects, as condition is assumed to be a major indicator of health and therefore disease resistance (Beldomenico *et al.* 2008), yet we saw that parasites were either aggregated on 'source' hosts of high condition, or had transferred to hosts of higher relative condition. Further investigation into why a high host initial relative condition translated to a greater number of parasites is required, as well as further investigation of the effects of absolute condition on disease resistance.

It is also possible that innate immunity (as all our fish were naïve to *G. turnbulli* infection acquired immunity could not have been an issue here) influenced epidemic dynamics within our populations. A large amount of variability in the resistance of individual guppies to *Gyrodactylus* sp. has been observed (Madhavi and Anderson, 1985; Van Oosterhout *et al.* 2003; Cable and van Oosterhout, 2007), and more recent work has identified major histocompatibility (MHC) class IIB genes to be an important part of guppy innate immunity which may be impacted by parasite-mediated selection (Sato *et al.* 1995; Fraser *et al.* 2009; Fraser and Neff, 2010). This issue deserves further research, and we acknowledge that innate immunity may have interacted with host condition in our populations, we believe it to be unlikely that significant genetic variability existed among tanks, since all fish had been obtained from aquarium stocks bred in the laboratory for several generations, and MHC class IIB genotypes tend to have low variability in aquarium stocks when compared to wild populations (Sato *et al.* 1995). Moreover our fish were selected for the experiment and assigned a feeding regime at random and therefore genetic variability should have been similar in all tanks.

Our study also revealed the importance of food availability in driving epidemic dynamics. The most dramatic relationship was observed at the low food treatment where both population peak burden and variance to mean ratio increased more dramatically with 'source' and average K_n , respectively, than at other food treatments. Although it is likely that larger fish would be able to acquire more food than the smaller ones, one can also assume that these larger fish also had greater food requirements than the smaller ones. As such, especially for the low food availability treatment, the larger fish may have been more limited in food intake on a per gramme weight basis than the smaller ones. This, together with competition among guppies for food when the

average K_n was high and food availability low, may have exaggerated inter-fish differences in host suitability, thus explaining the higher variance to mean ratio among the fish at the low food treatments. Our results are consistent with those of Kolluru *et al.* (2006) who found that low food availability led to higher parasite burdens. However, we have shown that initial condition of the fish plays an important role in this relationship.

Furthermore, being infected may also alter the individual's appetite. It has been documented in some cases that infected hosts may reduce their food intake as a defence mechanism, and this infection-induced anorexia may increase host resistance to the disease (Exton, 1997), as observed in guppies by Van Oosterhout *et al.* (2003). It is also possible that infected individuals may try to increase their food intake in order to compensate for the energetic costs of fighting infection (Kolluru *et al.* 2009). Unfortunately, the design of our study did not enable us to record food intake or weight gain of individual fish, and as such we do not know whether parasite infection, or parasite load, or host body condition altered food intake of the guppies. While it is unlikely that our host K_n would have changed significantly over the course of our short-term experiment, longer-term studies may benefit from observing how changes in K_n may alter epidemic dynamics.

This study attempted to bridge the gaps in our knowledge of the effect of individual nutritional status and body condition on basic epidemic behaviour. Our results indicate that several parameters related to the initial spread of an epidemic are determined as much by the current level of resource availability in an environment, as by individual factors such as host relative condition. Host relative condition exerted significant impacts on epidemic outcomes, especially when food availability was low. Importantly, we also found that the relative condition of the 'source' host was particularly important to the dissemination of infection through the host population. Further investigation into the effects of specific 'source' body condition on epidemics is required in order to better understand the spread of disease through naïve populations. These relationships may have significant implications for fisheries and disease management.

ACKNOWLEDGEMENTS

We are grateful to G. Fussmann for use of his laboratory space, Stanley King for help with parasite identification and to Mark Romer and Claire Cooney for assisting with administration and maintenance of our facilities.

FINANCIAL SUPPORT

Funding for this experiment was provided through a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) Special Research

Opportunity Program (SRO 356373-07), awarded to G.F. (PI), M.E.S., A.P.H. and P.B. Fish flow-through aquaria system was provided through an NSERC Research Tools and Instrument grant to A.P.H.

REFERENCES

- Bakke, T. A., Cable, J. and Harris, P. D.** (2007). The biology of gyrodactylid monogeneans: The “russian-doll killers”. In *Advances in Parasitology*, Vol. 64 (ed. Baker, J. R. and Rollinson, D.), pp. 161–376, 459–460. Academic Press, Elsevier B.V., Amsterdam, The Netherlands.
- Beldomenico, P. M., Telfer, S., Gebert, S., Lukomski, L., Bennett, M. and Begon, M.** (2008). Poor condition and infection: a vicious circle in natural populations. *Proceedings of the Royal Society of London, B* **275**, 1753–1759. doi: 10.1098/rspb.2008.0147.
- Brzek, P. and Konarzewski, M.** (2007). Relationship between avian growth rate and immune response depends on food availability. *Journal of Experimental Biology* **210**, 2361–2367. doi: 10.1242/jeb.003517.
- Cable, J., Scott, E. C. G., Tinsley, R. C. and Harris, P. D.** (2002). Behavior favoring transmission in the viviparous monogenean *Gyrodactylus turnbulli*. *Journal of Parasitology* **88**, 183–184. doi: 10.1645/0022-3395(2002)088[0183:bftriv]2.0.co;2.
- Cable, J. and van Oosterhout, C.** (2007). The impact of parasites on the life history evolution of guppies (*Poecilia reticulata*): The effects of host size on parasite virulence. *International Journal for Parasitology* **37**, 1449–1458. doi: 10.1016/j.ijpara.2007.04.013.
- Croft, D. P., Albanese, B., Arrowsmith, B. J., Botham, M., Webster, M. and Krause, J.** (2003). Sex-biased movement in the guppy (*Poecilia reticulata*). *Oecologia* **137**, 62–68. doi: 10.1007/s00442-003-1268-6.
- Dussault, G. V. and Kramer, D. L.** (1981). Food and feeding behavior of the guppy, *Poecilia reticulata* (Pisces: Poeciliidae). *Canadian Journal of Zoology* **59**, 684–701. doi: 10.1139/z81-098.
- Exton, M. S.** (1997). Infection-induced anorexia: Active host defence strategy. *Appetite* **29**, 369–383. doi: 10.1006/appe.1997.0116.
- Fraser, B. and Neff, B.** (2010). Parasite mediated homogenizing selection at the MHC in guppies. *Genetica* **138**, 273–278. doi: 10.1007/s10709-009-9402-y.
- Fraser, B. A., Ramnarine, I. W. and Neff, B. D.** (2009). Selection at the MHC class IIB locus across guppy (*Poecilia reticulata*) populations. *Heredity* **104**, 155–167. doi: 10.1038/hdy.2009.99.
- Gasparini, J., Roulin, A., Gill, V. A., Hatch, S. A. and Boulinier, T.** (2006). In kittiwakes food availability partially explains the seasonal decline in humoral immunocompetence. *Functional Ecology* **20**, 457–463. doi: 10.1111/j.1365-2435.2006.01130.x.
- Gheorghiu, C., Cable, J., Marcogliese, D. J. and Scott, M. E.** (2007). Effects of waterborne zinc on reproduction, survival and morphometrics of *Gyrodactylus turnbulli* (Monogenea) on guppies (*Poecilia reticulata*). *International Journal for Parasitology* **37**, 375–381. doi: 10.1016/j.ijpara.2006.09.004.
- Gordon, Swanne, P., Reznick, David, N., Kinnison, Michael, T., Bryant, Michael, J., Weese, Dylan, J., Räsänen, K., Millar, Nathan, P. and Hendry, Andrew, P.** (2009). Adaptive changes in life history and survival following a new guppy introduction. *The American Naturalist* **174**, 34–45. doi: 10.1086/599300.
- Harris, P. D.** (1986). Species of *Gyrodactylus von Nordmann*, 1832 (Monogenea Gyrodactylidae) from poeciliid fishes, with a description of *G. turnbulli* sp. nov. from the guppy, *Poecilia reticulata* Peters. *Journal of Natural History* **20**, 183–191. doi: 10.1080/00222938600770151.
- Harris, P. D. and Lyles, A. M.** (1992). Infections of *Gyrodactylus bullatarudis* and *Gyrodactylus turnbulli* on guppies (*Poecilia reticulata*) in Trinidad. *The Journal of Parasitology* **78**, 912–914.
- Hughes, S. and Kelly, P.** (2006). Interactions of malnutrition and immune impairment, with specific reference to immunity against parasites. *Parasite Immunology* **28**, 577–588. doi: 10.1111/j.1365-3024.2006.00897.x.
- Ilmonen, P., Hakkarainen, H., Koivunen, V., Korpimäki, E., Mullie, A. and Shutler, D.** (1999). Parental effort and blood parasitism in Tengmalm’s owl: effects of natural and experimental variation in food abundance. *Oikos* **86**, 79–86. doi: 10.2307/3546571.
- Kearn, G. C.** (1994). Evolutionary expansion of the Monogenea. *International Journal for Parasitology* **24**, 1227–1271. doi: 10.1016/0020-7519(94)90193-7.
- Kolluru, G. R., Grether, G. F., Dunlop, E. and South, S. H.** (2009). Food availability and parasite infection influence mating tactics in guppies (*Poecilia reticulata*). *Behavioral Ecology* **20**, 131–137. doi: 10.1093/beheco/arn124.
- Kolluru, G. R., Grether, G. F., South, S. H., Dunlop, E., Cardinali, A., Liu, L. and Carapiet, A.** (2006). The effects of carotenoid and food availability on resistance to a naturally occurring parasite (*Gyrodactylus turnbulli*) in guppies (*Poecilia reticulata*). *Biological Journal of the Linnean Society* **89**, 301–309. doi: 10.1111/j.1095-8312.2006.00675.x.
- Lall, S. P.** (2000). Nutrition and health of fish. In *Advances in Nutrition Aqua culture V. Proceedings of the Fifth International Symposium on Nutrition and Food Technology, 19–22. November 2000, Mérida Yucatán, Mexico*. ISBN 970-694-52-9.
- Landolt, M. L.** (1989). The relationship between diet and the immune response of fish. *Aquaculture* **79**, 193–206. doi: 10.1016/0044-8486(89)90461-4.
- Last, J. M. (Ed.)** (2001). *A Dictionary of Epidemiology*, Oxford University Press, New York, NY, USA.
- Le Cren, E. D.** (1951). The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology* **20**, 201–219.
- Madhavi, R. and Anderson, R. M.** (1985). Variability in the susceptibility of the fish host, *Poecilia reticulata*, to infection with *Gyrodactylus bullatarudis* (Monogenea). *Parasitology* **91**, 531–544. doi:10.1017/S0031182000062776.
- Møller, A. P., Christe, P., Erritzøe, J. and Mavarez, J.** (1998). Condition, disease and immune defence. *Oikos* **83**, 301–306.
- Murray, C. J. L. and Lopez, A. D.** (1997). Global mortality, disability, and the contribution of risk factors: global burden of disease study. *The Lancet* **349**, 1436–1442. doi: 10.1016/S0140-6736(96)07495-8.
- Peig, J. and Green, A. J.** (2010). The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology* **24**, 1323–1332. doi: 10.1111/j.1365-2435.2010.01751.x.
- Perez-Jvostov, F., Hendry, A. P., Fussmann, G. F. and Scott, M. E.** (2012). Are host–parasite interactions influenced by adaptation to predators? A test with guppies and *Gyrodactylus* in experimental stream channels. *Oecologia* **170**, 77–88. doi: 10.1007/s00442-012-2289-9.
- Poulin, R. and Rohde, K.** (1997). Comparing the richness of metazoan ectoparasite communities of marine fishes: Controlling for host phylogeny. *Oecologia* **110**, 278–283. doi: 10.1007/s004420050160.
- Pyke, G. H.** (1984). Optimal foraging theory: A critical review. *Annual Review of Ecology and Systematics* **15**, 523–575.
- R Development Core Team** (2011). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reno, P. W.** (1998). Factors involved in the dissemination of disease in fish populations. *Journal of Aquatic Animal Health* **10**, 160–171. doi: 10.1577/1548-8667(1998)010<0160:FIITDO>2.0.CO;2.
- Richards, E. L., van Oosterhout, C. and Cable, J.** (2010). Sex-specific differences in shoaling affect parasite transmission in guppies. *PLoS ONE* **5**, e13285. doi: 10.1371/journal.pone.0013285.
- Richards, G. R. and Chubb, J. C.** (1998). Longer-term population dynamics of *Gyrodactylus bullatarudis* and *G. turnbulli* (Monogenea) on adult guppies *Poecilia reticulata* in 50-l experimental arenas. *Parasitology Research* **84**, 753–756. doi: 10.1007/s004360050481.
- Sato, A., Figueroa, F., O’Huigin, C., Reznick, D. N. and Klein, J.** (1995). Identification of major histocompatibility complex genes in the guppy, *Poecilia reticulata*. *Immunogenetics* **43**, 38–49. doi: 10.1007/bf00186602.
- Schmid-Hempel, P.** (2011). *Evolutionary Parasitology: the Integrated Study of Infections, Immunology, Ecology, and Genetics*, Oxford University Press, Oxford, UK and New York, USA.
- Scott, M. E.** (1982). Reproductive potential of *Gyrodactylus bullatarudis* (Monogenea) on guppies (*Poecilia reticulata*). *Parasitology* **85**, 217–236. doi: 10.1017/S0031182000055207.
- Scott, M. E.** (1985a). Dynamics of challenge infections of *Gyrodactylus bullatarudis* Turnbull (Monogenea) on guppies, *Poecilia reticulata* (Peters). *Journal of Fish Diseases* **8**, 495–503. doi: 10.1111/j.1365-2761.1985.tb00964.x.
- Scott, M. E.** (1985b). Experimental epidemiology of *Gyrodactylus bullatarudis* (Monogenea) on guppies (*Poecilia reticulata*): short- and long-term studies. In *Ecology and Genetics of Host-Parasite Interactions* (ed. Rollinson, D. and Anderson, R. M.), pp. 21–38. Academic Press, New York, USA.
- Scott, M. E.** (1987). Temporal changes in aggregation: a laboratory study. *Parasitology* **94**, 583–595. doi: 10.1017/S0031182000055918.
- Scott, M. E. and Anderson, R. M.** (1984). The population dynamics of *Gyrodactylus bullatarudis* (Monogenea) within laboratory populations of the fish host *Poecilia reticulata*. *Parasitology* **89**, 159–194. doi: 10.1017/S0031182000001207.

- Scott, M. E. and Nokes, D. J.** (1984). Temperature-dependent reproduction and survival of *Gyrodactylus bullatarudis* (Monogenea) on guppies (*Poecilia reticulata*). *Parasitology* **89**, 221–228. doi: 10.1017/S0031182000001256.
- Smith, K. F., Acevedo-Whitehouse, K. and Pedersen, A. B.** (2009). The role of infectious diseases in biological conservation. *Animal Conservation* **12**, 1–12. doi: 10.1111/j.1469-1795.2008.00228.x.
- Van Oosterhout, C., Harris, P. D. and Cable, J.** (2003). Marked variation in parasite resistance between two wild populations of the Trinidadian guppy, *Poecilia reticulata* (Pisces: Poeciliidae). *Biological Journal of the Linnean Society* **79**, 645–651. doi: 10.1046/j.1095-8312.2003.00203.x.
- Van Oosterhout, C., Mohammed, R. S., Hansen, H., Archard, G. A., McMullan, M., Weese, D. J. and Cable, J.** (2007). Selection by parasites in spate conditions in wild Trinidadian guppies (*Poecilia reticulata*). *International Journal for Parasitology* **37**, 805–812. doi: 10.1016/j.ijpara.2006.12.016.
- Woo, P. T.** (2006). *Fish Diseases and Disorders*, 2nd Edn. CABI Publishing, Oxfordshire, UK.