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Author for correspondence:
Davide Thambithurai
e-mail: davide.thambithurai@glasgow.ac.uk

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Fish vulnerability to capture by trapping is modulated by individual parasite density

Davide Thambithurai[1,2], Isabel Lanthier[3], Eloi Contant[4], Shaun S. Killen[1] and Sandra A. Binning[3,5]

[1]Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK
[2]MARBEC, University of Montpellier, Ifremer, Sète 32400, France
[3]Département de sciences biologiques, l'Université de Montréal, Montréal, Québec, Canada
[4]École Pratique des Hautes Études, Université Paris Sciences et Lettres, 4-14 rue Ferrus, Paris 75014, France
[5]Ressources Aquatiques Québec (RAQ), Institut des sciences de la mer (ISMER), Université de Québec à Rimouski, 310 avenue des Ursulines, Rimouski, Québec, Canada G5L 2Z9

DT, 0000-0002-0338-3778; SSK, 0000-0003-4949-3988; SAB, 0000-0002-2804-9979

Commercial fishery harvest is a powerful evolutionary agent, but we know little about whether environmental stressors affect harvest-associated selection. We test how parasite infection relates to trapping vulnerability through selective processes underlying capture. We used fish naturally infected with parasites, including trematodes causing black spots under fish skin. We first assessed how individual parasite density related to standard metabolic rate (SMR), maximum metabolic rate (MMR) and absolute aerobic scope (AAS)—then used laboratory fishing simulations to test how capture vulnerability was related to parasite density. We further explored group-trapping dynamics using experimental shoals containing varying proportions of infected fish (groups of six with either 0, 2, 4 or 6 infected individuals). At the individual level, we found a positive relationship between parasite presence and SMR, but not MMR or AAS. While we saw no relationship between individual metabolic capacity and vulnerability to trapping, we found the length of time fish spent in traps increased with increasing parasite density, a predictor of trapping-related capture probability. At the group level, the number of infected individuals in a shoal did not affect overall group trapping vulnerability. Our results suggest that parasite infection has some capacity to shift individual vulnerability patterns in fisheries, and potentially influence the evolutionary outcomes of fisheries-induced evolution.

1. Background

Human impacts on animal populations are a major evolutionary force in both terrestrial and aquatic ecosystems [1–3]. Across contemporary anthropogenic processes influencing the evolution of wildlife, fishing is among the strongest [4,5]. Modern commercial fishing has become tremendously efficient, often exceeding exploitation rates of prey by natural predators [6]. Although debate still exists on how severely fish populations are affected by human fishing activity at an evolutionary level [7], some clear trends are apparent. For instance, fish body size is well-documented as being a strongly influenced by fisheries-associated selection [8,9]. In addition, studies on wild fish, fish in mesocosms [10–13], laboratory simulations using model species [14–16] and computational modelling [17] suggest fishing also selects on traits such as swimming performance, activity levels, shoaling behaviour, metabolism and habitat choice. In addition to the intrinsic selective processes that exist in fisheries, an important aspect that remains understudied is how fluctuating environmental conditions and/or biotic stressors influence fishing-associated

selection. While tremendous progress has been made in identifying and quantifying mechanisms underlying fisheries-induced selection and evolution (FIE), synergistic influences of additional stressors on selection could alter selective processes in ways yet to be fully understood [18].

Both selection, and the traits targeted by selection, are liable to fluctuate in the presence of abiotic and biotic stressors. Parasites are pervasive among wild animals and are known to affect host behaviour, physiology and performance [19–26]. Depending on context, parasites may constitute an important stressor, potentially altering trait expression and correlated selection. Importantly, little is known about how parasite infection relates to fishing-associated selection. There is clear evidence that parasites can influence predator avoidance through mechanisms that include decreased social responsiveness [20], decreased host condition [27], behavioural manipulation including increases in activity and risk-taking [28–31], and dampening of locomotory capacity [32,33]. Equally, parasites may influence host vulnerability to fishery harvest. Wilson *et al*. [34] showed that bolder fish are more likely to enter traps, and suggested this is principally a function of their behavioural phenotype along a shybold continuum. Interestingly, they also found differences in the parasite fauna among fish caught using different fishing methods (traps versus seines), trends which were likely driven by differences in fish behaviour when infected, such as increased exploration. Traps are a passive fishing technique deployed, left unattended and then recovered by fishers after some time interval. They vary greatly in design depending on habitat, and are used in both freshwater and marine fisheries. Even though fish are sometimes able to exit traps after entry [35], the probability an individual fish will be captured during trap retrieval increases with the amount of time they spend in the trap. For example, social responsiveness is an important factor modulating residence time in traps, with individuals following conspecifics into traps and even re-rentering traps after exiting to remain with their shoalmates [16]. If parasite infection were to positively influence the time a host remains within a trap by altering aspects of behaviour related to willingness to enter, or remain within a trap, then fishers may be inadvertently be selecting on individuals that are more vulnerable to parasites within a population.

In addition to effects on behaviour, parasites can affect host energy budgets as there are costs associated with mounting an immune/stress response, as well as repairing damaged tissue in response to infection [36]. Similarly, in a fishery context, metabolism is thought to be a target of selection given its links with whole-organism performance and maintaining homeostasis. For instance, in trap fisheries, a higher basal metabolic cost may induce greater activity and exploration, thus resulting in higher capture likelihood. Standard metabolic rate (SMR) is a proxy for the minimum energy expenditure in a resting, fasting and relaxed ectotherm, while maximum metabolic rate is the upper limit of an organism's aerobic metabolic capacity. The absolute difference between the two, termed absolute aerobic scope, is representative of the capacity to support aerobic activities beyond basic maintenance [37–39]. In ectotherms, parasite infection can influence both SMR and MMR [40,41], though parasite-associated effects on energy budgets remain unclear and significant among-system variance exists [42]. Importantly, energetic traits such as MMR and SMR have been recognized as potential targets for fishery selection given their links with whole organism performance [15,43]. The broad impacts of parasites on host physiology and behaviour mean we may be underestimating the influence they have on phenotypic variation, which is the material on which fishing-associated selection can operate.

Group living typically offers benefits including increased foraging efficiency and dilution of predation risk [44]. However, within a fishery context, group living can be deleterious, as fishing gears often specifically target groups of schooling fish. Thus, being in larger groups may render individuals more vulnerable to capture [16,17]. For example, purse seine fisheries target shoaling species, encircling whole schools, thus negating the anti-predator benefits of living in a large group [45]. There is also evidence that social cohesion can increase vulnerability to trapping, with individuals following groupmates into traps. However, the exact role of social dynamics in vulnerability to passive gears is largely unknown. Individual behavioural tendencies can be influenced by environmental stressors, which in term might affect the decision-making process of the whole group, given the presence of quorum responses in fish schools [46]. Given that parasite infection can increase shoal cohesion and size [47], parasitized fish may be more likely to be captured in trap fisheries, owing to increased social cues and denser shoals. On the on the other hand, if parasites were to disrupt shoaling behaviour [20,48–50] then parasitized individuals may be less likely to be captured. Moreover, the capture vulnerability of entire groups may be influenced by the proportion of infected individuals within the shoal and the overall effect on their collection behaviour and decision-making. Quantifying the impact of parasite infection on shoaling dynamics and group behaviour is fundamental in understanding the overall impact parasites may have on fishing-associated selection.

Using healthy sunfish (*Lepomis gibbosus*), and those naturally infected with black-spot trematode metacercaria, we explored the relationships among parasite infection, aerobic metabolism, group composition and capture vulnerability in a scaled-down trap fishery. Sunfish are a small shoaling species inhabiting the whole water column and displaying social behaviors similar to many commercially targeted species that are fished with traps (e.g. European perch (*Perca fluviatilis*)). Determining the relative importance of natural levels of parasitism in fishery selection is essential for understanding the synergistic impacts these two evolutionary pressures may have on fish populations. The study aims were threefold: (i) to explore the relationship between trematode density and aerobic metabolic traits (MMR, SMR AAS); (ii) to assess the relationship between parasite density and individual trapping vulnerability; and (iii) to assess whether overall group trapping vulnerability is influenced by the number of infected individuals within a shoal. To address these aims, we first measured SMR, MMR and calculated AAS for all fish. We then carried out a simulated trapping experiment varying the number of infected individuals within a group to either 0, 2, 4 or 6 in each trial (out of six fish total within each group). We hypothesized that standard metabolic rate (SMR) would be higher in more heavily infected fish, making them more likely to enter and remain in baited traps due to their high energetic requirements. We also predicted that heavy infection would be related to changes in MMR and AAS. Additionally, we predicted

groups with a higher number of infected individuals would have an overall higher vulnerability to trapping, as the presence of more infected individuals within a shoal could lead conspecifics to be more risk-prone and exploratory, independent of their own infection status.

2. Material and methods

(a) Experimental protocol

The experiment was conducted from mid-September to mid-November 2019. In addition to the quantification of encysted metacercaria (black-spot) on live fish, fish were euthanized and dissected following behavioural trials between June 2020 and March 2021 to quantify and identify other internal parasites.

(b) Animals

We used pumpkinseed ($n = 152$; mean ± s.d. body mass = 8.63 ± 2.99 ; mean ± S.D. standard length = 64.03 ± 7.61) collected from the three lakes surrounding the Université de Montréal's Laurentian Biological field station (Canada, 45° 59′ 17.8″ N, 74° 0′20.9″ W). Fish were captured using seine nets between the 11th and 21st of September 2019, and chosen based on their visible black-spot infections. Black-spot disease is a condition caused by trematodes (*Uvulifer and Apophallus sp.*) and characterized by conspicuous black spots formed by encysted metacercaria under the skin and fins of the fish. Collected fish from all three lakes were housed together in three large 600 L tanks supplied via a flow-through system pumping water from Lac Croche (45° 59′ 32.1″ N, 74° 00′ 38.6″ W; range = 15–18.3°C). They were fed daily with frozen bloodworms (Chironomidae) *ad libitum*. Upon arrival at the aquarium facilities, fish were treated in a peroxide bath (concentration = 2.5 mg l for 25 min) to remove any external pathogens; this did not influence the presence of black-spot metacercaria. Fish differed in their black-spot count: fish from Lac Croche and Lac Cromwell (45° 59′ 20.6″ N, 73° 59′56.4″ W) exhibited a gradient of trematode infection (respectively median = 196, range = 3–487, median = 112, range = 32–505), while fish in Lac Triton (45° 59′ 16.4″ N, 74° 00′28.5″ W) had no visible trematode parasites. Fish were visually assessed for signs of parasite infection and split into two categories: infected (with visible encysted black-spot trematode metacercaria on fish surface), and non-infected (no visible encysted black-spot metacercaria on fish surface), and tagged using a unique combination of coloured VIE elastomer (NorthWest Marine Technology Inc.) to allow individual identification during the trials. Fish were kept on a 12 h light : 12 h dark photoperiod throughout the experiment. In order to minimize any potential lake effects fish were housed and habituated together, thus having the opportunity to interact and shoal together prior to group-level experiments.

(c) Metabolic rate measurements

Following tagging, fish were rested for a minimum of three days prior to measuring metabolic phenotype. Twenty-four hours prior to testing, fish were removed from their home tank and transferred to a separate holding tank, where they were fasted for 24 h prior to respirometry measurements to minimize stress and reduce possible aerobic energy costs related to digestion.

We used intermittent flow respirometry to measure the instantaneous oxygen uptake (MO_2, in mg O_2 h^{-1}) of each fish, which we used to estimate MMR and SMR [51,52]. For full details of methods see electronic supplementary material, table S1 [53]. Eight fish were analysed each day over the course of 18 days, beginning on 29 September 2019. Owing to a system fault, no measurements were taken on 10 October 2019. Typically all fish were in their respective chambers by 13.00 daily, and were removed from the chambers between 8.00 and 9.00 the next day.

Individual animals were placed in one of eight acrylic respirometry chambers (empty volume = 449 ml; tubing = ~48 ml) immersed in two temperature regulated (mean ± s.d. = 15.88 ± 0.19 C°) baths each approximately 90 l in volume (i.e. four chambers in each bath). Temperature regulation was achieved by circulating water from the baths to a thermally controlled tank via two Eheim Universal 300 pumps, the thermal control loop made of plastic tubing included a metal coil which served to increase thermal exchange between the heated tank to the baths. A thermal controller switched the thermal control loop pump on or off depending on the desired temperature: when on, water was circulated through a chiller unit (Thermo Scientific Hakke EK20 immersion cooler) and into the coils, thus lowering thermal bath temperature, a further set of pumps circulated the thermal bath water into baths holding the respirometry chambers. System cleaning was achieved via a recirculating loop in the thermal bath hooked to a pond UV lamp, and regular cleaning (approx. every 5 days) using a mild bleach solution. Chamber mixing was done via small in-line pumps (Aquapro AP200LV, 200 l h^{-1}) linked via non-permeable tubing to each chamber, flushing was achieved by a single small pump split between all chambers in each bath. A digital timer periodically switched on the pump, which flushed chambers with fully aerated water for 4 min, and then switched off for 6 min.

Both MMR and SMR were estimated for each fish. MMR was estimated following a standard chase protocol [54]: individual fish were removed from their holding tank each morning around 10.00 and transferred to a circular trough where they were chased manually for three minutes. Following the three-minute chase period, fish were air exposed for one minute. After the air exposure period, fish were immediately transferred to a respirometry chamber (less than 10 s). Water oxygen content was logged once every 2 s using a Firesting 4-channel oxygen meter and associated sensors (PyroScience GmbH, Aachen, Germany), all sensors were located within the re-circulation loops of the system. Each respirometry chamber was wrapped in black polyethylene to minimize visual disturbance, and following MMR measurements, each bath was shielded from external disturbance by covering them with black polyethylene sheeting. Following respirometry, fish were weighed to the nearest gram and returned to their home tank. Each Firesting oxygen metre also logged the temperature in each of their respective baths. The first slope of measurements was used to calculate MMR, the remaining slopes were used to calculate SMR. Slopes were visually assessed during the auto_rate function in respR [55], and discarded if found to be of poor fit (e.g. obvious deviations from linearity: less than 5% were discarded). To calculate oxygen uptake (SMR, MMR), we used respR, and corrected for background respiration using readings from each empty respirometry chamber at both the start and end of each run (i.e. a set of eight fish). SMR was estimated from MO2 measures taken overnight and was calculated as the mean of the lowest 10th percentile of adjusted rates [38]. Chamber volume and associated tubing were included in calculations of oxygen uptake.

(d) Trapping trials

(i) Setup

As well as investigating the relationships among individual parasite load, trap capture and metabolism, we tested whether varying the number of uninfected and infected individuals within a shoal influenced overall fishery vulnerability of the group. We created four treatment groups of six fish: six uninfected individuals (6u); four uninfected and two infected (4u-2i); two uninfected andfour infected (2u-4i); and six infected

(6i). Treatment groups were replicated, resulting in a total of 100 trials (6u = 24, 4u-2i = 24, 2u-4i = 27, 6i = 25).

Trials were conducted in an elliptical arena (major radius = 154 cm; minor radius = 93 cm) made from 3 mm white acrylic sheeting and filled to a depth of 17 cm. Arena water was supplied via a flow through system kept at the same temperature as the home tanks (approx. 15 C°). Three artificial plants were placed in the arena to encourage exploration and reduce stress. A clear 8 mm thick acrylic tube measuring 19 × 25 cm (W × H) was used as an acclimation area, this was connected to a pulley system which allowed remote lifting. A single trap 204 × 110 × 115 mm (L × W × H) was used during trials and baited using bloodworm to simulate fisheries capture. The trap was made from a metal frame (1.5 mm stainless steel) covered in green netting (less than 2 mm in size) with two inverted funnel entrances (22 × 45 mm; W × H) at each end. To allow recoding of fish entrance/exits, the top of the trap was constructed from clear 1.5 mm acrylic sheeting cut with a hole allowing the mounting of a GoPro Hero 4 (16:9 Full HD, 720p; GoPro, San Mateo, California, USA) camera. Each trial was also recorded from above using a Logitech HD Webcam c920 (Logitech Europe S.A., Lausanne, Switzerland) located approximately 130 cm above the water level and mounted on a wooden frame (189 × 120 × 150 cm; L × W × H) covered in canvas sheeting. Lighting within the behavioural arena was provided by four 8 watt 580 mm lights (Rona, Saint-Jérôme, Quebec, Canada).

In addition to elastomer tags, prior to each trial, fish were individually tagged with a small coloured paper tag (six different colours) to aid video identification, this was glued to the top of the head using a drop of super glue. These tags were removed at the end of the trials along with and residual glue. No fish experienced any noticeable effects from the procedure.

(ii) Trial procedure

Prior to each test day, treatment groups were fasted for 24 h and isolated from other fish to standardize hunger and minimize stress. At the beginning of the trial, each fish was removed from their home tank and tagged as described above. Following tagging (typically < 10 s), fish were immediately placed one by one in the acclimation area. As soon all the fish were tagged, video recording started and fish were given 10 min to habituate. The tube was then lifted via the pulley system and fish were allowed to interact with the trap in the arena for 40 min.

(iii) Dissections

Once all behavioural trials were completed, all fish were euthanized in an overdose of eugenol solution and frozen at −18°C. Fish were transported in ice to the laboratory facilities at the Université de Montréal's MIL campus for dissection. Whole fish were first observed under a stereomicroscope to accurately count the number of encysted black-spot metacercaria on the entire surface of the body. Fish were then dissected to quantify parasites in the digestive tract, abdominal cavity and muscle tissues; it should be noted that muscle dissections were not exhaustive but were consistent among fish. In sampled lakes, these endoparasites are mostly cestode *Proteocephalus ambloplitis* (bass tapeworm) and occasionally trematode *Clinostomum marginatum* (yellow grub) ([56], Binning unpublished data). Similarly to black-spot, Lac Croche and Lac Cromwell exhibited a gradient of endoparasite infection (respectively median = 0.5, range = 0–20, median = 16, range = 0–16), while fish in Lac Triton had no endoparasites. Raw numbers from these counts were divided by fish mass to yield parasite density (no. of parasites per gram of mass) separately for black-spot metacercaria and for other endoparasites.

(e) Statistical analysis

All analyses and figures were done in R v. 4.1.2 [57,58] primarily using packages 'tidyverse', 'rptR', 'glmmTMB', 'dabestr' and 'DHARMa' (see electronic supplementary material, table S5, for full package list). Where suitable, we checked model assumptions for homoscedascity and normality by inspecting residual and quantile plots. Broadly, analyses were split into three sections: (i) the relationship between parasite infection and aerobic metabolic traits, (ii) how consistently individuals that were parasitized and unparasitized entered traps calculating repeatability across trials for each fish, and (iii), whether individual trapping vulnerability, as well as group trapping vulnerability, differed as a function of individual parasite density or the number of parasitized individuals within a shoal.

We used a binary score based on whether a fish entered or did not enter a trap for repeatability calculations at an individual level. For all other individual based analyses, we used individual capture vulnerability (V_I), defined as time in seconds a fish spent inside a trap during a trial (range = 0–2400 s). For all group analyses, we used group capture vulnerability (V_G), which we defined as the sum of all individual trapping vulnerability times during a trial (range = 0–14 400 s).

To investigate whether fish condition was related to trap entry, we calculated the scaled mass index (SMI) for each fish [59]. We also calculated coefficients of variation (s.d./mean) of summed time spent in traps for group-level analyses.

(f) Individual models on metabolism

To test whether there was a relationship between parasite density and host metabolic rate, we used three linear regressions, one each for SMR, MMR and AAS (O_2 mg h^{-1}). Each metabolic variable was log-transformed and used as response variable in models, while density of black-spot metacercaria, density of other endoparasites, collection lake and log(mass) were used as explanatory variables. Candidate models were compared using Akaike's information criteria (AIC) [60]; scripts to reproduce all models with a delta AIC < 2 are presented in the electronic supplementary material, but only the results from the top models are presented in the result section. For all linear regressions, we checked model assumptions of homoscedasticity and normality by visually inspecting residual and quantile–quantile plots.

Oxygen measurements from two fish (gggr and ryyp) were identified as extreme outliers. Models were initially run on datasets including and excluding the fish, which led to no differences in model interpretation; ultimately the fish were removed from analyses which included metabolic rate data.

(g) Individual repeatability

We calculated repeatability of trap entry using the rptR package, which uses mixed-effects models to model repeatability (R) [61]. Repeatability using binary data for entry/non-entry was calculated between infected and non-infected groups. We controlled for mass-specific variation by including it as a fixed effect in the estimate calculations and included fish ID as a random effect in all models to account for inter-individual variance. Iterations for bootstrapping and permutation were set to 10 000.

(h) Individual models on trapping vulnerability

We modelled trapping vulnerability for each fish using a series of zero-inflated hurdle models in the package glmmTMB [62]. Hurdle models treat zero and non-zero outcomes in data as two separate categories. In this case, models show which predictors increase the probability of capture versus non-capture (zero or not zero), but also how each predictor influences non-zero values in the data (1–2400) – thus how much time a fish spent in the trap. Structurally there are three components to the

analysis: a conditional formula (for non-zero values), a zero-inflated formula (for zero-values), and a dispersion formula (to address overdispersion in data). Across all models, we used V_I as the response variable. Three separate models were fitted, one for each of three metabolic variables (SMR, MMR, AAS) to avoid any collinearity issues between metabolic variables. Given we were interested in understanding how both trematode and other parasite density might be related to trap vulnerability, we included respective parasite densities as two different factors in each model as explanatory variables. We also included fish mass (g), lake of capture and treatment group (6u; 4u-2i; 2u-4i; 6i) as explanatory variables. Fish ID and trial number were included as random effects. Zero-inflation structure for the models was kept the same as the conditional effects formula by specifying *zi* = ∼. in the model call, and a zero-truncated negative binomial distribution was used for the conditional model. We used the default glmmTMB dispersion structure in all models.

To select final models, we dropped fixed terms individually from full models and refitted them. All structurally nested models were then compared using the 'AICtab' function from the package bbmle. Candidate models were compared using Akaike's information criterion (AIC) [60]; again, scripts to reproduce all models with a delta AIC < 2 are presented in the electronic supplementary material, but only the results from the top models are presented. In all cases where metabolic variables were kept in the final model, mass was also kept to account for the scaling effects of mass on metabolism.

(i) Group model on trapping vulnerability

To analyse the effect of treatment (6u; 4u-2i; 2u-4i; 6i) on V_G, we used a zero-inflated model with a negative binomial distribution. Treatment was included as a categorical explanatory variable, whilst test number was included as a random effect. The default dispersion structure was used, and zero-inflation structure was specified as *zi* = ∼*behavioural_treatment*, signifying the probability of producing a zero was based on the behavioural treatment group.

3. Results

(a) Individual models on metabolism

SMR was higher with increased black-spot metacercaria density: SMR (adj $R = 0.63$, 95% CI = 1×10^{-04}, 0.012, $p = 0.01$); this was not the case for MMR (adj $R = 0.52$, 95% CI = -1.32×10^{-03}, 9.06×10^{-02}, $p = 0.132$), nor AAS (adj $R = 0.39$, 95% CI = -2.96×10^{-03}, 1.07×10^{-02}, $p = 0.262$). Each unit increase in trematode density contributed to an approximate relative increase of 0.69, 0.42 and 0.39 mg h % in SMR, MMR and AAS, respectively. None of the final models included other endoparasite density, but included collection lake and fish mass (electronic supplementary material, table S2; figure 1).

(b) Individual repeatability

Adjusted repeatability of parasitized individuals ($R = 0.202$, 95% CI: 0.094–0.284, $p < 0.001$) was higher than non-parasitized individuals ($R = 0.041$, 95% CI: 0–0.064, $p = 0.173$). Confidence intervals of repeatability estimates for non-parasitized fish overlapped zero.

(c) Individual trapping vulnerability

The most parsimonious models for trapping vulnerability across metabolic variables SMR, MMR and AAS included all covariates with the exception of collection lake. Density of black-spot metacercaria was found to positively relate to (V_I) in all conditional models, while density of other endoparasites was negatively related to (V_I) across conditional models. Neither parasite densities were strongly related to the binary component of the model, meaning parasite load did not influence trap entry. Metabolic variables SMR, MMR and AAS did not have any influence on whether fish entered traps, nor the time they spent in traps. This was in contrast to log(mass), which across models was strongly related to trap entry, with larger fish entering traps less often (electronic supplementary material, table S3 and figure S1(a)). While fish body condition was not related to the likelihood of trap entry (electronic supplementary material, figure S1(b)).

(d) Group trapping vulnerability

The number of parasitized individuals within a group did not strongly influence V_G (electronic supplementary material, table S4; figure 2). Groups wholly consisting of individuals with parasites or without parasites had, on average, higher residency times within traps than mixed groups (6u V_G mean ± s.d. = 3565 ± 2968; 6i V_G mean ± s.d. = 3367 ± 2420; 2u-4i V_G mean ± s.d. = 2938 ± 2505; 4u-2i V_G mean ± s.d. = 2729 ± 2670). Among treatment groups, 4u-2i had the highest coefficient of variation (CV = 97.8%), followed by 2u-4i (CV = 85.3%), 6u (CV = 83.3%) and 6i (CV = 71.9%).

4. Discussion

We found that black-spot density positively correlates with some measures of capture vulnerability at an individual level. Specifically, fish with a higher density of black-spot metacercaria spent more time within traps but were equally likely to enter traps as fish with fewer or no metacercaria. Density of other endoparasites showed a weak, negative correlation with time fish spent in traps at the individual level. We hypothesized that being infected with black-spot trematode metacercaria would be related to an increased individual likelihood of capture through a mechanistic link with metabolic rate. However, although we found a positive relationship between black-spot trematode metacercaria density and SMR, we found no evidence of SMR being related to trap vulnerability. This suggests parasite density may be directly affecting trap vulnerability, but not via effects on metabolism. At the group level, the number of parasitized individuals had no effect on vulnerability. Our results suggest that in a full-scale fishery harvest scenario, parasite infection could shift selection patterns around traps with more heavily infected fish spending more time in traps, and thus being more vulnerable to capture. If this effect is sufficiently strong, it could not only serve to alter the selective landscape in fishing, but also have wider scale repercussions on parasite dynamics [63]. In addition, preferential removal of heavily parasitized fish may also lower the palatability of captured fish, potentially influencing the economic value of the catches [64]. These results provide an excellent example of how stressors acting in synergy with fishing, can potentially influence broad-scale selective processes in fishery harvest.

Adjusted repeatability of trap entry in parasitized individuals was considerably higher than in non-parasitized individuals. Meaning the consistency of either entering or not entering traps is greater in individuals that have black-spot metacercaria. Previous work has shown behavioural

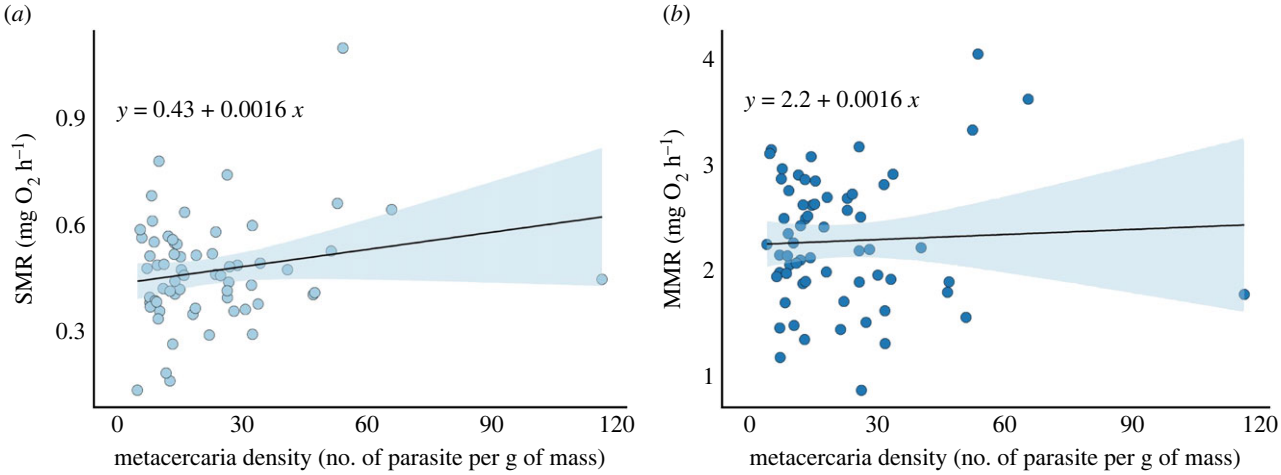

Figure 1. Relationship between mass controlled whole organism metabolic variables (*a*) SMR and (*b*) MMR, and density of encysted black-spot metacercaria. Lines represent linear regressions between each respective metabolic variable and black-spot metacercaria density, and shaded areas represent upper and lower 95% confidence intervals. Panels include only individuals infected with black-spot disease. Note that metabolic rates have been standardized to the mean fish mass to aid interpretation. (Online version in colour.)

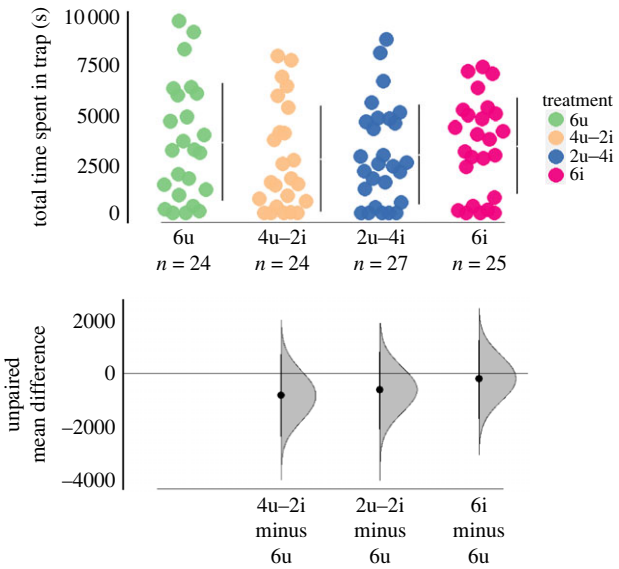

Figure 2. Shared-control estimation plots showing raw data and mean difference between 6u and other treatment groups for total time spent in traps. Top panel shows swarm plots with all data points and 95% confidence intervals as indicated by vertical error bars, with group means shown as gaps in bars. Bottom panel shows 95% confidence intervals and distributions of bootstrapped effect sizes between the groups. (Online version in colour.)

consistency in some traits, such as aggression, can increase in response to greater infection from parasites [65]. Therefore, there is potential for our repeatability results to be a direct effect of black-spot infection. The strength of such homogenizing effects on behaviour are very likely related to both the type of parasitic infection and host species. Here, we did not quantify the specific trematode species found in our fish. However, some trematodes only encyst dermal and epidermal tissue, while others are known to encyst in the muscle or brain of their hosts [66]. Thus, the impact from different species of trematode on capture vulnerability could vary substantially from what we observed here. Although the mechanism influencing our repeatability estimates remain unknown, it is clear that individuals with parasites demonstrate more consistent behaviour around traps, either consistently entering or not-entering across trials. Given repeatability can represent the upper bound of heritability [67], which is a key parameter dictating responses to selection [68]; our results indicate parasitized fish may be under increased selection pressure when compared to unparasitized individuals. Not only could this lead to direct selection on phenotypes vulnerable to parasite infection, but also on correlated physiological and behavioural traits. It should be noted confidence intervals for repeatability estimation were large, thus the precision of these estimates can be considered relatively low. Further work is needed to elucidate how parasites may influence the repeatability of capture in fisheries.

We observed a positive relationship between SMR and the density of black-spot metacercaria, while the relationship between these parasites and MMR/AAS was negligible. Importantly, we found no relationship between metabolic traits and fishing vulnerability. This suggests that despite the positive relationship between black-spot intensity and aerobic metabolism, no clear trend exists between metabolic phenotype and trap capture. This finding is in line with previous work testing how metabolism influences trapping vulnerability, showing no clear link between aerobic energy consumption and the length of time fish spent in traps [16]. By contrast to our results, other recent work, has shown no relationship between aerobic metabolism and black-spot count [56]. Previously, it has been shown that oxygen consumption rates of bluegill sunfish (*Lepomis macrochirus*) increased approximately one month following black-spot infection, and that energetic costs from this disease may only influence energy consumption during this period [69]. Here, aerobic energetic demand correlated positively with black-spot metacercaria density, perhaps indicating that during the period in which fish were captured and tested, black-spot metacercaria had recently infected the host, thereby affecting host metabolism. In addition, whereas Guitard *et al*. [56] found a negative relationship between other endoparasites and metabolic traits, here we found no strong relationship between the two. These discrepancies may be explained by differences in the sampling dates, and thus temperatures at which these relationships were tested (July versus October), with different thermal conditions serving to affect parasite activity. In addition to activity, black-spot infection intensity is also seasonal, with counts being highest during the autumn months [48]. Here, we found higher median black-spot counts ($n = 127$), than in the Guitard

et al. [56] study ($n = 112$; doubling numbers as only one side was sampled). It is possible that a metabolic cost is only evident after a specific threshold of black-spot infection is reached, perhaps in relation to an associated stress response in the host [69,70]. It is unknown whether black-spot causes a stress response in fish, but this could be a possible mechanism driving the higher basal metabolic costs witnessed. Overall, our results suggest that dynamics between fishing, parasite infection and metabolism are complex, and more work is needed, particularly using wild fish populations, to elucidate this relationship.

The number of parasitized individuals within a group had no strong effect on time fish spent in traps at the group level, nor whether they entered enter traps. Across our four treatment groups, shoals of individuals composed of either wholly infected (6i), or wholly uninfected (6u) fish, were most similar in terms of the sum of time they spent in traps. This suggests there is some conformity in behaviour that arises in uniform groups; but that this trend is not present in mixed shoals. Parasites are thought to maximize inter-individual variation in behaviour, contributing to the maintenance of 'animal personalities' [71,72]. In relation to trap entry at the individual level we found the opposite of this trend: individuals with parasites showed more consistency in behaviour. However, at the group level, results here support the idea that parasites may increase within-group variation in fishing vulnerability, as shoals composed of mixed infection phenotypes had high coefficients of variation in group trapping vulnerability. It is worth noting that unlike for individual-based analyses, in our group analyses we did not use a random effect to control for origin as metrics tested were a product of fish from different lakes. Therefore, it is possible that the shoaling behaviour could be confounded by the ratio of individuals from different lakes in each shoal. We tried to minimize the chance of this occurring by housing and habituating fish from different lakes together prior to the start of all experiments. Further work quantifying how parasite infection renders individual behaviour more repeatable, but also how this translates into group decision making, is needed to elucidate possible mechanisms influencing selection.

Aerobic metabolic phenotype was not related to the time fish spent in traps, nor likelihood of trap entry. Meaning that at the scale tested, the influence of aerobic metabolism on trap capture is negligible. Previous work using active gears has found links between vulnerability to fishing and aerobic metabolism. However, this is thought to arise owing to correlations between aerobic and anaerobic metabolism [15,73]. By contrast to active gears such as trawls, which are through to select on performance traits, trapping vulnerability likely selects on behavioural traits [48,74,75]. Studies assessing how metabolic phenotype influences capture in both trapping and rod and line angling have found little evidence of these fishing techniques selecting on aerobic capacity (e.g. SMR [16,76]). Although here we found parasite density to positively relate to SMR, we also found no evidence to suggest metabolism relates to capture at the scale tested. However, given that aerobic metabolic phenotype can be associated with higher activity levels and aggression [77,78], it is still possible that selection on SMR, which here we found to be related to parasite load, may occur. This may only influence selection at wider spatial scales, something not tested in this study. For instance, assuming that individuals with higher energetic requirements need to forage more often and across larger ranges, then the probability of these individuals encountering traps, becoming infected and being caught is higher than that of individuals with lower energy requirements. Indeed, black-spot, has been found to increase both the home range and activity levels of Atlantic cod (*Gadus morhua*) [79]. Although the mechanism promoting this behavioural change was not identified, increased activity could directly increase the likelihood of parasitized individuals being captured compared to unparasitized individuals. Further work is needed to determine if metabolic phenotype is under selection in trap fisheries, when considering wide-scale movement and activity patterns of fish.

We found a strong effect of body mass on trap entry, independent of fish body condition (scaled mass index), with larger fish entering traps less often. Given all fish comfortably fit within the inverted funnel trap entrances - which were approximately 31% deeper and approximately 44% wider than the largest fish, reluctance of some fish to enter traps was likely behavioural, and not a physical limitation. Recent work suggests that continued exploitation of large fish might be driving a long-term global decline in parasite numbers [63]. This might indeed be the case in instances where larger fish, which tend to have greater absolute parasite abundance and richness, are preferentially targeted. However, we saw that larger fish had both a lower density of parasites, and were less likely to be captured. This suggests that no wide-scale impact on parasite population dynamics is likely to occur with this method of fishing as a function of size. Why some fish entered traps more frequently may be linked to their internal hunger state. The terms hunger and condition (body condition) are often used interchangeably in fish studies [80], though work denoting how these two traits relate to one-another is scarce. Presumably, fish in lower condition have higher hunger levels, and vice versa. Here, we expected fish in lower condition to be more attracted to the traps, and incur higher trapping rates, due to links that exist between hunger and activity/exploration rates [81]. However, although overall body size was negatively correlated to trap entry, no such trend was present for body condition and trap entry. Therefore, in this case, hunger, as indicated by lower body condition, did not play a strong role in trap capture. All fish in our trials were fasted for 24 h, meaning their immediate hunger states were possibly similar, this could have served to homogenise capture regardless of condition if proximate hunger state has more influence on behaviour than overall condition. It should be noted that we calculated scaled mass index based on the weight of both parasites and fish, which can in some cases lead to an overestimation of condition [82]. We found no relationship between body condition and black-spot metacercaria density (electronic supplementary material, figure S2), therefore we do not expect our condition indices to be inflated by parasite mass.

The dynamics among fishing-associated selection, parasites and their hosts, are a function of both fishing method and the species in question. Our study focused on a freshwater centrarchid fish species that is not commercially targeted. Although global captures in marine fisheries are greater than those from freshwaters, freshwater fisheries are critically important across the globe with regard to food and economic security, as well as cultural importance [83].

While centrachids are not commercially fished, Percidae including walleye (*Sander vitreus*), zander (*Sander lucioperca*) and European perch are all freshwater species targeted by commercial trap fisheries, are prone to black-spot infection, and occupy similar ecological niches as centrarchids. Our results are thus particularly relevant for these fishes, but should also be considered important within the context of other fisheries, such as those centering on South American and African cichlids (e.g. the ornamental fish trade). There are numerous other freshwater fish taxa targeted by smaller-scale artisanal fisheries across the globe, and our results suggest that interactions between parasite infection and vulnerability to passive fishing gears should be examined in these fisheries. Furthermore, given the variety of parasite species, and the varied effects they have on their host, such as affecting sensory ability [84], influencing habitat selection [19,85], increasing hydrodynamic drag [86], and damaging fins [87], it is clear that parasites could significantly disrupt the ability of fish in sensing and responding to fishing gears. We hope our results will provide a catalyst for further work directly addressing how parasite influence capture within commercially exploited species.

Fisheries-induced evolution remains a debated issue [7]. If fisheries-associated selection on traits other than fish size does occur, it is likely influenced by a multitude of extrinsic factors, which may either accentuate or dilute the evolutionary potential of fishing. Passive gears, such as pots/traps, are considered more environmentally friendly methods of fishing compared to gears such as trawls, which have a high energy consumption, significant habitat impacts and high bycatch levels [88]. Pots/traps have shown to be viable in several demersal fisheries including species such as pacific cod (*Gadus macrocephalus*), sablefish (*Anoplopoma fimbria*) and groupers [35,88,89]. Yet, almost nothing is known on how selection on behavioural or physiological traits in trap fisheries may occur. For the first time, we show that parasite presence and density in fish relates to individual susceptibility to capture in passive traps. Importantly, in this study, we assessed the final moments before capture occurs. However, the potential impacts to fishery selection from parasites are not restricted to the immediate time before capture, but may include spatially and temporally extensive windows [73]. The extent to which synergistic stressors may influence selection in the wild remains largely unknown.

Ethics. Animals were collected following protocols approved by UdeM's Comité de déontologie de l'expérimentation sur les animaux (protocol number 21-028) and permits were granted by the Ministère des Forêts, de la Faune et des Parcs (Permit number: SEG#2021-05-18-1833-15SP).

Data accessibility. Data are included as electronic supplementary material.

The data are provided in electronic supplementary material [90].

Authors' contributions. D.T.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, supervision, visualization, writing—original draft, writing—review and editing; L.I.: data curation, methodology, resources; C.E.: formal analysis, writing—review and editing; S.S.K.: conceptualization, methodology, validation, writing—review and editing; S.A.B.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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