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ABSTRACT

In most fisheries, larger fish experience substantially higher mortality than smaller fish. Body length, life-history and behavioral traits often correlate, such that fisheries-induced changes in size or life-history can also alter behavioural traits. However, empirical evidence regarding how size-selective harvesting alters the evolution of behavioural traits in exploited stocks is scarce. We used experimental lines of zebrafish (*Danio rerio*) that were exposed to positive, negative or random size-selective harvest over five generations. Our aim was to investigate whether simulated fishing changed the mean personality of the surviving females five generations after initial harvesting halted. We found that mean boldness, activity, and sociability were significantly altered relative to a randomly harvested control line. Harvest-induced changes in individual-level personality were only detected in the negatively size-selected line. By contrast, we did not detect harvest-induced evolution of personality in the positively size-selected line. We conclude that size-selective harvesting alters individual fish personality in a social fish.

INTRODUCTION

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In most exploited fish stocks, fishing mortality on adults is substantially larger than natural mortality (Brown et al. 2008). In addition, most fishing gears and harvest regulations operate in a size-selective manner (Jørgensen et al. 2007; Kuparinen et al. 2009; Pierce 2010). Such selection can lead to life history adaptations within just a few generations (Heino et al. 2015; Jørgensen et al. 2007; Laugen et al. 2014; Uusi-Heikkilä et al. 2015; van Wijk et al. 2013). Fast life history traits - characterized by fast juvenile growth, early maturation at small size and elevated reproductive investment (Stearns 1992) - are generally (but not necessarily, Dunlop et al. 2015; Gíslason et al. 2017) favored under intensive harvesting in both unselective and positively size-selective scenarios (i.e., large individuals are preferentially harvested), leading to reduced post maturation growth and terminal length (Jørgensen et al. 2007) and yielding elevated natural mortality (Andersen et al. 2018; Jørgensen and Holt 2013). Most research on fisheries-induced evolution (FIE) has focused on life-history adaptation (Devine et al. 2012; Sharpe and Hendry 2009), with much less attention devoted to the evolution of behavioral and physiological traits (Arlinghaus et al. 2017; Heino et al. 2015; Heino and Godø 2002; Hollins et al. 2018; Philipp et al. 2009; Uusi-Heikkilä et al. 2008).

In this context, fish personality traits (individual behavioral differences that are consistent over time and/or across situations; Reale et al. 2007) are candidates for FIE of behavior through two main pathways (Arlinghaus et al. 2017; Biro and Post 2008; Uusi-Heikkilä et al. 2008). First, traits such as boldness are related to fitness (e.g., Smith and Blumstein 2008) and often correlate with life-history traits (growth rate, reproductive investment, maturation size and longevity; Dammhahn et al. 2018; Réale et al. 2010), and thus behavioural traits can evolve whenever the fitness landscape changes (Andersen et al.

2018; Claireaux et al. 2018; Jørgensen and Holt 2013). For example, life history adaptations to fishing pressure selecting for a fast life history favor individuals that forage intensively and/or aggressively to reap fitness benefits early in life (Andersen et al. 2018; Claireaux et al. 2018; Jørgensen and Holt 2013). Second, heritable traits including boldness or aggression (Dochtermann et al. 2015) are often systematically related to vulnerability to fishing; thus personality traits can be under direct selection by fisheries (Alós et al. 2016; Arlinghaus et al. 2017; Diaz Pauli and Sih 2017; Diaz Pauli et al. 2015; Härkönen et al. 2014; Klefoth et al. 2017; Rudstam et al. 1984; Sutter et al. 2012; Wilson et al. 2011; Wilson et al. 2015). Importantly, the heritability of personality traits is comparable to or even higher than the heritability of life-history and morphological traits (Dochtermann et al. 2015; Mousseau and Roff 1987; Stirling et al. 2002). Therefore, direct selection on personality can lead to adaptive evolution of behavior to fishing without corresponding changes in life histories (Alós et al. 2016; Arlinghaus et al. 2017; Biro and Post 2008; Biro and Sampson 2015; Monk and Arlinghaus 2017; Sutter et al. 2012). Finally, behavior can also plastically change in exploited fish stocks, due to learning or due to relaxation of density-dependence (e.g., Januchowski-Hartley et al. 2011; Klefoth et al. 2013; Özbilgin and Glass 2004; Raat 1985; Sbragaglia et al. 2018).

Irrespective of the exact mechanism (genetic or plastic), it is important to consider both evolutionary and ecological aspects of fisheries-induced effects on stock dynamics (Eikeset et al. 2016). Fish personality can have profound consequences for social functioning, population dynamics, ecosystem processes and fisheries (Arlinghaus et al. 2017; Conrad et al. 2011; Diaz Pauli and Sih 2017; Mittelbach et al. 2014; Palkovacs et al. 2012; Palkovacs et al. 2018; Ward et al. 2016; Wolf and Weissing 2012). However, the findings of

empirical studies investigating the relationship between behavior and vulnerability to fishing are inconsistent and therefore, a conclusive understanding of FIE of personality traits is currently lacking (e.g. Alós et al. 2016; Biro and Sampson 2015; Diaz Pauli et al. 2015; Härkönen et al. 2014; Kekäläinen et al. 2014; Monk and Arlinghaus 2017; Sutter et al. 2012; Thambithurai et al. 2018; Vainikka et al. 2016; Wilson et al. 2011; Wilson et al. 2015). Moreover, there are only a few theoretical studies focused on the effects of selective harvesting on the evolution of fish personality, and these studies have largely focused on boldness as the focal trait under selection (Andersen et al. 2018; Claireaux et al. 2018). Therefore, there is limited knowledge of the evolutionary effects of fishing on personality traits.

Selection experiments in the laboratory can provide cause-and-effect evidence regarding FIE of both life-history and personality traits (Diaz Pauli and Heino 2014). The few existing experimental harvesting studies focused on personality and behavioural traits suggest that negative size-selective harvesting increases the propensity to take risks (Uusi-Heikkilä et al. 2015; Walsh et al. 2006), in agreement with theoretical models (Andersen et al. 2018; Claireaux et al. 2018). We built on the results presented by Uusi-Heikkilä et al. (2015) to investigate the evolutionary change of a range of personality traits in response to both positive and negative size-selective harvesting using zebrafish (*Danio rerio*) as a model organism. Earlier work using zebrafish selection lines that were created by imposing a 75% per generation mortality rate based on size revealed substantial changes in life histories, size variation, allele frequencies and transcriptome profiles, but no change in metabolic rates after just five generation of harvesting (Uusi-Heikkilä et al. 2016; 2017; 2015). Negative size-selection triggered evolutionary adaptations typical of a slow life history (in

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particular, a lower degree of reproductive investment compared to the control), while positive size-selection triggered adaptations characteristic of a fast life history (young age and small size at maturation, high relative fecundity, small terminal length). Most importantly, Uusi-Heikkilä et al. (2015) documented that negative size-selection led to evolutionary changes of behavior by increasing of boldness at the juvenile stage. However, sexual maturation is a critical transition during life history (Bernardo 1993) and is known to alter animal personality traits, such as boldness and aggression (e.g., DiRienzo et al. 2012; Gyuris et al. 2012; Niemelä et al. 2012), both of which are important for reproduction (McPeck 2004; Niemelä et al. 2012). It is thus unclear whether the evolutionary changes in boldness reported for the juvenile stage by Uusi-Heikkilä et al. (2015) hold for the adult life-stage and whether personality traits other than boldness (i.e. sociability, aggression and activity) also changed in response to size-selective harvesting.

Our objective was to examine the effects of five generations of intensive directional size selection (both positive and negative) on four different adult personality traits (activity, boldness, aggression, and sociability) measured at the individual-level (i.e., not in a group context). Because sex-specific behavioral differences have been described in zebrafish (Spence et al. 2008) and pace-of-life syndromes can be sex-specific (Hämäläinen et al. 2018), we tested our hypotheses only with females. Following the theoretical model of Andersen et al. (2018), we predicted that positive size selection (mimicking a fishery with a minimum length limit) favored the evolution of shy adult individuals. By contrast, we expected the evolution of bold adult individuals in the negative size selection line (mimicking a fishery with a maximum size limit). We also formulated predictions regarding evolutionary change in three additional personality traits (activity, aggression and sociability), assuming that

these traits are linked to boldness by a behavioral syndrome (Conrad et al. 2011; Réale et al. 2010; Sih et al. 2004). Specifically, we predicted that fishes exposed to positive size selection (where small fish had a selective advantage) would be (i) less active, (ii) less aggressive and (iii) more social than fishes of the control line. We expected opposing adaptations in relation to negative size selection (where large fish had a selective advantage). We also predicted that all four behavioral traits would be repeatable over time (i.e., indicative of personality traits; Reale et al. 2007) and correlated amongst one another (i.e., indicative of a behavioral syndrome; Sih et al. 2004), as already demonstrated in previous studies on zebrafish (e.g., Ariyomo et al. 2013; Dahlbom et al. 2011; Moretz et al. 2007; Toms and Echevarria 2014). Given that personality is correlated with body size in zebrafish (Polverino et al. 2016a), and knowing that the zebrafish selection lines we studied differ in adult body size (Uusi-Heikkilä et al. 2015; see also Fig. 1), it is possible that size differences among the selection lines could mask evolutionary adaptation in personality. We thus included and excluded body size (total length) as a co-variate in our analysis to reveal whether selection treatment *per se* affected the evolution of personality, or whether changes in the size of fish indirectly altered behaviors in the evolved lines.

MATERIALS AND METHODS

Selection lines

Four experimental zebrafish lines (two lines per treatment) were exposed to directional selection pressures (a 75% per-generation harvest rate) acting on either large body size (large-harvested line; N = 2) or small body size (small-harvested line; N = 2). Two additional replicated control lines were harvested randomly with respect to size (random-harvested line; N = 2; Uusi-Heikkilä et al. 2015). Size-selective harvesting occurred during the first five

generations ($F_1 - F_5$) once 50% of the randomly harvested control fish were mature. Harvesting was stopped for the following generations to remove any “maternal” effects and allow singling out the evolutionary outcomes of selection as well as the maintenance of evolutionary adaptations (Uusi-Heikkilä et al. 2015). Zebrafish lines were reared in groups in six separate tanks in a common recirculation system under the following conditions: water temperature was maintained at 26 ± 0.5 °C, photoperiod was set to a 12-12 h light-darkness cycle (light on at 07:00 am), and the fish were fed *ad libitum* with dry food (TetraMin, Tetra) five times per day during daylight.

Given the common-garden design and a single factor being different among the selection lines (i.e. harvesting), comparisons among lines starting from F_8 (i.e. three generation after initial harvesting halted) onwards are indicative of evolutionary adaptations to size selective harvesting, and earlier analysis have revealed that genetic changes have indeed taken place (Uusi-Heikkilä et al. 2015). The first life-history and life-time growth outcomes were assessed at F_9 , revealing that the large-harvested line evolved a smaller adult length due to altered energy allocation patterns and increased relative fecundity (Uusi-Heikkilä et al. 2015; Fig. 1), while the small-harvested line evolved a lower reproductive investment (Uusi-Heikkilä et al. 2015). Despite the potential for evolutionary rebound (Conover et al. 2009; Salinas et al. 2012), the evolved differences in life histories and terminal length in the zebrafish lines were still maintained at F_{13} (see supplementary material and Fig. 1), demonstrating that recovery has not taken place for the life-history traits affecting life-time growth.

Experimental procedure

We used individuals from the F₁₀ generation of the selection lines (Uusi-Heikkilä et al. 2017; Uusi-Heikkilä et al. 2015). One month before the beginning of the behavioral experiment, about 50 fish for each of the six selection-line replicates were randomly selected from the common recirculation system and moved to six acclimation aquaria (30x40x30 cm) and fed twice per day (dry food at 2% of fish biomass). At the beginning of the behavioral experiments, 15 females from each of the six selection lines were randomly selected from the acclimation aquaria, measured for total length, and kept in social isolation tanks (30x12x12 cm) for 24-36 hours before the experimental trials started.

We used three individual-level experimental trials to study four different individual behaviors in the following order: total activity (swimming activity in the test tank) and boldness (i.e., activity in a risk zone measured in the same test environment as total activity), aggression, and sociability. We determined the repeatability score of each behavior (an indicator of consistent between-individual differences in behaviors; Bell et al. 2009) by repeating the assays after 24 hours in the same order. All trials ran between 13:00 and 18:00. The fish were transferred from the individual isolation tank to the experimental arena with a dip-net. A web camera (C920 HD Pro, Logitech; <http://www.logitech.com>) was placed above the experimental arena, and a 5 min video was recorded for each individual trial. The video recording started 60 s after the fish was placed into the experimental arena to allow for a brief acclimation period.

Activity and boldness trial

Total activity and boldness were tested in the same experimental trial in a standard open field arena (30x30 cm, 4 cm water level) in which all the walls were covered with black foil

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to avoid reflections. An open field test is a common approach for studying zebrafish behavior and can also be associated with exploration of a novel environment (Polverino et al. 2016a; Stewart et al. 2012). In our study, activity was defined as the total distance traveled by fish in the entire area of the arena, while risky activity was defined as the total distance traveled by fish in the central area of the arena, a square area with edges at a distance of two body lengths from all four walls for each fish. The central part of the arena is usually associated with risk by zebrafish (Kalueff et al. 2013). The total distance covered in the arena was estimated using automated tracking of zebrafish with EthoVision XT 9 (Noldus). Ethovision tracks were subsequently analyzed using a customized R script (R version 3.2.2) to automatically correct for the size of the fish and account for any shifts in camera perspective.

Aggression trial

Aggressive behavior was assessed using a mirror test, a common test to study zebrafish agonistic behavior (e.g., Gerlai et al. 2000; Pham et al. 2012). Trials were run in an experimental arena (30x30 cm, 4 cm of water level) in which all the walls were covered with black foil except for one, over which a mirror was placed. Levels of aggression were estimated as the number of charges the fish displayed towards its image on the mirror (Larson et al. 2006). A charge was scored when the fish suddenly accelerated towards the mirror from a distance of at least two body lengths, as defined in previous zebrafish studies (Ariyomo and Watt 2012; Gerlai et al. 2000).

Sociability trial

Social behavior was tested in an experimental arena (68x30cm, 4 cm of water level) that was subdivided into two areas by means of a transparent plastic divider. One area (38x30 cm) was occupied by the focal fish, while the other area (30x30 cm) was occupied by a stimulus shoal, a group of 13 randomly selected female fish (replaced every day). All arena walls except the wall occupied by the plastic divider were covered with black plastic. Sociability in zebrafish has been previously assessed using similar methods (Nunes et al. 2017; Pham et al. 2012). Sociability was estimated as the number of attempts the focal fish made to join the stimulus shoal. An attempt was scored when the fish suddenly accelerated towards the divider from a distance of at least two body lengths.

Statistical analysis

We used generalized linear mixed effects models (GLMM) to (i) test for differences among selection lines (large-harvested, small-harvested and random-harvested) in the four behaviors (total activity, risky activity, aggression and sociability), and (ii) decompose the variance into between- and within-individual sources and estimate the repeatability scores of these four traits while controlling for significant differences in selection lines (adjusted-R).

We fit two different GLMMs using the R library MCMCglmm (Alós et al. 2017; Dingemanse and Dochtermann 2013; Hadfield 2010; Harrison et al. 2014) for each of the four behaviours. The first GLMM included selection line (as a factor with three levels) as a fixed effect, and the identity of the fish and the replicate of the selection line as random intercept terms. In this model, we used the entire dataset without considering differences in size of the fish among lines (model 1, global treatment model). The second GLMM (model 2, size-matched model) included selection line (as a factor with three levels) and total length of the fish as fixed effects, and the identification of the fish and the replicate of the selection line

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as random intercept terms. Because selection lines and fish sizes were correlated (Fig. S1), we selected a subsample of individuals to create a new size-matched data set in which there were no differences in the mean size and size range among the three selection lines (Fig. S1). The parameters, 97.5% credibility intervals and p -values were estimated using a Bayesian Markov Chain Monte Carlo (MCMC; Hadfield 2010) approach and uninformative priors. We drew 30,000 posterior samples, discarded the initial 20,000 iterations (burning period), and one out of 10 of the remaining iterations were kept to prevent autocorrelation (thinning strategy). The convergence of the MCMC chains was assessed by visual inspection of the chains and was tested using the Gelman-Rubin statistic (Plummer et al. 2006). A threshold value of 1.1 or less was assumed to indicate convergence (Gelman and Rubin 1992; Hadfield 2010).

Adjusted- R was estimated as the quotient of the between-individual variance (the variance across random intercepts attributed to the individuals, V_{ind_0}) and the sum of V_{ind_0} and the within-individual or residual variance (the variance associated with replicate and the measurement error and phenotypic flexibility, V_{e_0}) for a given behavioural trait, following previous studies (Dingemanse and Dochtermann 2013; Nakagawa and Schielzeth 2010). We extracted V_{ind_0} and V_{e_0} from the four fitted GLMMs and computed adjusted- R s and their 95% CIs using the posterior probability distributions. To assess the significance of the adjusted- R scores, a reduction in the DIC (Δ DIC) provided by the GLMM, where V_{ind_0} was constrained to zero, was used to detect significant V_{ind_0} , with any Δ DIC reduction larger than 2 considered to be significant. Total activity, log-transformed risky activity and sociability models were initially fit assuming a Gaussian distribution of errors. By contrast, a Poisson

distribution of errors was used for aggression data in both models (overdispersion of both models was close to 1 in both cases, see Results). For the first model (global treatment model), we restricted the analysis to individuals with two observations (trials) resulting in a sample size of $n=22$ individuals for large-harvested line, $n=18$ for random-harvested line and $n=22$ for small-harvested line (size range 20 – 34 mm; see Fig. S1). For the second model (size-matched model), we further restricted the individuals to those with overlapping size, resulting in a smaller sample size of $n=15$ individuals for large-harvested line, $n=18$ for random-harvested line and $n=11$ for small-harvested line (size range 22 – 28 cm; see Fig. S1). Finally, we tested for correlations among repeatable behaviours using Kendall's coefficient (r_{τ}) to examine evidence of behavioural syndromes (i.e., correlations among the personality traits).

RESULTS

During the five min experimental trials, total activity ranged from 1 to 29 m, while activity in the risk zone (i.e., boldness) ranged from 0 to 11 m. Aggressive behaviour ranged from 0 to 84 charges. Finally, sociability ranged from 0 to 81 attempts to join the shoal. With the exception of aggression, all behavioural traits tested with model 1 (global treatment model without controlling for length, Fig. 2) were found to be repeatable (total activity: mean $R = 0.43$; boldness: mean $R = 0.17$; sociability: mean $R = 0.37$; Tables 1 and 2), and all repeatable traits were interpreted as personality traits (Table 2). Similar results were obtained with model 2 (size-matched model) where all the traits except for aggression were repeatable (total activity: mean $R = 0.42$; boldness: mean $R = 0.32$; sociability: mean $R = 0.46$; Tables 1 and 2). Thus, the aggression test we used did not result in a stable personality trait.

In both models 1 and 2, the small-harvested line was found to be significantly less active ($p < 0.01$) and less social ($p < 0.05$) compared to the control line (Tables 1 and 2, Fig. 3). The small-harvested line was significantly less bold ($p < 0.01$) than the control in model 1, and marginally significantly less bold ($p = 0.06$) according to model 2 (Table 1 and Fig. 3). In all cases, there was no significant effect of zebrafish length as indicated by the results of model 2 (Tables 1 and 2). The large-harvested line did not differ with respect to the control line in any of the personality traits we examined (Table 2). Aggression was not compared among lines because it was not found to be repeatable (Table 2).

Correlation analysis among the three personality traits indicated that total activity and risky activity were the traits with the strongest positive correlation (r_T between 0.49 and 0.52; Table 3). Total activity was also significantly positively correlated with sociability (r_T between 0.34 and 0.39; Table 3). Risky activity and sociability were weakly, yet also significantly positively correlated (r_T between 0.21 and 0.26; Table 3), overall revealing evidence for behavioural syndromes.

DISCUSSION

We found that negative size-selective harvesting (the small-harvested line) led to altered mean personality traits in individual female zebrafish when tested five generations after harvesting halted. By contrast, and contrary to our predictions, positive size-selective harvesting (the large-harvested line) did not alter any of the personality traits that we measured in individual-assayed zebrafish. Our data indicate that activity, boldness, and sociability decreased in the small-harvested line, while the large-harvested fish did not show differences with respect to the controls. We also found that the differences observed in the

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personality traits of the small-harvested line did not depend on size and hence constituted an evolutionary adaptation to negative size-selection at the behavioural level that was not affected by differences in the average adult sizes among the selection lines. Our findings for adult zebrafish females generally agreed with an earlier study on juvenile zebrafish that also found that there was no significant difference in average boldness between the large-harvested and control lines (Uusi-Heikkilä et al. 2015). We offer three alternative explanations for our results. The first relates to the pace-of-life syndrome, the second relates to social modulation of individual behaviour and the last to predation risk. To underscore our argument we present additional preliminary results from ongoing experiments in a social context.

Repeatability and behavioural syndromes

All behaviors except aggression were found to be repeatable in both models. We used experimental tests previously applied to zebrafish, such as the open field test (e.g., Ariyomo and Watt 2012; Polverino et al. 2016a) and the social preference test (e.g., Moretz et al. 2007; Nunes et al. 2017; Pham et al. 2012). Total activity and boldness were most strongly correlated, forming a behavioral syndrome; however, the fact that both measurements were taken in the same experimental trial could mean that we measured two facets of behaviors that are both indicative of one trait primarily (i.e., total activity or boldness). Total activity and sociability also formed a syndrome, indicating that more active/bold zebrafish are also more social. Our results agree with previous documented behavioral syndromes in fish (Conrad et al. 2011).

Although the mirror test has been used previously to measure the repeatability of aggression in zebrafish (e.g. Ariyomo and Watt 2012), we did not find significant repeatability for this trait. Therefore, our results cannot be used to draw conclusions on aggression as a stable personality trait. Similar results have been obtained by Way et al. (2015), who compared five different behaviors of zebrafish using a mirror test and found that charges displayed by zebrafish resulted in a non-repeatable behavior. Despite the fact that charges were described as an aggressive display in other zebrafish studies (Larson et al. 2006), the mirror test that we used could have been insufficient to consistently motivate individuals across trials (Way et al. 2015). Moreover, a recent study in the mangrove rivulus, *Kryptolebias marmoratus*, demonstrated that the non-reversing mirror was the only device able to elicit a behavior that predicted fish agonistic behavior during a real fight (Li et al. 2018). For our experiment, we used a normal mirror instead of a non-reversing one, which could have reduced the repeatability of aggression.

Boldness and activity

Boldness is related to the ability to acquire food resources under risk (Reale et al. 2007). This trait strongly contributes to mediating growth-mortality trade-offs in fishes and other animals (Ahrens et al. 2012; Enberg et al. 2012; Stamps 2007). We documented the existence of behavioral syndromes between boldness and the other repeatable behavioral traits (i.e., activity and sociability), however our predictions with respect to harvest-induced evolution of average boldness in the large- and small-harvested lines were only partly supported. Although F_{10} juveniles of the small-harvested line were documented earlier to be bolder than controls (Uusi-Heikkilä et al. 2015), we found that, contrary to our predictions,

F₁₀ adult females of the small-harvested line displayed lower levels of average boldness than female zebrafish in the control line.

Our findings could be related to the pace-of-life syndrome and in particular to a correlation between fast/slow life history and bold/shy personality (Réale et al. 2010; Wright et al. 2018). Previous studies on the same selection lines documented that the small-harvested line maintained fast post-maturation growth at the cost of reduced reproductive investment (Fig. 1), indicative of slow life-history adaptation (Uusi-Heikkilä et al. 2015). While the small-harvested line was found to be bolder than the control line at the juvenile stage, we found that adult small-harvested females were shyer than the controls. Thus, the transition at maturation appears to have reversed the personality expressed by the small-harvested line. The pace-of-life-hypothesis suggests that fish with slow life histories should be shy to reduce the risk of mortality in favour of future reproduction (Réale et al. 2010; Wright et al. 2018) – a prediction agreeing with our results. Personality changes across ontogeny have also been reported in other fish species, such as the Eastern mosquitofish, *Gambusia holbrooki* (Polverino et al. 2016b), and similarly in largemouth bass (*Micropterus salmoides*) boldness was found to affect fitness differently across life stages (Ballew et al. 2017). A clear switch in boldness expressed across ontogeny has also been described in the field cricket (*Gryllus integer*), for which boldness was consistently repeatable across the juvenile stage but changed considerably after maturation (Niemelä et al. 2012). Our interpretation is in accordance with a recent conceptual refinement of the pace-of-life concept (Dammhahn et al. 2018), which assumes the existence of several independent trade-offs that can be differentially shaped by ecological conditions (e.g., different size-

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selective mortality schedules, as in our experimental system) and stage-specific correlations of boldness and fitness (Ballew et al. 2017). Indeed, we found no change of boldness in adult females of the large-harvested line compared to controls, a result which agrees with the lack of personality changes revealed at the juvenile stage by Uusi-Heikkilä et al. (2015). This finding is noteworthy because we expected the evolution of shy individuals to be strong in the positive size-selection line following Andersen et al. (2018). Fast life histories (such as the life histories shown by the large-harvested line) should indeed be characterized by elevated boldness (Réale et al. 2010), but the positive size-selection treatment could have created a counterforce after maturation leading to no changes in boldness relative to the control. In particular, elevated mortality of large fish during selection in the large-harvested line could have disfavoured bold phenotypes in this line because these fish grow faster through a food acquisition mechanism and thus might be more likely to be harvested (Enberg et al. 2012). In fact, during the size selection ($F_1 - F_5$) individuals were mainly fed with clumped food at the surface of the water, which can be considered a risky environment for zebrafish (Spence et al. 2008). Therefore, individuals with bold personality traits could be able to grow faster by having more access to food and at the same time be disfavoured under the positive size-selectivity scenario. Our work underscores that the predictions of the pace-of-life-hypothesis with respect to personality and life-history correlations can be context-dependent and can vary among ecological conditions, thereby complicating generalizations (Polverino et al. 2018; Royauté et al. 2018; Wright et al. 2018). In fact, our results suggest that positive and negative size-selective mortality create diverse evolutionary pressures triggering boldness outcomes that cannot be easily predicted with a simple correlation framework between fast/slow life history and bold/shy personality traits (Claireaux et al. 2018).

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An alternative explanation for our results relates to the fact that we measured boldness of a social fish during individual experimental trials. Isolation creates physiological stress in zebrafish (Forsatkar et al. 2017), which can lead to outcomes that do not represent what a particular fish expresses in a group or in less stressful situations (Killen et al. 2013). Moreover, the mean individual-level personality traits that we measured might not necessarily correspond with the collective phenotype exhibited by shoals of zebrafish as in the original selection environment. For example, Jolles et al. (2017) found that stickleback (*Gasterosteus aculeatus*) that showed high levels of proximity to confined shoals in an individual social preference test displayed weak social interactions and polarization when in shoals. Therefore, it is conceivable that in a social context the selection lines could display a different level of boldness and also a different level of activity and sociability compared to when tested individually. Preliminary results of ongoing experiments in our group indeed suggest that when in mixed sex shoals the small-harvested fish take collectively more risks than control fish (Fig. S2), while large-harvested fish did not differ from the control. These initial findings suggest that one must be cautious with classical personality tests of focal individuals when the actual selection environment is a social setting, as was the case in our harvesting experiment. Therefore, future work of FIE of personality traits should focus on individual personality traits expressed in a group context and across ontogeny, particularly because given that many fish species form shoals (Pitcher 1986), the phenotypes expressed in a social environment represent the ecologically relevant outcome of adaptation to natural and fisheries-induced selection pressures.

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A last possible explanation could be related to the fact that in zebrafish, as in other small bodied species, larger individuals could be under stronger natural predation risk than small ones (Brown and Braithwaite 2004; Polverino et al. 2016a) because they offer more energy to gape-limited predators than smaller individuals (Persson et al. 2003). Genotypes programmed for investing into somatic instead of gonadal growth are able to attain larger maximum size (e.g., as in the individuals of the small-harvested line; Uusi-Heikkilä et al. 2015). As such, taking less risk could be a strategy for avoiding predation in favour of future reproduction. Indeed, Polverino et al. (2016a) demonstrated that larger zebrafish of the same cohort were less active and less risk prone in a potentially dangerous open field. We can exclude that the changes in boldness observed in our study were due to a correlated response to differences in body length among selection lines. Instead, we conclude that the lower average boldness of the small-harvested line represented an evolutionary response by the intrinsically larger-growing individuals to negative size-selective mortality. We propose this response can be explained, at least in part, by the fitness benefit of more cautious behaviour in relation to natural predators by larger sized zebrafish – a behavioural strategy that appears more common in the small-harvested line compared to the control.

Despite the possibility that total activity and risky activity could be measures of the same latent personality trait (i.e., boldness), it is also possible that they represent the same latent measures of total activity, or alternatively, that total activity represents a separate personality trait that is merely correlated with boldness (Reale et al. 2007). In both cases, the fact that we found lower activity in the small-harvested line compared to the control line suggests that a mechanism related to conserving energy could be at play. Swimming produces energetic costs in fishes (Kitchell et al. 1977), and individuals that swim less might

allocate energy surpluses more efficiently to somatic growth (Enberg et al. 2012). Such a mechanism could explain why the small-harvested line, which evolved a larger terminal size than the large-harvested line, evolved a lower average activity compared to the control line when focal fish were assayed individually.

Our work constitutes the first empirical test of two recent theoretical life-history models of FIE of boldness (Andersen et al. 2018; Claireaux et al. 2018). Andersen et al. (2018) predict the evolution of shy individuals when fishing mortality is directed exclusively at large adult fish, and evolution of bold individuals when fishing mortality also or mainly captures juveniles. Our work only partially supports these predictions. We did not directly determine the degree to which our size-selection treatments captured adults versus juveniles, but, in all likelihood, fishing mortality in the large-harvested treatment could have been more adult-oriented than in the small-harvested treatment. It is important to consider that the size-selective harvesting occurred when 50% of the individuals of the control line were mature (Uusi-Heikkilä et al. 2015). All fish that survived the size-selective harvesting were then allowed to mature and contribute to the next generation. Earlier results reported rapid evolution of smaller size and younger age at maturation in both size-selected lines relative to controls (Uusi-Heikkilä et al. 2015). This finding suggests that the timing of harvest (i.e., when 50% of the control line was mature) could have created a condition where size-selection targeted mainly (negative size-selection) or exclusively (positive size-selection) adults in both size-selection treatments, and that these effects were reinforced over generations as maturation continued to shift toward smaller sizes and younger ages. Assuming that only body size determines the harvest probability (i.e., without other covarying behavioural traits, which appears somewhat unlikely in the wild; Arlinghaus et al. 2017), the model by Andersen et al. (2018) suggests that the evolution of shy individuals

should occur in both size-selection treatments. We found evidence for the evolution of shy individuals only in the small-harvested line, but not in the large-harvested one. However, this result for the large-harvested adults still agrees with previous findings for juveniles of the same line (Uusi-Heikkilä et al. 2015).

Sociability

The negative size-selection treatment resulted in evolutionary changes in the sociability of adult female zebrafish – a trait that has received only cursory treatment so far in the literature on fisheries-induced selection and evolution (but see; Hollins et al. 2018; Louison et al. 2018; Thambithurai et al. 2018). We predicted that the large- and small-harvested females would evolve higher and lower sociability than control females, respectively. Only the latter prediction was supported by our results: the small-harvested line evolved lower average sociability compared to the control line, while no changes were revealed in the large-harvested line. The small-harvested treatment could have favored low sociability because reduced social interaction would likely lead to increased consumption during the clumped and hence scramble competitive feeding environment that happened in the original harvest experiment (Uusi-Heikkilä et al. 2015). As mentioned above, individual-assayed social personalities could result in different phenotypic outcomes at the group level (e.g., Jolles et al. 2017), and preliminary results of our research group indeed support the notion that the small-harvested line forms tighter shoals than the control line when assayed in groups (Fig. S2). This is noteworthy because shoaling behavior facilitates foraging efficiency in zebrafish (Nunes et al. 2017). Thus, less social small-harvested individuals may have attained larger sizes during the harvesting experiment because individually asocial personality traits might collectively lead to more cohesive groups, but this assumption necessitates a proper future test on the group differences of large- and small-harvested fish

relative to control fish. Moreover, we need to better understand how the fish shoals of the different lines use the surface of the water which is the area where the feeding occurred during size selection. An alternative interpretation could be that what we measured in the sociability test (attempts of the focal fish to join the shoal) is in fact indicative of boldness (e.g., Moretz et al. 2007; Roy et al. 2017). However, the sociability trait was more tightly correlated to total activity than to risky activity, suggesting that this interpretation may be unlikely.

Limitations and further study

We provide the first experimental evidence on how size-selective harvesting may trigger the evolution of fish activity, boldness and sociability in a social species. However, our study has a number of limitations. First, our results were confined to females. Given that males and females can display different behaviours in zebrafish (Spence et al. 2008) our findings cannot be generalized to males. Second, in our sociability test, we used a shoaling stimulus composed of zebrafish coming from the control line. It is possible that the subpopulations evolved preferences for their own line (Engeszer et al. 2007), which could have affected our results. Third, we did not measure the evolution of personality using a longitudinal approach (i.e., measuring the same individual at different ages), and thus our inferred explanation that maturation reversed personality in the small-harvested line remains speculative. Finally, we may have overlooked important behaviours that relate to growth variation and that might have changed together with size-selection. For example, rank in dominance hierarchies determines food monopolization in zebrafish (Hamilton and Dill 2002). In fact, in a separate experiment with the same selection lines at F₁₁ (Fig S3), we detected a significant difference in dyadic agonistic interactions (i.e., bites) among the selection lines using size-

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matched males and females (Fig. S3). The results indicate that the small-harvested line displayed more agonistic interactions than the control line. This suggests that other behavioral traits not measured in the present study might differ among the selection lines, indicating a need for further research. One of the key dimensions that needs to be studied is how zebrafish groups use vertical space, and in particular, the surface of the water column, which is not only risky (e.g., to avian predators) but also profitable for feeding (at least in the harvesting experiment as conducted here). These and other traits should be studied in groups rather than individuals to better measure phenotypes in the original environment that the selection experiment operated on.

CONCLUSIONS

We demonstrate that five generations of size-selection in zebrafish induced evolutionary changes in individual-level personality in females, but in unexpected ways and not consistently with respect to the negative or positive size-selection treatments. Our results suggest that positive size-selection may not alter average individual personality, while negative size-selection has left a legacy in relation to activity, boldness and sociability. Clearly, our results must be interpreted with caution and may not translate directly to real-world fishing scenarios, where the fish live in groups, have multiple spawning events, and/or have overlapping generations. Further, behavior might be under direct selection by fisheries, but our experiment strictly selected based on size. Nevertheless, at a broad level, our work suggests that exclusively size-selective harvesting has the potential to alter the evolution of personality traits within just five generations and such effects are maintained for further five generations after harvesting was stopped. In that sense, our work supports recent theoretical work that predicts how elevated and size- and behavior-selective fishing

evolutionarily alters boldness and other personality traits (Andersen et al. 2018; Claireaux et al. 2018). Fisheries-induced evolution of personality traits can have consequences for social groups, populations, food webs and fisheries, and thus demands careful empirical study (Arlinghaus et al. 2017; Diaz Pauli and Sih 2017).

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Contributions

RA, SUH and AW conceived the experiment. VS, KF, CTM and CD-G conducted the experiment and behavioral analysis. VS, JA, and AEH performed statistical analyses. VS and RA mainly interpreted the results and wrote the manuscript, with feedback from all other authors.

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Table 1. Estimates of the parameters (posterior mean showed), confidential intervals (lower-CI and upper- CI) and p-MCMCs of the two generalized linear mixed models (model 1 using all individuals and model 2 using individuals with overlapping size and size as covariate) fitted for total and risky activity. Estimates for positive (large-harvested line: LH) and negative (small-harvested line: SH) size-selected lines are shown with respect to the control line that was randomly selected for size (RH), and fish total length (cm). ID of the fish and selection lines replicate were treated as random intercept. The table also shows the deviance information criterion of the constrained model (DIC) and for the unconstrained model (DIC-un), as well as the adjusted-R scores, their confidential interval and significance of the test (†: p value < 0.10; *: p value < 0.05; **: p value < 0.01; ***: p value < 0.001).

Total Activity				
Model 1	Estimate	Lower-CI	Upper-CI	p-MCMC
Intercept	14714	12348	16715	<0.001***
Selection line (LH)	-1080	-3771	2172	0.481
Selection line (SH)	-5984	-8864	-2769	<0.001***
DIC: 2468.9				
DIC-un: 2498.3				
Adjusted-R: 0.43[0.22-0.45]*				
Model 2				
Intercept	24890	3050	48818	0.032*
Selection line (LH)	-1498	-5248	2150	0.414
Selection line (SH)	-5843	-9496	-1903	0.005**
Fish total length (cm)	-4002	-12984	4804	0.383
DIC: 1759.1				
DIC-un: 1781				
Adjusted-R: 0.42[0.10-0.45]*				
Log (Risky activity + 1)				
Model 1	Estimate	Lower-CI	Upper-CI	p-MCMC
Intercept	8.02	7.60	8.38	<0.001***
Selection line (LH)	-0.11	-0.66	0.34	0.672
Selection line (SH)	-0.68	-1.15	-0.14	0.009**
DIC: 353.7				
DIC-un: 355.8				
Adjusted-R: 0.17[0.12-0.29]*				
Model 2				
Intercept	10.39	7.22	13.22	<0.001***
Selection line (LH)	-0.31	-0.74	0.13	0.17
Selection line (SH)	-0.47	-0.98	0.01	0.06†
Fish total length (cm)	-0.93	-2.06	0.25	0.12
DIC: 188.7				
DIC-un: 272.1				
Adjusted-R: 0.32[0.1-0.37]*				

Table 2. Estimates of the parameters (posterior mean showed), confidential intervals (lower-CI and upper- CI) and p-MCMCs of the two generalized linear mixed models (model 1 using all individuals and model 2 using individuals with overlapping size and size as covariate) fitted for sociability and aggression. Estimates for positive (large-harvested line: LH) and negative (small-harvested line: SH) size-selected lines are shown with respect to the control line that was randomly selected for size (RH), and fish total length (cm). ID of the fish and selection lines replicate were treated as random intercepts. The table also shows the deviance information criterion of the constrained model (DIC) and for the unconstrained model (DIC-un), as well as the adjusted-R scores, their confidential Interval and significance of the text (*: p value < 0.05; **: p value < 0.01; ***: p value < 0.001).

Sociability				
Model 1	Estimate	Lower-CI	Upper-CI	p-MCMC
Intercept	30.95	23.25	38.85	<0.001***
Selection line (LH)	2.08	-8.64	12.95	0.692
Selection line (SH)	-14.55	-24.43	-3.76	0.011*
DIC: 1064.2				
DIC-un: 1097.2				
Adjusted-R: 0.37[0.28-0.48]*				
Model 2				
Intercept	53.595	-20.317	132.832	0.187
Selection line (LH)	-2.307	-14.649	10.95	0.71
Selection line (SH)	-15.993	-28.544	-1.834	0.019*
Fish total length (cm)	-8.974	-39.503	20.349	0.555
DIC: 742.7				
DIC-un: 768.9				
Adjusted-R: 0.46[0.23-0.5]*				
Log (Aggression +1)*10				
Model 1	Estimate	Lower-CI	Upper-CI	p-MCMC
Intercept	2.45	1.67	3.21	<0.001***
Selection line (LH)	0.15	-0.86	1.23	0.772
Selection line (SH)	-0.83	-1.93	0.20	0.13
DIC: 720.5				
<i>Over-dispersion of the model = 1.02</i>				
DIC-un: 973.5				
Adjusted-R: 0.1[0.04-0.22] ^{n.s.}				
Model 2				
Intercept	4.61	-3.49	11.63	0.229
Selection line (LH)	0.07	-1.09	1.15	0.893
Selection line (SH)	-0.85	-2.13	0.42	0.18
Fish total length (cm)	-0.84	-3.59	2.28	0.571
DIC: 720.6				
<i>Over-dispersion of the model = 0.92</i>				
DIC-un: 721.05				
Adjusted-R: 0.15[0.05-0.28] ^{n.s.}				

Table 3. Correlation among repeatable behaviours (Total activity, risky activity and sociability) in each experimental trial (1 and 2) and model (global treatment and size-matched model) expressed as Kendall's coefficient. (*: p value < 0.05; **: p value < 0.01; ***: p value < 0.001).

	Total activity	Risky activity	Sociability	Total activity	Risky activity	Sociability
Model 1 – Global treatment model						
	Trial 1			Trial 2		
Total activity	-	0.50***	0.34***	-	0.52***	0.34***
Risky activity	-	-	0.21**	-	-	0.13 ^{ns}
Sociability	-	-	-	-	-	-
Model 2 – size-matched model						
	Trial 1			Trial 2		
Total activity	-	0.49***	0.39***	-	0.52***	0.37***
Risky activity	-	-	0.26*	-	-	0.23*
Sociability	-	-	-	-	-	-

Figure 1. Differences in size (standard length expressed in mm, SL) among positive (large-harvested line: LH) and negative (small-harvested line: SH) size-selected lines with respect to the control line (RH) that was randomly selected for size are presented across ontogeny. At F_9 (a; $N =$ LH: 19; RH: 15; SH: 21) at 210 days post fertilization (DPF), F_{10} (b; $N = 100$) at 230 DPF and F_{11} (c; $N = 30$) at 450 DPF. Results of the Lester biphasic growth model are also presented for generations F_9 and F_{13} (d). Letters above the boxplots indicate the output of the Tukey's post hoc test ($a < b$). More details regarding the statistical approach are presented in the supplementary material.

Figure 2. Density population plots (left column), trial individual values (mid column) and among-individuals differences (right column) for each of the behaviors studied using model 1 (all individuals have been used): aggression, sociability, risky activity and total activity. The adjusted-R scores, their confidential interval and significance test for each trait are shown.

Figure 3. Density population plots (left column), trial individual values (mid column) and among-individuals differences (right column) for each of the behaviors studied using model 2 (size-matched individuals): aggression, sociability, risky activity and total activity. The adjusted-R scores, their confidential interval and significance test for each trait are shown.

Figure 4. Differences among the selection lines in four behavioural traits (total activity, risky activity, sociability and aggression) among the positive (large-harvested line: LH) and negative (small-harvested line: SH) size-selected lines with respect to the control line (RH) that was randomly selected for size. Boxplots represent the mean values across the two trials for Model 1 ($N =$ LH: 44; RH: 36; SH: 44) and Model 2 ($N =$ LH: 30; RH: 36; SH: 22).

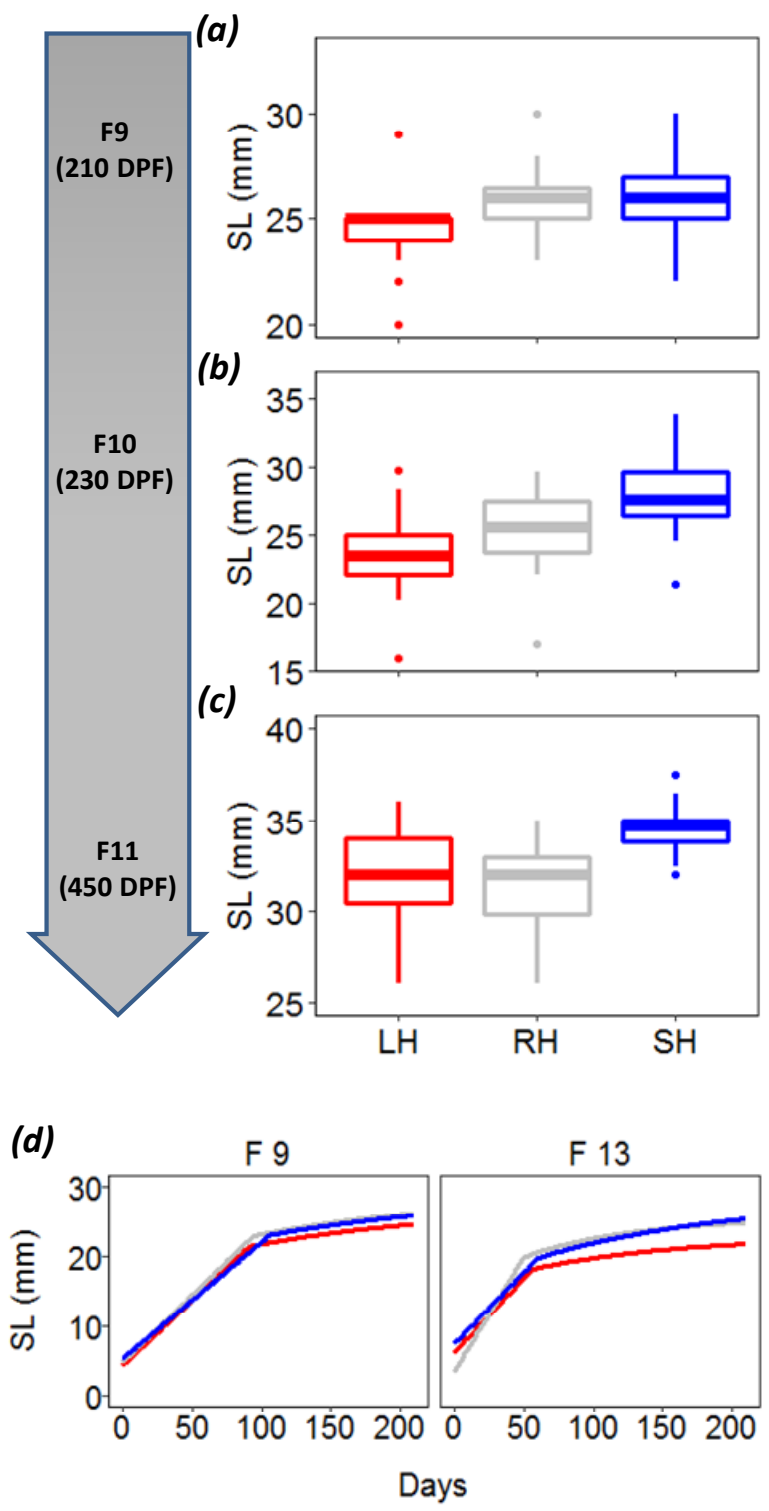


Fig. 1

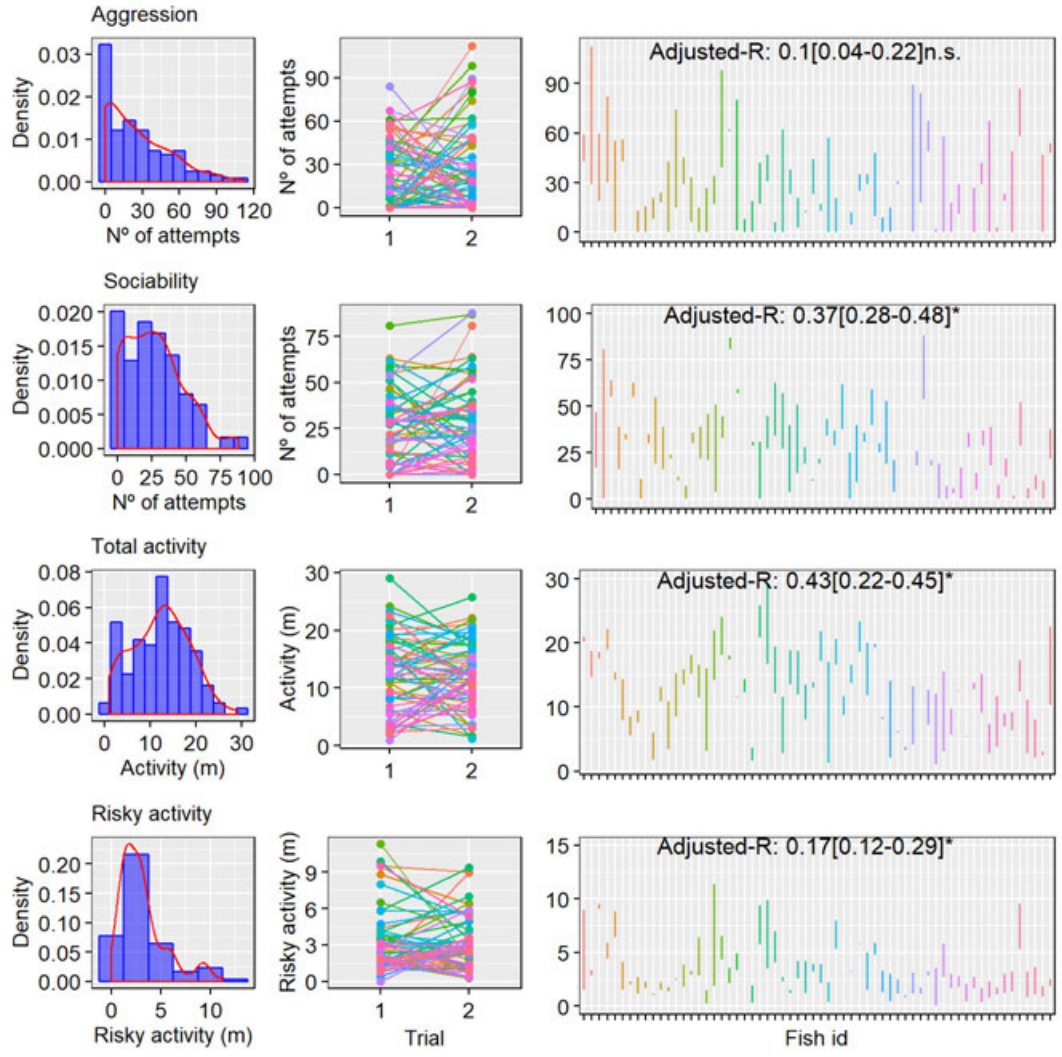


Fig. 2

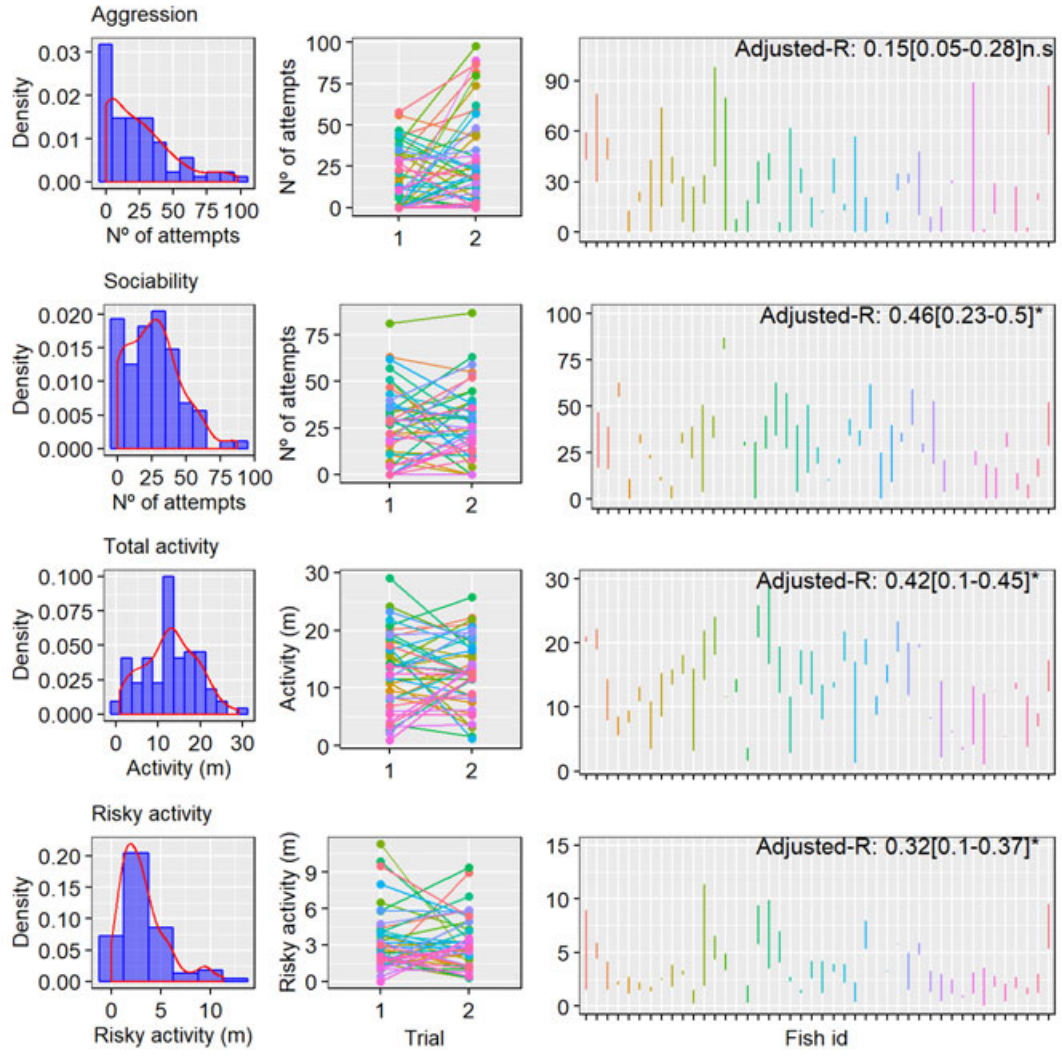


Fig. 3

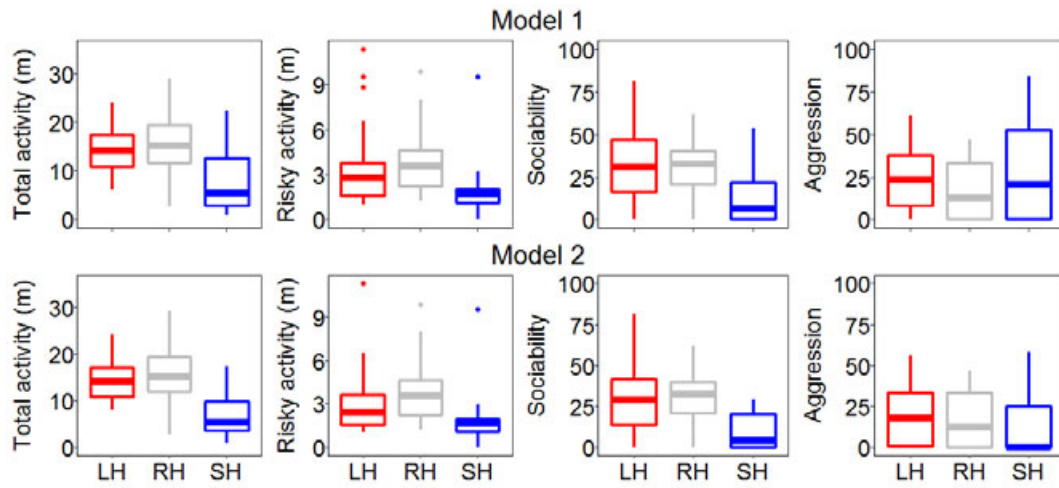


Fig. 4