

Size-selective harvesting affects the immunocompetence of guppies exposed to the parasite *Gyrodactylus*

Vitalija Bartuseviciute¹, Beatriz Diaz Pauli¹, Anne Gro Veia Salvanes^{1,2}, Mikko Heino^{1,3,4}

¹University of Bergen

²Bjerknes Centre for Climate Research, Norway

³Institute of Marine Research, Bergen, Norway

⁴International Institute for Applied Systems Analysis, Laxenburg, Austria

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Abstract

Harvesting is typically size-selective, targeting large individuals. This is expected to lead to reduced average body size and earlier maturation, i.e., faster life histories. Such changes can also affect traits seemingly unrelated to harvesting, including immunocompetence. Here we test four hypotheses on how harvesting affects immunocompetence based on the pace-of-life syndrome, habitat area limitation, and energy allocation and acquisition, respectively. We empirically evaluate these hypotheses using an experimental system consisting of the ectoparasite *Gyrodactylus turnbulli* and lines of guppies *Poecilia reticulata* that had been subjected to either small, random, or large size-selective harvest for over 12 years. We followed the infection progression of individually infected fish for 15 days. We found significant differences between the harvested lines: fish from the small-harvested lines had the highest parasite loads. During the early phase of the infection, parasite loads were the lowest in the large-harvested lines, whereas the terminal loads were the lowest for the random-harvested lines. These results agree with the predictions from the energetic trade-off and surface area hypotheses. To our knowledge, this is the first demonstration of the consequences of size-selective harvesting on immunocompetence.

Keywords: parasite resistance, life-history trade-offs, exploitation, Pace-of-life-syndrome (POLS)

Introduction

Humans can induce and accelerate evolution in the species around us (Palumbi, 2001). In particular, harvesting, both hunting (Coltman et al., 2004; Jachmann et al., 1995) and fishing (Conover & Munch, 2002; Diaz Pauli & Sih, 2017; Jørgensen et al., 2007), is a potent agent of evolution because it directly affects survival, a key component of fitness. From the prey perspective, harvesting is just another form of predation. However, humans are particularly efficient predators, and typically exploit higher proportions of prey populations than their natural enemies do. Moreover, harvesting frequently targets specific phenotypes, often differently from natural predators (Darimont et al., 2015). Such harvesting has direct demographic effects, but also creates selection against traits that make succumbing to harvest more likely.

In aquatic systems, fishing represents a major source of mortality. Moreover, fishing is selective by nature, usually targeting large fish that are least likely to succumb to natural predation (Law, 2000), and results in populations consisting of fewer, smaller, and younger fish. The typical response to such selection is evolution towards maturing earlier and at smaller size (Heino et al., 2015; Jørgensen et al., 2007). Strong selection pressure over multiple generations, despite the generally low heritability of life-history traits (as it is typical for traits closely related to fitness; Mousseau & Roff, 1987), can cause substantial evolution in a few generations (Conover & Munch, 2002; Law, 2000; Uusi-Heikkilä et al., 2015; van Wijk et al., 2013).

Wild populations have to navigate the potentially conflicting challenges of how best to deal with human predation and their natural enemies, which include not only predators but also parasites and disease. Developing and maintaining immune system is costly (Lochmiller & Deerenberg, 2000; Schulenburg et al., 2009; Sheldon & Verhulst, 1996), competing for the same resources that individual uses for growth and reproduction. This suggests that harvest-induced changes in growth and maturation lead to correlated responses in the immune system. Moreover, harvesting can also influence immunocompetence by changing a population's size structure and its density.

Here we use the *Gyrodactylus*–guppy system to investigate the trade-offs between adaptation to size-selective harvesting and parasite resistance. *Gyrodactylus* is a specialist monogenean ectoparasite common in many fish species, including guppies where prevalence can exceed 75% (van Oosterhout et al., 2007). Resistance to *Gyrodactylus* is genetically based (Madhavi & Anderson, 1985), with both innate and acquired immunity playing a role (Cable & Van Oosterhout, 2007). *Gyrodactylus* have a complex reproduction system, where embryos develop one inside the other and are hence known as “Russian-doll killers” (Bakke et al., 2007; Cable & Harris, 2002). As ectoparasites, *Gyrodactylus* can directly be observed and counted, instead of relying on invasive methods preventing multiple observations of the same host, or alternatively, using indirect proxies of parasite load to obtain repeated observations. Therefore, several studies have used the *Gyrodactylus*–guppy

system to investigate host-parasite interactions (Dargent et al., 2013; Kolluru et al., 2006; Stephenson et al., 2018; Tadiri et al., 2013). Yet, whether size-selective harvesting affects immune response to *Gyrodactylus* remains unstudied.

It is challenging to predict what the expected relationship between harvesting and immunocompetence should be. Harvesting affects targeted populations in multiple ways. The most readily observed changes are in body size, but there can be many other, less obvious changes in other life-history traits, behaviour, and physiology. If we assume that individual parasite loads can be used as a proxy of immunocompetence, the available theory can predict either a positive or negative relationship between host body size and parasite load (Fig. 1).

A larger surface area allows larger hosts to harbour more parasites (Poulin & Rohde, 1997). This *surface area hypothesis* leads us to predict a positive correlation between host body size and parasite load. Thus, if harvesting selects for smaller body sizes, then individual parasite loads should be reduced. Another mechanism that could lead to a positive relationship is related to the energetic trade-off between growth and investment in immunocompetence (van der Most et al., 2011). Therefore, the *energy allocation hypothesis* predicts a positive correlation between body size and parasite loads because individuals that allocate more resources to growth will have less resources available to immunocompetence. These two hypotheses are not mutually exclusive — changes in body size could be in part caused by the energetic trade-off between growth and immunocompetence.

Other hypotheses suggest a negative correlation between host body size and parasite loads. The *energy acquisition hypothesis* builds on the observation that harvesting can affect the total amount of energy available for functions such as growth and immunocompetence: harvesting favours shy behavioural types, which are associated with lower energy acquisition rates (Walsh et al., 2006). Hence, there would be less energy available for both the immune system and growth/reproduction, leading small individuals to suffer from the highest parasite loads. The *pace-of-life syndrome (POLS) hypothesis* (Montiglio et al., 2018; Réale et al., 2010) also predicts a negative correlation between host body size and parasite loads, but the underlying logic is based on inter-temporal trade-offs: a faster pace of life is generally correlated with reduced investment in traits with delayed fitness pay-offs in terms of improved survival and/or reproductive capacity. Such traits include investment in somatic growth and in immunocompetence (Stephenson et al., 2015). Harvesting large individuals favours faster pace of life and is therefore expected to lead to both reduced body size (Law, 2000) and immunocompetence, the latter having been documented with natural predators (Stephenson et al., 2015).

We investigated the relationship between harvesting and immunocompetence by using laboratory populations of experimentally harvested guppies representing three treatments: large-harvested (removing large individuals), random harvest (no size selection), and small-harvested (removing small individuals). This has resulted in an array of populations along a gradient where large-harvested populations are showing small body size and early maturation, small-harvested ones large body size and late maturation, with random-harvested ones in between (Table 1). We infected female guppies from our experimentally harvested populations with parasites from a laboratory culture of *Gyrodactylus turnbulli* and followed the development of the parasite loads in individual hosts. Using parasite loads as a proxy of the host's innate parasite resistance, a component of its immunocompetence, we test the hypotheses outlined above. Figure 1 shows the characteristics of the experimental fish and the specific predictions on their parasite loads following our hypotheses.

Methods

Experimental fish

Experimental fish are from size-selectively harvested guppy lines at the University of Bergen. The lines originate from the low-predation Yarra River in Trinidad and have been maintained in a laboratory since 2009 and were subjected to three types of size-selective harvesting. Large-harvested (removal of $x\%$ of individuals larger than 16 mm in each harvesting event), small-harvested (removal of $x\%$ of individuals of individuals bigger than 16 mm), random-harvested (removal of $\frac{1}{2} x\%$ of the entire population in each harvesting event). Harvesting was started in 2010 and typically conducted every 6–12 weeks. Harvesting intensity has been varied between 25% and 50% to maintain roughly constant population sizes (see Diaz Pauli et al. (2014), Diaz Pauli et al. (2017) and Diaz Pauli (2012) for more details). The 16 mm size threshold corresponds to male standard length at maturation

in Yarra river (Reznick, Rodd, et al., 1996). Each size-selectively harvested line had 3 replicates, resulting in total 9 laboratory populations of mixed age and sex guppies in 400 L tanks. Table 1 summarizes the population characteristics at the initiation of the parasite experiment (May 2021).

Experimental set-up

On May 3–6th 2021 we separated 12 representative adult females randomly from each of the nine populations (n=108). These were housed separately by population in a 2-litre aquaria (n=12 in each) in flow-through environments. The fish were fed *ad-lib* daily with newly hatched *Artemia salina* (Silver Star Artemia) for two weeks until experimental infections. Water temperature was $26 \pm 1^\circ\text{C}$ and the photoperiod was 12:12 h (L:D).

Length (mm, as standard length) was measured on the first (day 0) and last experimental day (day 15). Figure S2 shows a full timeline for the experiment. The mean SL of all fish used in the experiment was 20.0 ± 0.1 mm (mean \pm SE; range: 15.5 mm–24.5 mm). Before measuring, the fish were anesthetized individually in MS-222 (concentration: 0.03%, buffered with 0.02% NaCO_3).

Table 1. Life-history characteristics of size-selectively harvested guppy lines (populations) and females chosen for the parasite experiment. SL refers to mean standard length (\pm SE). Population values are based on subsamples of $\frac{1}{4}$ of all fish. Because female maturity cannot be reliably detected non-invasively, we conservatively assumed that all females larger than 16 mm SL were mature.

Size-selection	Males				Females			
	Length at 50% maturity (L50) [†]		Mature males [‡]		Mature females (≥ 16 mm SL) in populations		Experimental females	
	SL (mm)	n	SL (mm)	N	SL (mm)	n	SL (mm)	n
Large-harvested	13.8 ± 0.18	389	15.3 ± 0.07	320	18.4 ± 0.23	405	17.6 ± 0.11	36
Random-harvested	15.2 ± 0.18	120	16.7 ± 0.13	88	19.2 ± 0.28	74	20.9 ± 0.14	36
Small-harvested	15.6 ± 0.17	169	17.8 ± 0.10	137	21.0 ± 0.16	218	21.4 ± 0.13	36

[†] Estimated with a generalized linear mixed model with binomial error distribution, Maturity $\sim 0 + \text{Length} + \text{Size-selection} + 1|\text{Population}$. SE was estimated with bootstrapping.

[‡] Observed males were identified as mature by anal fin morphology, as described in Turner (1941), when the fleshy hood passes beyond the tip of the gonopodium (stage 4).

Infection and monitoring of parasites

Gyrodactylus turnbulli were obtained from guppies bought in a pet shop in Bergen, Norway in 2019. The species was identified by an expert (Egil Karlsbakk, pers. comm. *University of Bergen, Norway*) based on parasite morphology. The attachment areas were also consistent with *G. turnbulli* (Harris & Lyles, 1992). Parasites were transferred to wild-strain laboratory guppies via co-habitation, similar as in Harris (1988). *Gyrodactylus* were kept on laboratory guppies in mixed sex and age tanks until the experiment started, supplementing the tanks with naïve fish to maintain parasite numbers when needed, as in King & Cable (2007).

For infection *Gyrodactylus* worms were transferred to the caudal fins of experimental females. This was done individually by bringing heavily infected donor fish that has been given an overdose of MS-222 into physical contact with the experimental fish, confirming the establishment of three parasites under a microscope, and facilitating the transfer with Dumont tweezers No.5 when needed. This method is similar to the ones used before (Cable & Van Oosterhout, 2007; Dargent et al., 2013, 2015; Stephenson et al., 2018; van Oosterhout, et al., 2003).

Infected females were fed *ad-lib* daily with newly hatched *Artemia salina* (Silver Star Artemia) and housed in $24 \pm 2^\circ\text{C}$ water temperature and a 12:12 (L:D) photoperiod. Parasite loads were inspected every 3 days (Fig. S1, S2), which was the shortest fish handling interval permitted by the Norwegian Food Safety Authority. The water

was changed at the same time. Counting of parasite loads was done with a manual click counter under a stereomicroscope using magnification x12, after fish were anesthetized in buffered MS-222. A painting brush was used to separate fins from the body (Tadiri et al. 2013; Pérez-Jvostov et al. 2012) and to allow systematically scanning all body surfaces for parasites.

All fish were initially infected with three worms. On day 3 we reinfected nine fish as their parasite loads were less than 3 worms. This was done to account for the possibility that *Gyrodactylus* were old or damaged and therefore unable to establish (King & Cable, 2007). Similar reinfection has been used in other studies (Cable & van Oosterhout, 2007; Smallbone et al., 2016), except that we did not treat reinfections as new day 0.

In the end of the experiment, all individuals were sacrificed using an overdose of MS-222. A total of eight individuals had to be removed from the experiment following guidelines of humane endpoints (i.e., abnormal behaviour) and did not complete all 15 days of the experiment. Only four individuals presented abnormal behaviour linked to the parasite infection, while the remaining four were sacrificed due to reasons unrelated to our experimental set-up (e.g., problems while giving birth).

Data analysis

We modelled parasite loads as the population dynamical process $N_{t+1,i} = \lambda_i N_{t,i}$, where $N_{t,i}$ is the parasite count at time t in population i and λ_i is parasite population growth ratio. Logarithmic transformation of the equation gives $\ln(N_{t+1,i}) = \ln(\lambda_i N_{t,i}) = \ln(\lambda_i) + \ln(N_{t,i})$. The parameters of this model can be estimated with a regression model of type $\ln(N_{t+1,i}) = c_i + \ln(N_{t,i}) + \epsilon_i$, where ϵ_i is an error term. This implies that model coefficients $c_i = \ln(\lambda_i)$ can be interpreted as population growth rates and that $N_{t,i}$ should enter the model as an offset term, without a regression coefficient. We fitted this model using a generalized mixed effect model with a flexible representation of time course and accounting for length effects. We initially fitted the model assuming Poisson error distribution using package lme4 (Bates et al., 2021). Because our Poisson models were over-dispersed (checked with the package blmeco, Komer-Nievergelt et al., 2019), the final models were fitted assuming negative binomial error distribution using package MASS (Ripley et al., 2022). We used three random effects reflecting the experimental set-up (non-independence of fish originating from the same population, block structure and multiple measures of the same fish). The fixed effects include two variables reflecting the experimental design (SIZE-SELECTION and TIME) and one confounding variable, LENGTH. TIME is measured in the increments of 3 days. TIME² was used to account for non-linear time dependencies. LENGTH was mean-standardized and ln-transformed. Model also included the two and three-way interactions of the fixed effects. Goodness of the model fit was evaluated with a package MuMIn (Bartón, 2022). Data analysis was conducted in R (v. 4.0.3, R Foundation for Statistical Computing, 2020).

We conducted backward model selection based on likelihood ratio testing, starting from the model with all main effects and their two-way interactions, and the interaction between time, length, and treatment. Final model selection was done by AIC comparisons (Supp. Table S1), but we kept all terms representing our study design (all random effects and the fixed effects SIZE-SELECTION and TIME when main effects). Confidence intervals were obtained by bootstrapping (1000 replicates) and the 2.5% and 97.5% percentiles were extracted as lower and upper confidence limits.

Results

Harvested lines and experimental fish

The size-selectively harvested lines differ in their size structure and life-history traits (Table 1). These differences follow the slow–fast continuum, with the large-harvested lines having the fastest life histories (characterized by small adult size and size at maturation) and the small-harvested lines having the slowest ones. These differences are replicated in the experimental females exposed to the parasite infection (Table 1, Fig. S3).

Host surface area constrains growth of parasite loads

Individual body size had a large effect on the development of the parasite load (Fig. 2). Because experimental fish differed significantly in length, the initial parasite load (3 parasites per fish) corresponded to large

differences in parasites loads relative to the surface area of the fish (Fig. 2A). However, already 3 days after the infection the relative parasite loads were almost equalized. At the end of the experiment, the relative parasite loads varied greatly between individuals but were independent of length. These results show that host surface area limitation is an important factor affecting *Gyrodactylus* loads in our guppies.

Size-selective harvesting affects parasite loads

The increase of parasite loads over time differed between the three size-selectively harvested treatments (Fig. 3A). The differences in the terminal parasite loads were prominent: in day 15, the observed parasite loads were 116 ± 17 (mean \pm SE) for the large-harvested lines, 122 ± 22 for the random lines, and 196 ± 22 for the small-harvested lines, i.e., the terminal parasite loads in the negative lines were about 60% higher than in the other lines (Fig. 3B).

Because there were systematic differences in fish body size between the lines (Table 1, S4), the differences in parasite loads are potentially confounded by size differences. However, even after controlling for the effect of body size, our statistical model shows significant differences in the parasite loads between the treatments (Table 2), as illustrated by the model-predicted average parasite loads for a 20.0-mm fish (the mean length across all experimental fish) in Fig. 2A.

In addition to the large differences in terminal loads, the time courses of parasite infections were also qualitatively different: the model-predicted parasite load for length-standardized fish peaked at day 12 in the random-harvested lines but continued to increase in the other size-selectively harvested lines, even rapidly so in the small-harvested lines (Fig. 3A). Nevertheless, in all cases parasite load growth rates were decelerating over time, consistent with surface-area limitation of parasite loads.

Host body size affects parasite load in harvested treatments

Size had significant effects on parasite load in all treatments. Patterns were consistent in all size-selectively harvested lines. Small individuals had higher parasite loads during the first 9 to 12 days of the experiment. By the end of the experiment, parasite loads in small fish were stable or declining (Fig. 2B). In contrast, parasite loads of large individuals were still increasing in the end of the experiment in all but random-harvested lines. The largest individuals had the highest model-predicted terminal parasite loads (Fig 2B).

Although our results show significant effects of host body size, it accounts for only a relatively small proportion of variation in parasite loads. Our main model explains 32% of variability in the data (marginal pseudo- R^2 ; Table 2); dropping LENGTH (including its interactions) reduces this value to 30%.

Table 2. Summary of the final generalized linear mixed effect model for *Gyrodactylus turnbulli* parasite loads in female guppies. The model assumes negative binomial error distribution. SIZE-SELECTION refers to the three size-selectively harvested treatments of guppies. TIME is measured in the increments of 3 days. LENGTH refers to ln-transformed standardized length ($\ln(l/\bar{l})$), hence the effects including this term can be omitted when focusing on a fish with an average standard length ($\bar{l} = 20.0$ mm). *P*-values <0.05 are bolded. Standard deviation associated with the random effects was INDIVIDUAL ID: $1.99 \cdot 10^{-8}$, POPULATION: $4.96 \cdot 10^{-9}$, BLOCK: $1.78 \cdot 10^{-8}$. Marginal pseudo- $R^2 = 0.321$.

Fixed effects	Estimate	Standard error	Z	P
Intercept	0.886	0.147	6.0	< 0.0001
LARGE SIZE-HARVESTED				
RANDOM SIZE-HARVESTED	0.422	0.165	2.6	0.0106
SMALL SIZE-HARVESTED	0.476	0.172	2.8	0.0057
TIME	0.102	0.083	1.2	0.2217
TIME ²	-0.055	0.015	-3.7	0.0002
LENGTH	-1.887	0.890	-2.1	0.0340
RANDOM SIZE-HARVESTED:TIME	-0.180	0.066	-2.7	0.0060
SMALL SIZE-HARVESTED:TIME	-0.141	0.068	-2.1	0.0381
RANDOM SIZE-HARVESTED : LENGTH	0.086	1.185	0.1	0.9424
SMALL SIZE-HARVESTED: LENGTH	0.308	1.232	0.3	0.8023
LARGE SIZE-HARVESTED:TIME: LENGTH	0.084	0.354	2.4	0.0175
RANDOM SIZE-HARVESTED:TIME: LENGTH	0.649	0.315	2.1	0.0389
SMALL SIZE-HARVESTED:TIME:LENGTH	0.790	0.339	2.3	0.0197

Discussion

We empirically evaluated the trade-off between life-history adaptations and immunocompetence in experimental guppy lines exposed to different size-selective harvesting regimes. Using parasite loads as a proxy of immunocompetence, we found significant differences between hosts deriving from the different lines. Our findings suggest that size-selective harvesting leads to evolution in parasite resistance.

Our results are consistent with two of our initial hypotheses: differences in parasite loads are associated with differences in host surface area (hypothesis 2), and small-harvested lines had the highest parasite loads, in agreement with the energetic trade-off between growth and immunocompetence (hypothesis 4). While the host

size was important in determining individual parasite loads, in agreement with previous studies in guppies by Cable and van Oosterhout (2007) and Tadiri et al. (2013), it could not explain differences between the size-selective harvest treatments. We conclude that harvesting small individuals affects parasite resistance through two jointly acting mechanisms, by changing the size structure of the host population and by altering energy allocation of individual hosts.

Guppies exposed to sustained large size-harvest, which favours faster life histories described by early maturation at small sizes, had higher parasite resistance than guppies from lines with small size-selective harvest favouring slow life histories. This finding is the opposite to the pace-of-life syndrome hypothesis (POLs) (Montiglio et al., 2018; Réale et al., 2010), and energy acquisition hypothesis (Walsh et al., 2006). Our results are in agreement with the trade-off hypothesis emphasizing the energetic competition between investment in growth and immunity (Lochmiller & Deerenberg, 2000) and with the surface area hypothesis – the bigger the individual, the more parasites it can acquire (Poulin & Rohde, 1997).

While POLs is a good framework for understanding life-history variation in guppies, it is only to be expected that not all traits can be aligned with a single gradient. Previous studies on pace-of-life syndrome and trade-offs of immunocompetence vs. other life history traits show mixed results across taxa. Although Martin et al. (2006) found only partial support of stronger immune defences in slow-living house sparrows, a meta-analysis of 14 studies of poultry lines by van der Most et al. (2011) found that experimental selection for accelerated growth had a large and significant negative effect on immune function. Previtali et al. (2012) found evidence of pace-of-life hypothesis in rodents for adaptive immunity measured by antibody response, which was greatest in squirrels, intermediate in chipmunks, and lowest in mice, while innate immune responses were the opposite. Coltman et al. (2001) found a positive genetic correlation between parasite resistance and body size in Soay sheep (*Ovis aries*), suggesting that genetically resistant individuals also experience superior growth. Therefore, we suggest that the validity of the pace-of-life syndrome is sensitive to the exact nature of selection driving trait variation. Artificial selection experiments can target single traits and create patterns that could not emerge in the wild, where selection always affects multiple traits simultaneously. Selection in our experimental populations falls in between these extremes: while harvest selection was strictly size-based, the populations are self-renewing and subject to semi-natural selection related to cannibalism avoidance, feeding, and mating.

Previous studies on parasite resistance in guppies have also yielded mixed results. For example, van Oosterhout et al. (2003) found clear differences between two Trinidadian guppy populations in susceptibility to *Gyrodactylus turnbulli*. Those from the low-predation site (with slow life histories) lost parasites at a slower rate and had higher parasite loads than guppies from the high-predation site (with fast life histories). These results are consistent with our findings on size-selectively harvested guppies. However, Pérez-Jvostov et al. (2012) evaluated the adaptive responses to infections of wild guppy populations adapted to different predation regimes and found no interaction between infections and the predation regimes. One possible reason for these differences could be different study designs. While Pérez-Jvostov et al. (2012) used local parasites to infect their guppy populations in a semi-wild setting with less control of individual infections, the present study and that of van Oosterhout et al. (2003) had similar experimental designs based on individually-infected fish in a laboratory setting. While the latter approach is less natural and could introduce some biases, the benefit is that we then were able to have repeated observations of each fish and could thus quantify the development of parasite infections on individual fish over the experimental period. Both of these studies were based on naturally existing variation, which makes it impossible to isolate the agent of selection. In contrast, in our study the principal agent of selection, size-selective harvesting, was strictly controlled.

Despite controlled initial start of infection, there were significantly different responses in establishment and continuation of the infection. Small individuals had higher initial parasite loads in all size-selectively harvesting lines, while large ones had lower initial parasite loads but acquired higher parasite loads than small individuals over time. One explanation could be that small individuals are less resistant, but also that growth of the parasite populations could be constrained by host size, leading to the lower observed parasite loads in small individuals at the end of infection. Larger individuals have larger surface area and are therefore offer more habitat for ectoparasites (e.g., Poulin & Rohde, 1997). Our observations are consistent with study of Cable & van Oosterhout (2007), which found that large guppies carried the highest parasite loads and experienced the highest mortality rates when experimentally infected with different *Gyrodactylus* strains. Observed parasite loads

standardized for host surface area (Fig. 2) were roughly constant at the end of our experiment. However, because we terminated our experiment before parasite-induced mortality occurred, we could not evaluate the full cost of parasitism in our guppies.

Our experiment leaves open how harvesting affects immunocompetence in males, and whether innate and acquired resistance are similarly affected. Males are known to be more susceptible to infections than females (Stephenson et al., 2016; Zuk, 2009). Resistance to *Gyrodactylus* is known to include both innate and acquired immunity (Cable & Van Oosterhout, 2007). Another important venue is to understand the roles of local adaptation and multiple agents of selection – in wild and laboratory systems. Laboratory environments are by design benign, but exposing animals to non-local parasite strains is a stress that wild populations usually do not face.

We demonstrated that size-selective harvesting has significant effects on a trait which was not under direct selection, namely parasite resistance. Such correlated responses to selection are generally expected due to life histories having correlations with other traits, reflecting both trade-offs and underlying genetic pleiotropic effects (Roff, 1993; Stearns, 1989, 1992; van Noordwijk & de Jong, 1986). We found that small size-harvested lines had lower parasite resistance, suggesting a trade-off between higher growth rate and immunocompetence. Interestingly, our study delivers positive news for the harvest management: preferential harvest of large individuals, as is common in both fisheries and hunting, does not seem to compromise parasite resistance. Yet care is needed in extrapolating our results to nature, as our study reveals only a small fragment of innate immunocompetence experienced by exploited populations. Quantifying responses to different pathogens, while including both innate and acquired immunity responses, would allow forming a more complete picture of how costs of adaptations to harvesting and immunocompetence are being paid.

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Ethical considerations

The experiment followed the Norwegian and University of Bergen animal welfare regulations. The permission for experiment was made with basis in Regulation of 18 June 2015 No 761 concerning the use of animals for scientific purposes (the Regulation) § 37, cf. § 6 was given by Norwegian Food Safety Authority (Decision regarding the use of animals in procedures - FOTS ID 21812, accepted 2020 02 12).

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Figures

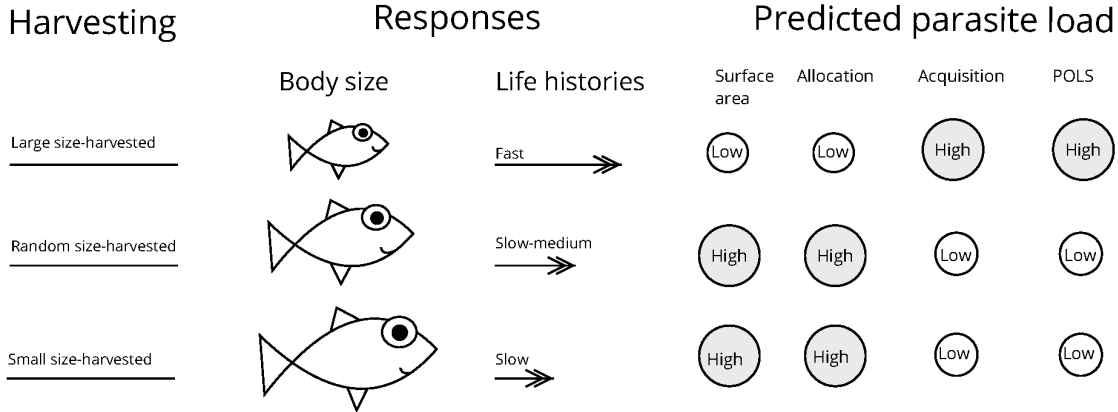


Figure 1. Predictions on size-selective effects on immunocompetence in terms of predicted parasite load.

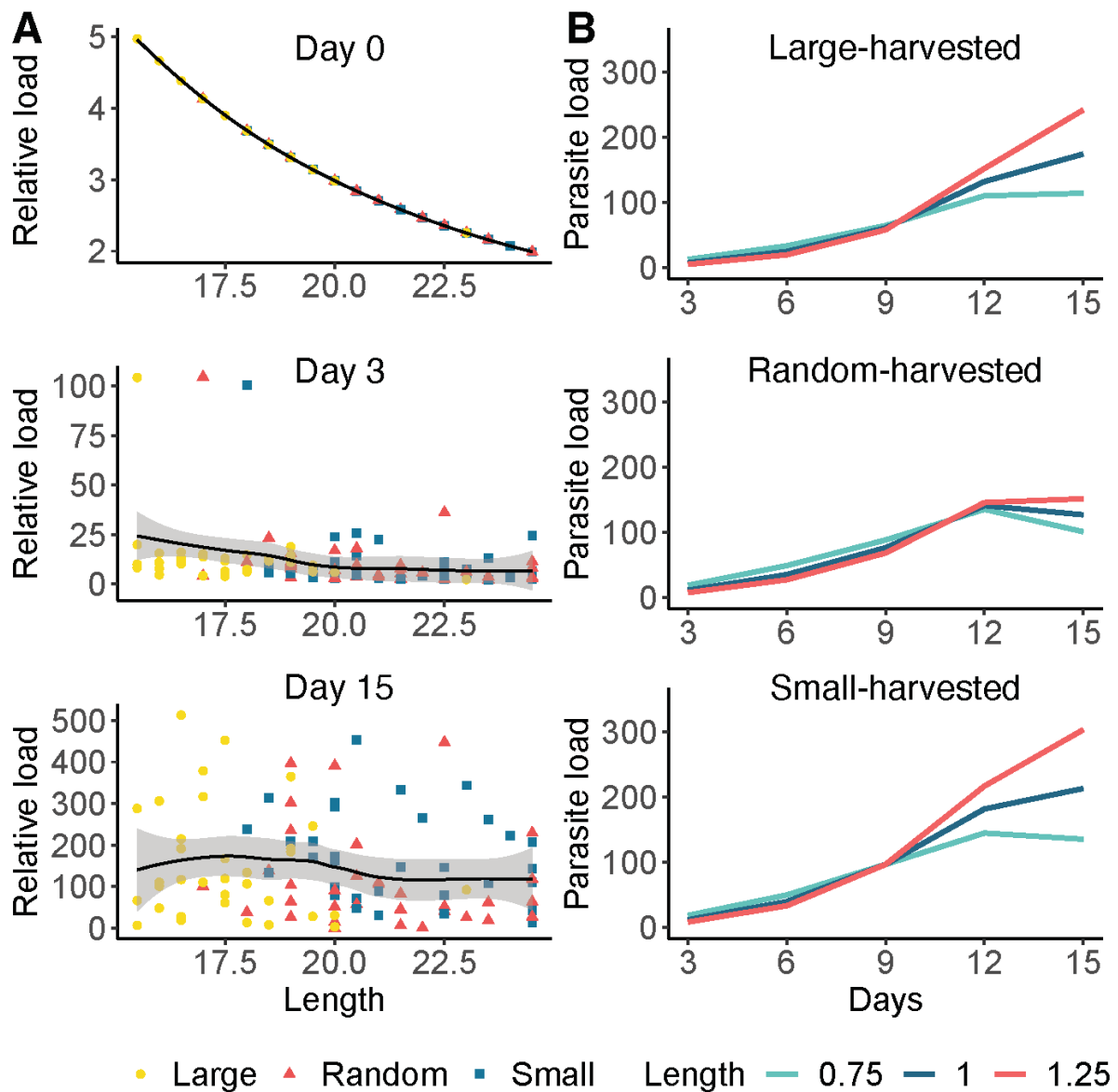


Figure 2. (A) Relative parasite loads versus fish length with LOESS-curves. Relative load is parasite density normalized relative to the surface area of fish of the average size (20.0 mm), assuming an isometric length–surface area relationship. For relative parasite loads on all days see Figure S4. (B) Model predictions (see Table 2) for different lengths within size-selectively harvested lines; predictions are also shown for a fish of the average size (1= 20.0 mm; blue) and 25% smaller (0.75=15 mm; green) and 25% larger (1.25=25 mm; red) fish; this corresponds to the size range of the experimental fish (Fig S3).

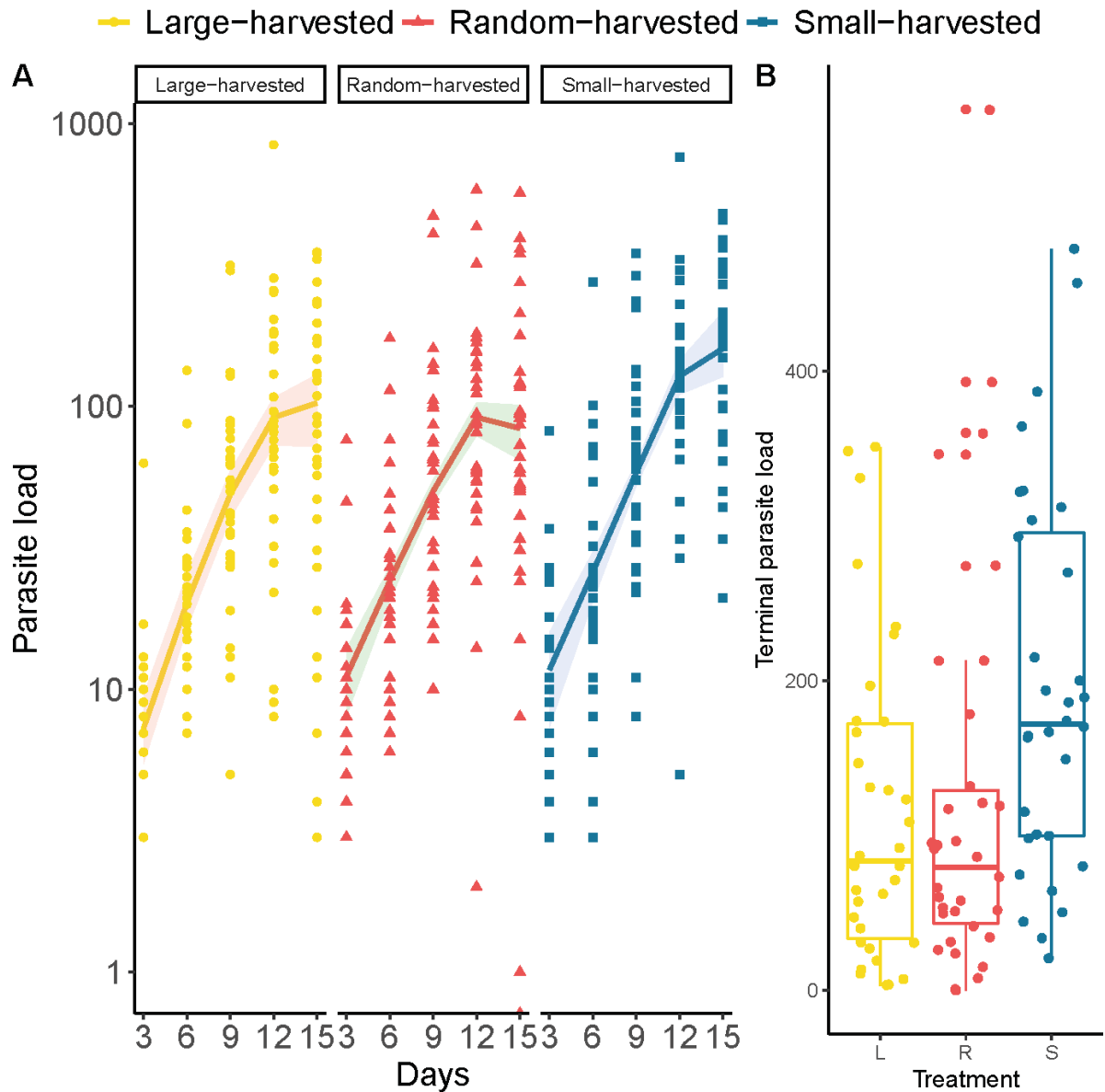


Figure 3. (A) Observed parasite loads (symbols) in individual female guppies ($n=108$) originating from three size-selectively harvested lines and the corresponding model-predicted (see Table 2) parasite loads for a 20.0-mm fish, the mean body length of all experimental fish. The shapes and colours correspond to the three size-selective harvested treatments. Note that the y-axis is on logarithmic scale. An individual in the random treatment managed to clean the parasite loads and had zero loads on day 15; this observation is plotted on the x-axis. Confidence intervals for the model predictions were estimated using bootstrapping ($n=1000$). (B) Terminal parasite loads (day 15) in size-selectively harvested lines.