

Disentangling the causality between parasite infections and poor host conditions in the wild population

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January 18, 2023

Abstract

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Title page

Submitted to *Ecology Letters* as Letter

(42 pages with 5 Figures, 1 Table, 1 Supplemental file, 3572 words in the main body, 74 references)

Title

Disentangling the causality between parasite infections and poor host conditions in the wild population

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A short running title: Disentangling the causality between parasite infections and poor host conditions

Keywords:

Body condition, Host-parasite relationship, Infection dynamics, Mark-recapture, Path analysis, *Salmincola*, Salmonid

Author ships:

All authors conceived the ideas and study design. Also, all contributed to collect data. RH analyzed datasets and wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data accessibility: The data are available from figshare (link: <https://doi.org/10.6084/m9.figshare.21868203.v1>).

Abstract

Although parasites reduce host health, parasite infections also occur as a consequence of compromised host health. Both causalities could induce positive feedback, in which infected hosts with poor body conditions may suffer further infection, but it has rarely been demonstrated in the wild, possibly due to methodological difficulties. We used a mark-recapture survey combined with structural equation modelling (SEM) to examine whether both causalities and positive feedback occurred in stream salmonid and parasitic copepod systems. We found that parasitic copepods reduced host conditions and hosts with poor conditions were likely to be infected, suggesting that positive feedback can occur in the wild. Importantly, heavily infected hosts with poor body conditions showed lower apparent survival rates. Our findings provide robust evidence showing host condition–parasite infection dynamics, offering novel insights into how positive feedback could strongly undermine the wild host population via reduction of host survival (145 words).

1 | Introduction

Parasites account for more than one-third of species on Earth and a great deal of biomass in ecosystems (Lafferty *et al.*, 2006; Dobson *et al.*, 2008; Kuris *et al.*, 2008); hence, host–parasite relationships are one of the most common biotic associations in nature (Hudson *et al.*, 2006; Dobson *et al.*, 2008; Kuris *et al.*, 2008). Parasites damage host health via directly exploiting resources from hosts or indirectly causing physiological burdens (Poulin, 2011; Sheldon & Verhulst, 1996) and can be major drivers of host evolutionary changes (Paterson *et al.*, 2010) and host population dynamics (Hudson *et al.*, 1998; Poulin, 2011). Parasite infections also occur as a consequence of poor host health (Lochmiller, 1996; Pederson & Greives, 2008; Beldomenico *et al.*, 2008). Given that gaining or maintaining immunity is nutritionally costly for hosts (Lochmiller, 1996; Sheldon & Verhulst, 1996), host individuals without enough available food resources can be easily predisposed to higher parasite loads (Forbes *et al.*, 2016). These opportunistic infections in epidemiology may cause parasite outbreaks and finally crush wild populations (Lochmiller, 1996). Therefore, parasite infections and host health synergistically affect wild host and parasite dynamics.

Elucidating the synergy of parasite infections and host body conditions in the wild can advance our understanding of wild host population dynamics. However, most field studies have only examined cross-sectional correlations and have discussed one-sided causalities (Beldomenico *et al.*, 2008). Field studies suggest a negative correlation between host body condition, and infection parameters generally indicate that parasites are causes of poor host condition (Harper *et al.*, 1999; Vicente *et al.*, 2004; Sala-Bozano *et al.*, 2012; Hasegawa *et al.*, 2022a), although some showed poor condition situations such as food limitations may increase parasite prevalence and intensity because hosts compromise their immune functions under such situations (Forbes *et al.*, 2016). Most importantly, when parasite infections are both the cause and consequence of a poor host condition, we can also expect positive feedback: an infected host with a poor body condition due to the parasite infection will be more susceptible to further infection (Beldomenico *et al.*, 2008; Beldomenico *et al.*,

2009 a, b; Beldomenico & Begon, 2010). Positive feedback may create heavily infected hosts, which could be “super spreaders” among the populations (Beldomenico & Begon, 2010). Further, positive feedback can decrease host survival and eventually undermine the host population (Beldomenico & Begon, 2010).

Both causalities and positive feedback are likely to occur but have rarely been demonstrated in natural populations. This is probably because tracking small and cryptic parasite infections is usually difficult without sacrificing host individuals, although longitudinal studies are one of the best ways to estimate the causalities in natural systems (Beldomenico *et al.*, 2008; Telfer *et al.*, 2010). Only a few studies have overcome these problems and specifically tested their causalities in wild conditions. A series of studies by Beldomenico *et al.* (2008, 2009a, 2009b) successfully detected parasite infections on field voles *Microtus agrestis* in the field using a haematological method, and they monitored the infection status and host body condition combined with mark-recapture analysis of the host, clearly demonstrating positive feedback. A haemogram can be a useful indicator of infection; however, the authors did not observe parasites directly in the blood, and specific changes in infection intensity were not clarified. Blanchet *et al.* (2009) also demonstrated the causal relationships between parasite infections and host growth rates by estimating the growth of two host fishes from scales and otoliths, although these methods have potential estimation errors (e.g. Neilson, 1992), and the duration, frequency, and intensity of parasites before sampling were unknown. Moreover, these previous studies failed to evaluate host survival rate, even though positive feedback could likely cause host death in natural populations and, hence, affect wild host population dynamics (Beldomenico & Begon, 2010). Thus, previous findings have not sufficiently demonstrated the existence of condition–infection causality and positive feedback, necessitating more rigorous empirical evidence.

Here, we provide the first rigorous evidence of both causalities and positive feedback in wild populations by using a mark-recapture survey combined with structural equation modelling (SEM) in a wild stream fish–parasitic copepod system. SEM analysis is a powerful method for estimating the causalities in longitudinal datasets because of its simplicity and robustness (Fan *et al.*, 2016). In fact, several studies have applied this approach to longitudinal studies and have revealed complex natural interactions (Almaraz, 2005; Byrnes *et al.*, 2011). Our focused ectoparasitic copepod, *Salmincola* cf. *markewitschi*, is ideal for examining the causality between host body condition and parasite numbers because of their relatively large body size (2–5 mm; Kabata, 1969) and characteristic of attaching to the mouth cavities of host salmonid, white-spotted charr (Kabata, 1969), enabling us to track the change in infection intensity and host body condition longitudinally without sacrificing host fish. Further, previous studies have suggested that *Salmincola* spp. have negative impacts on host fitness components under rearing conditions, such as decline of fecundity (Gall *et al.*, 1972), appetite (Nagasawa *et al.*, 1994; Hiramatsu *et al.*, 2001), and body condition (Nagasawa *et al.*, 1998). Our previous studies also showed clear negative correlations between *Salmincola* cf. *markewitschi* loads and fish conditions in natural streams (Figure 1; Hasegawa & Koizumi under review 1). We conducted a mark-recapture survey of white-spotted charr *Salvelinus leucomaenis* and *Salmincola* cf. *markewitschi* infecting the host mouth cavity in the Shiodomari River in southern Hokkaido. We also evaluated the apparent survival rate of host fish during the mark-recapture period to assess whether positive feedback reduces host survival in the wild.

2 | Materials & Methods

2.1 | Study species

White-spotted charr (Figure 1) is a common salmonid fish inhabiting mountain streams in the Japanese archipelago (Hosoya, 2013). Like many other salmonids, they have two types of life history in Hokkaido Island: some individuals remain and reproduce in their natal river throughout their lives (i.e. stream residents), whereas others migrate to the sea or lakes and later come back to the natal rivers for reproduction (i.e. migrants) (Morita, 2001; Morita *et al.*, 2009). Above natural waterfalls or man-made dams, most individuals mature as residents (Morita *et al.*, 2009).

In our study systems, white-spotted charr have frequent infections by parasitic copepods in their mouth cavities (Hasegawa & Koizumi, 2021). These copepods were identified as *S. cf. markewitschi* based on

morphological observations and molecular analysis in a previous study (Figure 1; Hasegawa *et al.*, 2022b).

2.2 | Study area

Mark-recapture surveys were conducted at the headwater tributary of the Ito River, Shiodomari River system, southern Hokkaido, Japan. The study reach was located between two waterfalls (both are about 2 m high). Since the waterfall prevents the upstream migration of most, but not all, sea-run migrants (Hasegawa unpublished data), the population was mainly composed of residents. The study reach was 536 m, and it was divided into 22 sections (i.e. 25 m section $\times$ 21 + 11 m section $\times$ 1). The water temperature was measured hourly with a HOBO data logger (Onset Computer Corporation, Bourne, MA) from 2 June 2020 to 7 July 2021, and the average water temperature in the study reach was 8.4 °C (min 0.0 °C–max 18.9 °C). No other fish species were observed in the study reach, apart from white-spotted charr (Hasegawa unpublished data).

2.3 | Mark-recapture survey

During the study period of 2 and 6 June 2020 (hereafter the period called “June 2020”), we captured white-spotted charr by two-pass electrofishing using a backpack Electrofisher unit (300 V DC, Model 12-B, Smith-Root Inc., Vancouver, WA, USA) and a dip net (2-mm mesh) at each section to estimate the charr abundance by the removal method (e.g. Riley & Fausch, 1992). Block nets were set at the start and end points of each section to prevent fish from entering or leaving during electrofishing. Captured fish were anaesthetised using FA100 (DS Pharma Animal Health Co., Ltd.), and body length (fork length; FL) and body weight (BW) were measured to the nearest 1 mm and 0.1 g, respectively. We checked the presence and number of copepods by observing the fins, body surface, and mouth cavity of each fish. Fluorescent elastomer tags (North-west Marine Technology Inc., Shaw Island, WA, U.S.A.) were injected with a unique combination of six colours at four landmarks in each fish (four landmarks at the head and posterior points to each eye). Photographs of all individuals were taken on the left side with a digital camera (TG4, Olympus, Tokyo, Japan) to double-check the individual identification based on the variation of the white-spot pattern (Watz *et al.*, 2019). After fish recovery, we gently released the fish into the middle of each section from which they were captured. As age-0 fish were rarely infected by the copepod in previous studies (Hasegawa & Koizumi, 2021), we only captured and marked age-1 and older fish individuals.

Recapture sessions were conducted three times: July 2020 (4–9 July 2020), October 2020 (31 September–3 October 2020), and July 2021 (5–9 July). Fish were recaptured and treated in the same manner as the marking session (i.e. June 2020), except for the July 2021 survey, in which we captured marked fish by angling and two-pass electrofishing (Hasegawa & Koizumi under review 2). For individuals with partly fading elastomer colours or exhibiting body length shrinkage, we confirmed and identified them by checking the photographs. A few individuals were initially captured but eventually excluded from the analysis due to undetermined identity. During the recapture session, we also captured unmarked fish for host abundance estimation and parasite prevalence calculation, but we did not mark the fish. Given the relatively long interval between October 2020 and July 2021 (i.e. 9 months), we did not use the data of July 2021 in the estimation of causality by SEM; however, they were used for the survival rate estimation (see Section 2.4.3). All capture histories are represented in Figure 2 and Supplement 1.

2.4 | Statistical analyses

2.4.1 | Calculating variables

The infection level (prevalence, intensity, and mean intensity) was calculated following Bush *et al.*’s (1997) method. The estimated charr abundance in each section was calculated using the removal method implemented in the program CAPTURE (White *et al.*, 1978; available at <http://www.mbr-pwrc.usgs.gov/software/index.html>). The host density in each section was calculated from estimated charr abundance, and each section area (m²) calculated from mean stream width and section length (i.e. 25 m or 11 m). For the accurate evaluation of the host body condition, we used the residual index (Jakob *et al.*, 1996): we calculated residual distances of individual points from the regression of ln (BW) with ln (FL). As fish body condition is assumed to be different among seasons in salmonids (e.g. Morita *et al.*, 2011), we

calculated residuals in each capture session (i.e. June 2020, July 2020, October 2020, and July 2021). We also calculated the growth rate (mm / day) for each host individual for each capture-recapture interval.

2.4.2 | Structural Equation Modelling

All statistical analyses were performed using R 4.1.2 (R Core Team, 2021). To estimate the causalities among host body conditions, parasite infections, and other possible factors, we used piecewise structural equation modelling using package “*piecewise SEM*” version 2.1.2 (Lefcheck, 2016) based on the hypothetical scheme shown in Figure 2. Piecewise SEM allowed us to test the effects of parasite numbers and host body conditions on several parameters in subsequent months simultaneously and to use mixed effects. The whole model (i.e. basis set) is composed of several generalised linear (mixed) models (Shipley, 2009; Lefcheck, 2016). The goodness of fit of the whole model (i.e. basis set; Lefcheck, 2016) was evaluated by Shipley’s test of direct separation using Fisher’s C value (Shipley, 2009; Lefcheck, 2016). If that value did not fall below a significant level ($p < 0.05$), the model was fitted and explained our datasets well. Since unexpected correlations, such as temporal correlations between parasite numbers and body conditions among months (Figure 2), severely reduced the model fitting due to collinearity, we treated these correlations as correlated errors and removed them from the basis set (Shipley, 2009). All linear mixed models in piecewise SEM were constructed using the R package “*lme4*” version 1.1 (Bates *et al.*, 2015), and all responses and explanatory variables were standardised before the analysis. We analysed our datasets for each of two separate seasons (i.e. from June 2020 to July 2020 and from July 2020 to Oct. 2020).

Based on the hypothetical schema (Figure 3), we constructed four linear mixed models. We expected that host body conditions could affect parasite numbers, and vice versa, and there should be time lags across seasons (Figure 3). Fish with higher growth rates may show higher body conditions in the post month (Figure 3). Therefore, in the first model, the response variable is host body condition in the post month, and an explanatory variable is parasite numbers and host growth rate in the pre month to check if parasite infections reduce host body condition (i.e. parasite are cause of host body condition; Figure 3). In the second model, the response variable is parasite numbers in the post month, and the explanatory variable is body condition in the pre month to check if the prior host body condition affects parasite numbers (i.e. parasite are a consequence of poor condition; Figure 3). Host density could affect individual host body condition, and body condition also affects host growth rate (e.g. Gabelhouse, 1991), which is generally affected by initial body size in salmonids (e.g. Morita, 2001). Therefore, we constructed two more models (Figure 3): a model that included body condition in the post month as the response variable, with its explanatory variable being host density in the pre month, and another model that included growth rate as the response variable, with its explanatory variables being body condition and body size in the pre month. The study sections were included as random effects in all constructed models.

2.4.3 | Cormack–Jolly–Seber model

We estimated the predictors for apparent survival using the Cormack–Jolly–Seber (CJS) model using the R package “*marked*” version 1.2.6 (Laake *et al.*, 2013). The CJS model enables us to estimate both capture probability (cp) and apparent survival (ϕ) by including both emigration and actual survival rates from capture histories (Lebreton *et al.*, 1992). We constructed models separately to estimate the factors predicting apparent survival and capture probability. For the model predicting apparent survival (ϕ), we included FL, body condition, parasite numbers, and their interactions (i.e. body condition $\times$ parasite numbers and FL $\times$ parasite numbers) in June 2020 as predictors, and we constructed models that included all possible additive and multiplicative interactions among predictors. Since fish size was the strongest predictor for estimating the capture probability of salmonids (Saunders *et al.*, 2011; Hedger *et al.*, 2018), we only included FL as an explanatory variable to estimate the capture probability (cp). The best model with the lowest Akaike’s information criterion value (AIC: Akaike, 1983) was selected.

3 | Results

The total marked and recaptured fish, infection parameters, and infection patterns of *Salmincola cf. marke-witschi* during the mark-recapture session are summarised in Figure 2 and Supplement 1.

From June 2020 to July 2020, the hypothesised model constructed by piecewise SEM fitted our datasets well (Fisher's $C = 7.22$, $p = 0.13$; Figure 4a). Both body condition and parasite numbers in the previous month had negative effects on parasite numbers and body condition in the next month, respectively (Figure 4a). Density had no significant effect on body condition (Figure 4a). Fish with higher body conditions exhibited higher growth rates, and growth rates were also affected by body size (Figure 4a).

From July 2020 to October 2020, the model also fitted our datasets (Fisher's $C = 7.12$, $p = 0.13$; Figure 4b). Individual fish that exhibited poor conditions were likely to gain further parasite infections in the post month, but opposite causality was not detected (Figure 4b). As in the previous period, the growth rate was also affected by host body condition and body size in the previous month (Figure 4b). Fish that showed higher growth rates had higher body conditions in the next month (Figure 4b).

The model that included the interaction term of body condition and parasite numbers was selected as the best model showing the lowest AIC value (Table 1, Figure 5), with heavily infected hosts (i.e. fish infected by more than six copepods) exhibiting apparently lower survival rates. The best model predicting capture probability (cp) included only FL (Table 1).

4 | Discussion

Although many studies have pointed out the negative impacts of parasites on wild host populations, most reported simple correlations and hence overlooked causal relationships (Harper *et al.*, 1999; Vicente *et al.*, 2004; Sala-Bozano *et al.*, 2012; Hasegawa *et al.*, 2022a). This is probably due to methodological difficulties in the long-term tracking of host individual and parasite infections. Only two studies have explicitly tested the causality using unique methods, such as haematological inspection and otolith/scale back-calculation (Beldomenico *et al.*, 2008, 2009 a, b; Blanchet *et al.*, 2009). Our study, by contrast, directly monitored the changes in infection intensity, host body condition, growth rate, and survival by the mark-recapture method, and therefore, serves more rigorous evidence of causal relationships and positive feedback in wild populations.

Strikingly, our study showed that both causalities were possible in wild populations, suggesting that positive feedback could occur in wild conditions; parasite infections reduced host conditions, and reduced conditions caused further parasite infections, and so on. The body condition index generally represents the host's overall health status, energy budget, and immune functions (Wilder *et al.*, 2016; Sánchez *et al.*, 2018). Although hosts commonly cope with parasite infections using innate and adaptive immune systems (Graham *et al.*, 2011; Fast, 2014), developing and maintaining these systems are very costly (Lochmiller, 1996; Sheldon & Verhulst, 1996), and therefore hosts with poor conditions, mainly due to parasite infections, cannot allocate their resources to immunity, resulting in higher parasite intensity. Our study clearly shows this trend.

Behavioural differences dependent on host body condition also explain positive feedback. Animals often show anti-parasite tactics such as dispersal from infection sources (Brown *et al.*, 2016; Terui *et al.*, 2017) and "parasite-removing behaviours" such as substrate rubbing (Kabata & Cousens, 1977; Atkinson *et al.*, 2018). However, these behaviours are commonly considered energy dependent (Krohn & Boisclair, 1994; Bonte *et al.*, 2012; Terui *et al.*, 2017); thus, hosts with poor conditions cannot employ these tactics.

How did the copepods in our study cause positive feedback? *Salmincola* spp. cause tissue damage, such as gill destructions and mouth cavity swellings (Kabata & Cousens, 1977; Nagasawa *et al.*, 1998; Hasegawa *et al.*, 2022a). These infections also induce the immune response of hosts (Hiramatsu *et al.*, 2001). Beyond developing immune systems, repairing damaged tissues also requires much energy (White *et al.*, 2020), eventually leading to loss of host body condition (Hasegawa *et al.*, 2022a). Physical attachment itself could induce body condition loss. In particular, since our focused copepods mainly attach to the mouth cavity, their infections reduce host foraging activity and strongly reduce host body conditions (Nagasawa *et al.*, 1994). Further, intraspecific competition may play an important role in susceptibility to infections. Poor condition fish are commonly outcompeted by other conspecifics in intra-specific competitions, especially among salmonids with a strong dominance hierarchy (Nakano, 1995). Whereas fish with a high hierarchy dominate at the centre of the flow (Nakano, 1995), outcompeted fish may be forced to move outside of the flow, where free-swimming copepodids may easily attach to the hosts under such low-flow environments

(Monzyk *et al.*, 2015). Under these mechanisms, positive feedback can easily occur, as demonstrated in our system.

We found that heavily infected hosts with poor conditions had lower apparent survival rates, suggesting that positive feedback could play important roles in host survival and ultimately undermine the host population (Beldomenico & Begon, 2010). Many studies have shown that heavily infected hosts, generally in poor conditions, tend to have lower survival rates in the wild (Ferguson *et al.*, 2011; Mayo-Hernández *et al.*, 2015). Given that body condition is continuously reduced as positive feedback occurs, host body condition eventually fails to meet the threshold for maintaining critical physiological and physical functions such as metabolism. Further, heavily infected hosts with poor conditions are likely to be preyed by predators (Temple, 1987) and outcompeted by conspecifics (Barber *et al.*, 2000; Filipsson *et al.*, 2018). These biological interactions indirectly reduce the host survival rate.

Finally, positive feedback should be carefully taken into account when considering host–parasite dynamics because this concept may also work at the population level (Beldomenico & Begon, 2010). Beldomenico and Begon (2010) predicted that populations with a large proportion of individuals in poor conditions are likely to have a higher prevalence and infection intensity, and this also increases the risk of further infections. Since average body condition and immune ability vary among populations (Cornet *et al.*, 2009; Becker *et al.*, 2020), such predictions are likely to occur in natural systems. Further, positive feedback may eventually cause host death, as discussed above, so this may affect host population dynamics. In this context, the southern salmonid populations, as in the present case, will be threatened by positive feedback. Such populations will especially be vulnerable to increasing water temperature induced by climate change (Nakano *et al.*, 1996) because temperature increment would be stressful for cold water-adopted salmonids and would ultimately decrease their body condition (Peterson *et al.*, 1979; Larsson, 2005). Under such a scenario, the proportion of fish individuals with poor conditions will increase, and parasites will expand more rapidly there. More case studies and monitoring are needed to verify this prediction.

Acknowledgements

We wish to thank Tomoaki Konno and Noriyuki Mineharu for helping with the fieldwork. Drs Kentaro Morita, Hiroyuki Munehara, and Takashi Noda gave us valuable comments on an earlier draft.

Figures

Figure 1

(A) *Salmincola* cf. *markewitschi* infecting the mouth cavity of white-spotted charr *Salvelinus leucomaenis*. (B) White-spotted charr not infected by copepods. (C) White-spotted charr infected by several copepods.

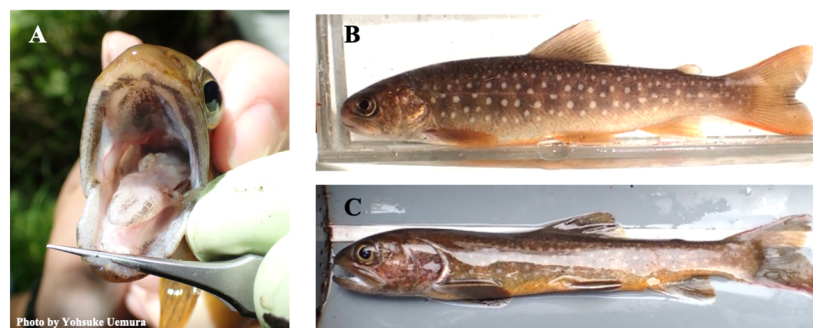
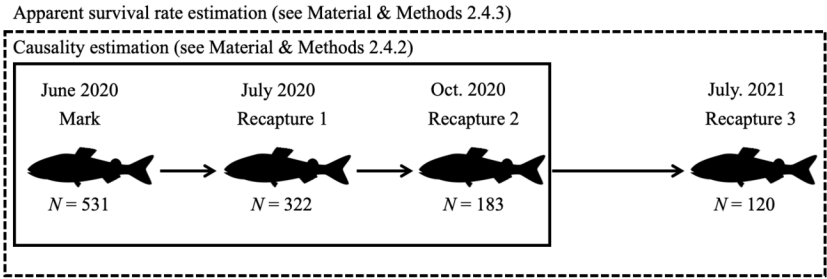


Figure 2



Summary of mark-recapture survey conducted from June 2020 until July 2021.

Figure 3

Hypothetical causal relationships among host body condition, parasite infections, and other potentially related factors of both host and parasite.

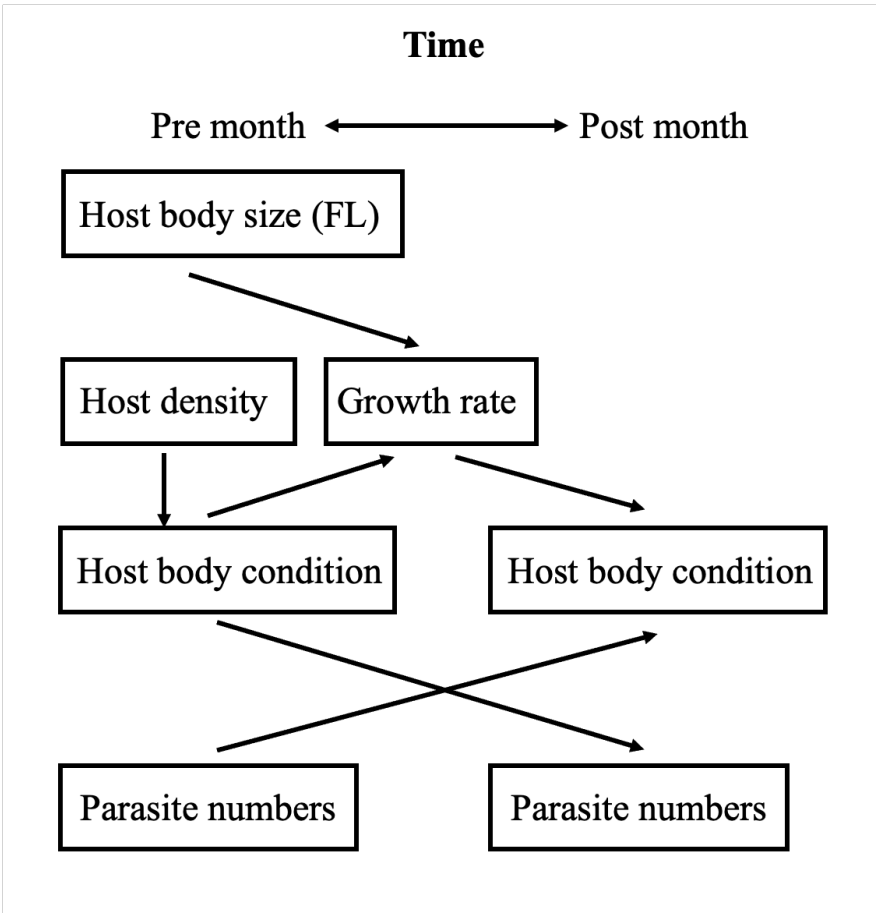
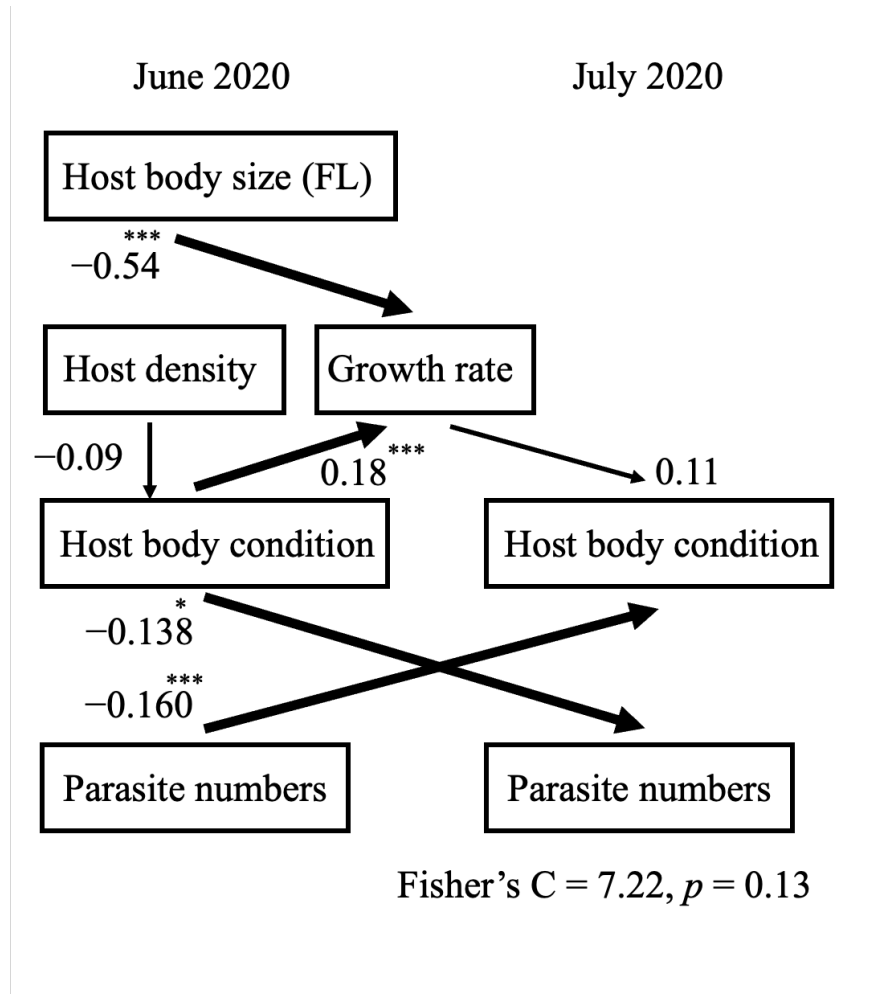


Figure 4

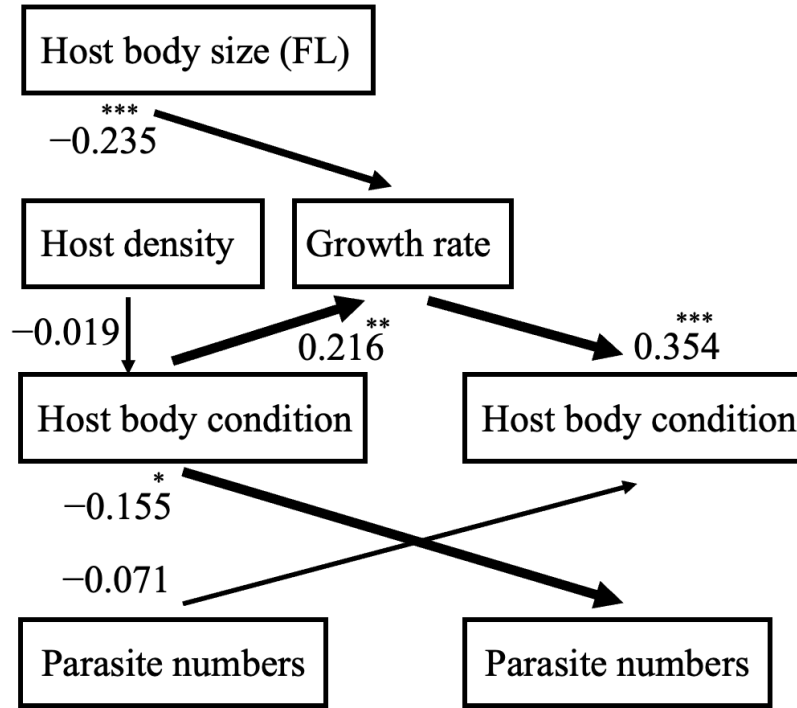
Causal relationships among factors of hosts and parasites inferred by piecewise SEM analysis. (A) Results from June 2020 to July 2020. (B) Results from July 2020 to October 2020. Bold arrows indicate significant

effects evaluated by the Wald test ($***p < 0.001$; $**p < 0.01$; $*p < 0.05$).



July 2020

Oct. 2020



Fisher's $C = 7.12, p = 0.13$

Fig. 5

Relationships between host apparent survival rate (φ), host body condition (residual index), and parasite numbers estimated by Cormack–Jolly–Seber (CJS) model. Colour differences among plots and estimated lines represent different parasite numbers.

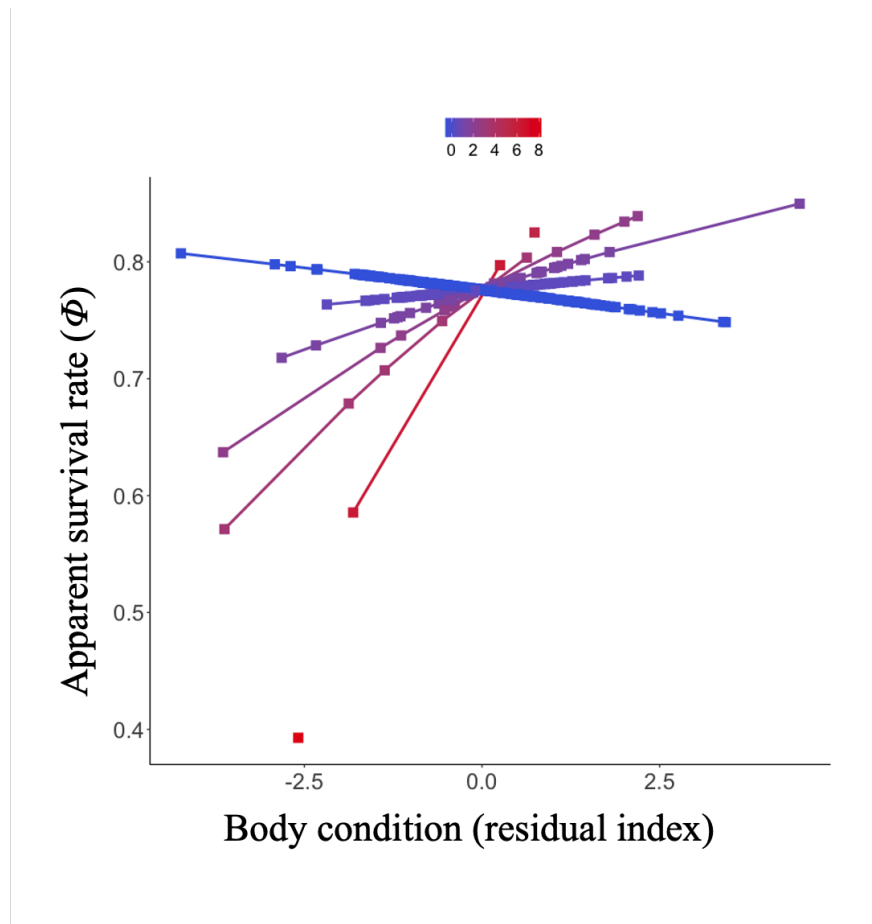


Table 1

Results of model selection of Cormack–Jolly–Seber models estimating host survival (ϕ) and capture probability (cp).

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