Post-release exploration and diel activity of hatchery, wild and crossbred strain brown trout in semi-natural streams

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Abstract: Behaviours that are adaptive in captivity may be maladaptive in the wild and hence compromise after-release survival of hatchery fish. Understanding behavioural differences displayed straight after the release could help improving hatchery protocols and developing behavioural tests for assessing the fitness of fish reared for releases. We characterized the post-release behaviour in two experiments using parr from wild, hatchery and crossed strains of brown trout (*Salmo trutta*): in small-scale channels and in high and low densities in mesocosm streams. Our results show that hatchery fish were more likely to disperse downstream from the natal stocking site compared to crossbred and wild fish. Small-scale experiment was not sufficient in discovering this ecologically pivotal difference in post-release performance between strains, and individual responses were inconsistent between experiments. Circadian activity patterns were not found to remarkably differ between strains. This detailed empirical evidence of post-release behaviour improves our understanding of the low success of captive-reared fish in the wild. Mixing locally adapted wild fish in the broodstock could rapidly mitigate some of the behavioural effects of hatchery selection.

Keywords: crossbreeding, domestication, fisheries, phenotypic plasticity, stocking

Introduction

Enormous numbers of captive-bred fish are released world-wide to support fisheries, enhance weakened natural populations or introduce new fish populations (Cowx 1994). In many cases, the stockings are performed without explicit aims and evaluation of their success (Naish et al. 2007). Often the hatchery-reared fish suffer from low survival in the wild, resulting in acute or long-term failures in compensation and restoration programs (Lorenzen et al. 2012, Glover et al. 2018). To increase stocking success, it is necessary to understand the mechanisms explaining the low after-release survival rates. Captive breeding leads to unintended domestication in very few generations (eg Araki et al. 2007, Christie et al. 2012, 2016, Mäkinen et al. 2015), and induces an inevitable loss of genetic variation

(Lorenzen et al. 2012). The simplified hatchery environment may also favour phenotypes that display, for instance, impaired anti-predatory behaviours (Petersson and Järvi 2006), increased boldness (Sundström et al. 2004) or fast growth that increases risk-taking behaviour (Biro et al. 2004, Biro and Post 2008, Saikkonen et al. 2011).

Whilst hatchery breeding typically aims to maximize genetic diversity, maintenance of local adaptations has been neglected (Neff et al. 2011). Due to precise natal homing, salmonid populations frequently (55−70%, (Fraser et al. 2011)) show significant local adaptations. Thus, the question is how the hatchery-broodstocks could be improved to better match with the local environmental requirements. However, it is yet unclear how to solve the trade-off between genetic diversity and maintenance of local adaptation when the aim is to re-introduce a naturally reproducing population (Houde et al. 2011). Controlled crossbreeding of hatchery broodstocks with locally caught wild fish might provide a solution (Houde et al. 2015).

The development of most behavioural traits depends strongly on the environment during ontogeny (Johnsson et al. 2014). As the dissimilarity of the environment is drastic between typical rearing tanks and natural environment (Huntingford 2004, Johnsson et al. 2014), the short period following release to nature represents a major habituation challenge with critical survival implications. Stocked, predator-naïve fish can sometimes be exposed to high predation (Hyvärinen and Vehanen 2004, Alioravainen et al. 2018); but see (Dahl et al. 2006). Further, hatchery-reared fish can have problems in learning to forage wild prey (Johnsen and Ugedal 1986, Sundström and Johnsson 2001), and their diet is often simpler than that of wild fish (Rodewald et al. 2011).

Multiple experiments have compared the post-release survival between fish from hatchery, wild and hybrid origins (Berg and Jørgensen 1991, Jonssonn et al. 1999, Jokikokko et al. 2006, Dahl et al. 2006, Pinter et al. 2017), but recapture data are insufficient to answer what mechanisms explain the observed differences. Acute survival of stocked fish depends often on post-release behaviour (Huntingford 2004, Johnsson et al. 2014), but studies focusing on detailed behavioural mechanism provoking survival differences are scarce (Rodewald et al. 2011, Rodewald 2013).

When fish are released in the wild, they are expected to accept the new habitat, start foraging and distribute naturally across the spatial scales. Stocking experiments performed in natural systems have shown that hatchery-reared parr (riverine juvenile) move downstream more than wild parr immediately after release (Jørgensen and Berg 1991). Brunsdon et al. (2017) showed that stocking density alters spatial distributions so that a high stocking density increases downstream dispersal distance from the stocking site. Likewise, low-density releases have been shown to result in higher survival rates compared to high-density releases (McMenemy 1995). However, density effects on post-release behaviour are not well known, even though the behaviour is suggested to associate with survival (Mittelbach et al. 2014), and density is recognised to affect behavioural development (Brockmark et al. 2010). As an adaptation to crowded rearing conditions hatchery-bred fish may display impaired territorial (Fenderson and Carpenter 1971) and unnatural schooling behaviour (Ruzzante 1994) that potentially results in downstream dispersal. The cost of territorialism in high density may exceed the benefits, and hence reduce agonistic behaviour with a survival cost (Bohlin et al. 2002).

Another behavioural mechanism potentially impaired by the hatchery conditions is the activity rhythm of the fish, which may have acute impacts on post-release performance. Behavioural activity of wild salmonids follows a circadian rhythm − feeding rates are low during the night when visibility is low and at mid-day when predation risk and light intensity are high (Hoar 1942). Circadian rhythmicity is an adaptation to environmental selection pressures (e.g., predation risk, food availability, thermal regimes, (cf. (Yerushalmi and Green 2009) driving salmonids to crepuscular foraging activity (Hoar 1942). In hatcheries, such rhythmicity is often lost as food may be constantly available, and fish may use all hours for foraging. Thus, hatchery-reared fish displaying maladaptive activity patterns may face fitness consequences due to high predation risk in nature (Metcalfe et al. 1999). Therefore it is important to consider full diel cycles when studying consistent behavioural differences among individuals (Závorka et al. 2016), and potential differences between hatchery and wild strain fish.

Here, we experimentally studied individual differences in post-release behaviour in relation to the genetic strain of the fish using one-year old brown trout (*Salmo trutta*) parr. We used fish from two originally philopatric populations, one captured from the wild, the other reared in a hatchery for stocking purposes for over five decades, and their reciprocal F_1 crosses. Previous studies have demonstrated that these strains differ in personality traits and in migration tendency (Alioravainen et al. 2018, Prokkola et al. 2019, Lemopoulos et al. 2019b) the hatchery strain being the boldest and the most migratory. Here, we hypothesized that the experimental populations would be strongly diverged in their behaviour, and that the hatchery population would represent a more (downstream) dispersive phenotype and display higher day-time activity than the wild strain. We studied post-release behaviour in two experiments, first in small-scale indoor channels, and then in larger seminatural streams in outdoors, using a high and a low fish density in both settings. We followed fish behaviour for five days after the release using short-range radio frequency identification (RFID) telemetry that enabled us to observe fish movements without disturbance. We analysed total movement activity and the duration of the exploration in the new environment and determined the individual circadian patterns. We quantified the individual plasticity in post-release behaviour between experimental contexts using the behavioural reaction norms (Dingemanse et al. 2010). We tested whether the individually assessed behaviour in the indoors indicates movements in the outdoors mesocosm. We expected the behaviour in the indoors experiment to predict behaviour in the outdoors both at the strain and the individual level. We expected high density to increase hatchery strain fish downstream movement in the mesocosm as a consequence of intensified competition for available territories. Hatchery strain fish were also expected to show high activity and rather unimodal circadian activity patterns, whilst wild strain fish were expected to obtain bimodal circadian activity patterns sooner after release. The hybrids have shown intermediate behaviour in bold−shy continuum compared to the purebred strains (Ågren et al. 2019, Alioravainen et al. 2019), and were expected to display intermediate responses also in this study.

Materials and methods

Fish

Experimentally bred fish originating from river Vaarainjoki (wild strain, mainly resident) and river Varisjoki (hatchery strain, mainly migratory) were reared in common garden conditions prior to the experiments. River Vaarainjoki is situated upstream Varisjoki in the same watershed. Detailed origin of the strains is described in (Lemopoulos et al. 2019a). We used F_1 generation pure strains produced using 3♀×3♂ full factorial breeding design (3 half-sib matrices) and both hatchery ♀ × wild ♂ and hatchery ♂ × wild ♀ crosses (two half-sib matrices per direction) as described in (Alioravainen et al. 2019). The fish, reared in two replicates per breeding batch (n = 20, 0.4 m^2 tanks) were tagged with 12mm HDX PIT-tags (Oregon RFID) under anaesthesia (benzocaine 40 ml L^{-1}) in September 2016 approximately 6 months after hatching. We maintained the tagged fish mixed in two 3.2 m^2 glass fibre hatchery tanks (n=450/tank) and fed them *ad libitum* with commercial fish feeds using automated feeders until the beginning of the experiments in April 2017. All animal collection, transport, and experimentation were conducted under licence from the national Animal Experiment Board of Finland (licence number ESAVI/3443/04.10.07/2015).

Indoor stream test

Between 26 April and 29 May 2017, we performed behavioural group trials in artificial indoor flow channels (length 6 m, width 0.4 m, depth 0.2 m, flowrate 1.60 L $s^{-1)}$ with gravel bottom, located in the Kainuu fisheries research station KFRS (www.kfrs.fi), to quantify individual open field movements in group context. In each trial, we released 12 fish (n_{strain} = 4) to acclimate in a sub-section separated with metal grid (mesh Ø=5 mm) in the lower end of each channel (n = 4) for 48 h before releasing them to explore the whole channel freely for five days (120 h). Hybrids were equally taken from hatchery × wild sire—dam and dam—sire crosses but considered as one group in the further analyses. The fish were not fed during the acclimation or the trial but natural food coming with the inflowing water (from Lake Kivesjärvi) was present. Altogether, we ran five consecutive trial periods testing 240 individuals.

Day length was set to 16 hours from 5:00 to 21:00 and light intensity to 13 lux. Each channel was equipped with four PIT-antenna coils covering half a metre area each (Fig. S1). The water to the channels was drained from the upstream lake and followed the natural temperature (range 3.0 – 5.0 °C) and oxygen dynamics (range 6.0 – 8.6 mg L^{-1}). After each trial, we measured the tested fish for total length (1 mm) and wet mass (0.1 g) under anaesthesia (benzocaine 40 ml L^{-1}). After the experiment, fish were maintained in the same hatchery tanks as previously until the outdoor experiment.

Outdoor stream test

One month after the end of the indoor experiments, on June 28, we introduced the same fish (n_{total} = 240) in eight circular riffle pools (Fig. S2., see details in Härkönen et al. 2019), located outdoors at the same research station. The fish were randomly divided into two different densities (n_{low} = 12 fish, 4 fish *per* strain and n_{high} = 48 fish, 16 fish *per* strain). Fish were fasting for one day before they were introduced to flow-through fish chests (0.50 m × 0.80 m, open in the both ends and covered with the grid Ø=5 mm mesh size) between 22:00 and 01:30. After 14.5–18h acclimation time in the chests, they were released into the

stream at 16:00. The fasting and fish chest procedure were used to minimize stress upon final release.

Every riffle pool had a gravity-driven flow (40.5 L/s), water depth of 0.30 m, and a similar set-up to monitor fish movement: four PIT-antennae loops across the whole riffle in every quarter of the pool (Fig. S2). The water temperature and oxygen content varied naturally within ranges 12.7 – 14.8 °C and 8.0 – 8.5 mg L^{-1}, respectively. The circular riffle section was 26.15 m long (from the middle) and 1.5 m wide. During the experiment the natural day length in the area was 21h 15 min from 2:35 to 23:50. We did not feed the fish with any additional food, since the pools had rich benthic macroinvertebrate fauna and drift along the incoming water (Rodewald et al. 2011). All pools were covered with a tent canvas to prevent avian predation and warming of water by direct sunlight. As in the indoor stream experiment, we monitored individual movements for the five first days in the streams, after which the fish were left in the outdoor streams for further data collection, (not used in this study).

Statistical analyses

The automatically collected raw PIT data were configured using TIRIS data-logger program (Citius solutions Oy, Kajaani, Finland; see details in (Vainikka et al. 2012). Antenna-specific ASCII-data were further aggregated to form movement data on 1-second resolution using software PIT-data (www.pitdata.net). From the processed 1-second-interval PIT-data, we analysed individual movements based on antennae by-passes *per* hour. Only antennae readings from a different location than the previous reading were considered as a movement. Further movement data processing was performed by self-made scripts (by N.A) by using *tidyverse*-package collection (version 1.2.1, (Wickham 2017). All the analyses were performed using R (version 3.5.2, (R Core Team 2018) through R Studio (RStudio Team 2016). Annotated scripts and data are available online (Open Science Framework; osf.org; DOI:).

One-way ANOVA was used to test for differences in fish body length between the strains, which we did not observe ($F_{2,\ 236}$ = 0.35, p = 0.7). From the outdoor experiment data, we tested how strain and density affected the total distance moved and movement ratio (upstream movement / total movement) by fitting a generalised linear model (GLM). Lower than 0.50 ratio value indicated that main direction was downstream and *vice versa* higher than 0.50 ratio value indicated that main direction was upstream. Both response variables were log-normal-transformed to meet the normality requirements of GLM. We calculated estimated marginal means i.e. least-squares means and 95% confidence intervals of GLM predictors using *emmeans*-package (Lenth 2019).

We fitted linear mixed effects models (LME, *lme4*-package, v1.1-21, (Bates et al. 2015)) to explain individual movements in both indoors and outdoors experiments. We tested the effects of strain, density (high vs. low) in outdoors experiment on total daily activity of the individuals (individual antenna by-passes *per* day). To control for the effects of individual length on movements, we divided movement measures by fish length. We standardised movement measures from indoors and outdoors mesocosm to make them comparable. Individual body length (left-centred) and experiment day were used as covariates in the models, individual and experimental streams as random factors. Additionally, in the outdoors model, we

wanted to test if behaviour in the indoors experiment explains the behaviour in the outdoors experiment. Therefore, we extracted individual residual scores of the model i.e. best linear unbiased predictors (BLUPs). We estimated model parameters and their 95% confidence intervals based on 10 000 posterior simulations of the parameters from fitted LME model by using *arm*-package v 1.10-1, (Gelman et al. 2018).

To measure the plasticity of individual behaviour between experimental contexts, repeated within-individual measures within each context were needed to partition the behavioural variation into individual reaction norms (Araya-Ajoy et al. 2015). Thus, we used model residuals as BLUPs to compare within-individual responses between indoor and outdoor experiments (reaction norms).

Type II (Wald's) test (*car*-package, v3.0-3, (Fox et al. 2010) were used to test the statistical significance in both LMM and GLM. All visualisations were made using *ggplot2*-package (v3.2.1, (Wickham 2017). To visualise and model how movement patterns changed over experimental days among strains, we used nonparametric Loess regression that uses local weighted regression to fit a smooth curve through points in a scatter plot. If estimated 95% confidence intervals of Loess fitted curves did not overlap, the differences were considered statistically significant.

For clarification, we considered downstream movement as 'dispersal', because fish relocate themselves from their stocking site. To-and-fro type of movement in indoor channels and outdoor mesocosm were considered as 'exploration', because the movement did not relocate the fish *per se*.

Results

Movement in the outdoors mesocosms

In the outdoor mesocosm experiment, the lowest movement direction ratio was in hatchery strain in low density (mean ± SD: 0.09 ± 0.06), and the highest ratio was in wild strain in high density (0.19 ± 0.15) indicating that direction of the movements were mainly downstream (Fig. S3). In the mesocosm riffle pools, strain (χ^2 = 30.065, d.f. = 2, $p < 0.001$) and density (χ^2 = 32.951, d.f. = 1, $p < 0.001$) had independent main effects on the total distance moved. Fish moved more in low than high density treatment, and hatchery strain fish moved clearly more than hybrid or wild strain fish (Fig. 1). Wild strain fish moved the least whilst hybrid expressed intermediate phenotypes in total movement (Fig. 1). Movement ratio was strain dependent (χ^2 = 10.682, d.f. = 2, $p < 0.01$), as wild strain fish showed lower dispersal tendency than hatchery strain fish (Fig. 1). Density (χ^2 = 0.7, d.f. = 1, p = 0.40) did not explain movement ratio in the mesocosm experiment.

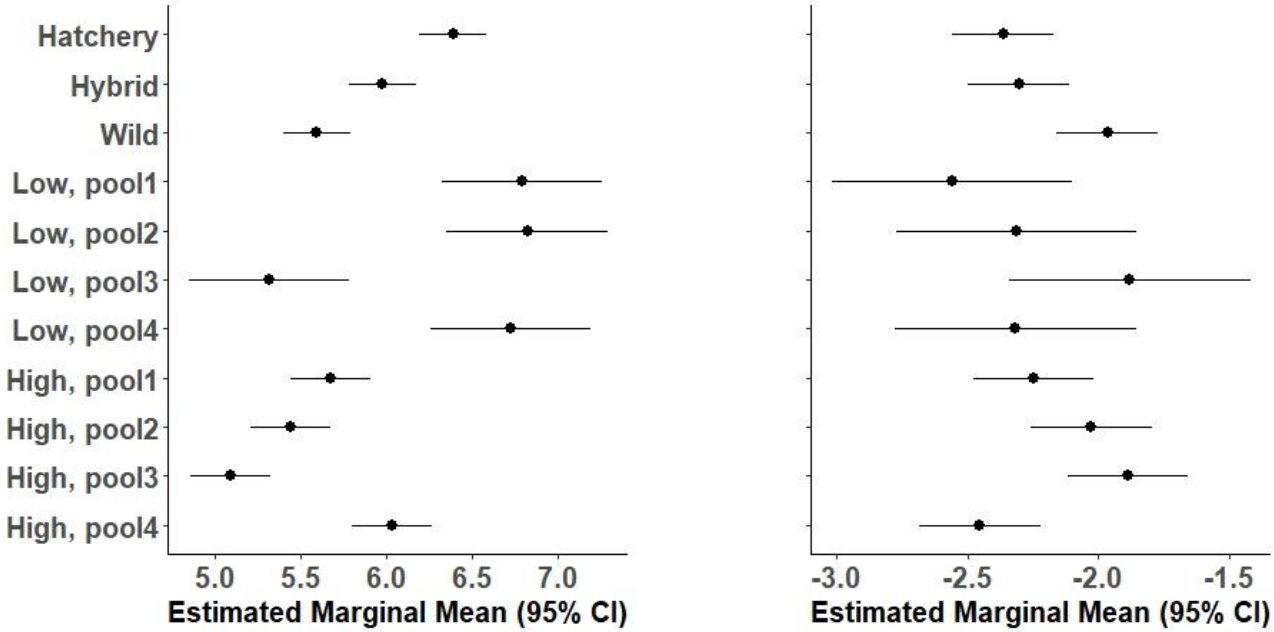

Figure 1. Estimated marginal means based on generalised linear model of log-normal transformed total individual distance moved (left) and movement ratio (right) of 240 individuals. The null deviance for the total distance moved GLM was 252.40 on 239 degrees of freedom, and the residual deviance was 157.03 on 230 d.f. Respectively the null deviance for movement ratio GLM was 171.41 on 239 d.f., and the residual deviance was 151.83 on 230 d.f.

Individual plasticity in movement behaviour

Strain did not explain the behaviour in the indoors experiment (χ^2 = 4.436, d.f. = 2, p = 0.11, Table 1). In the outdoors experiment strain had a string effect on behaviour (χ^2 = 44.374, d.f. = 2, $p < 0.001$), and it also has a strong positive interaction with the density (χ^2 = 18.490, d.f. = 2, $p < 0.001$, Table 1). Experiment day had a strong negative effect on individual daily total movements (indoors: χ^2 = 205.903, d.f. = 1, $p < 0.001$, outdoors: χ^2 = 549.421, d.f. = 1, $p < 0.001$), showing that highest movement rate occurred immediately after the release (Table 1). Individual body length had a significant positive effect on movement in the indoors experiment (χ^2 = 14.372, d.f. = 1, $p < 0.01$), but negative in the outdoors experiment (χ^2 = 27.732, d.f. = 1, $p <$ 0.001). The individual behaviour (as BLUPs) were found to have a mere but negative effect on outdoors behaviour (χ^2 = 9.790, d.f. = 1, $p <$ 0.01, Table 1). Hatchery strain fish showed the highest mean activity especially in the low-density pools and wild strain fish the lowest in outdoors mesocosms (Table 1). Loess regression curves showed that in the indoors streams there were no clear differences between strains in exploration, but in the outdoors mesocosm, strains had clear differences (Fig. 2). In high density, hybrid and hatchery strain fish were similar and more active than wild strain fish, whereas in low density, hatchery strain fish showed high activity and much higher than wild strain fish even until the end of the experiment (Fig. 2). Individual behavioural reaction norms indicate that extreme phenotypes may express the opposite behaviours in different the contexts (Fig. 3).

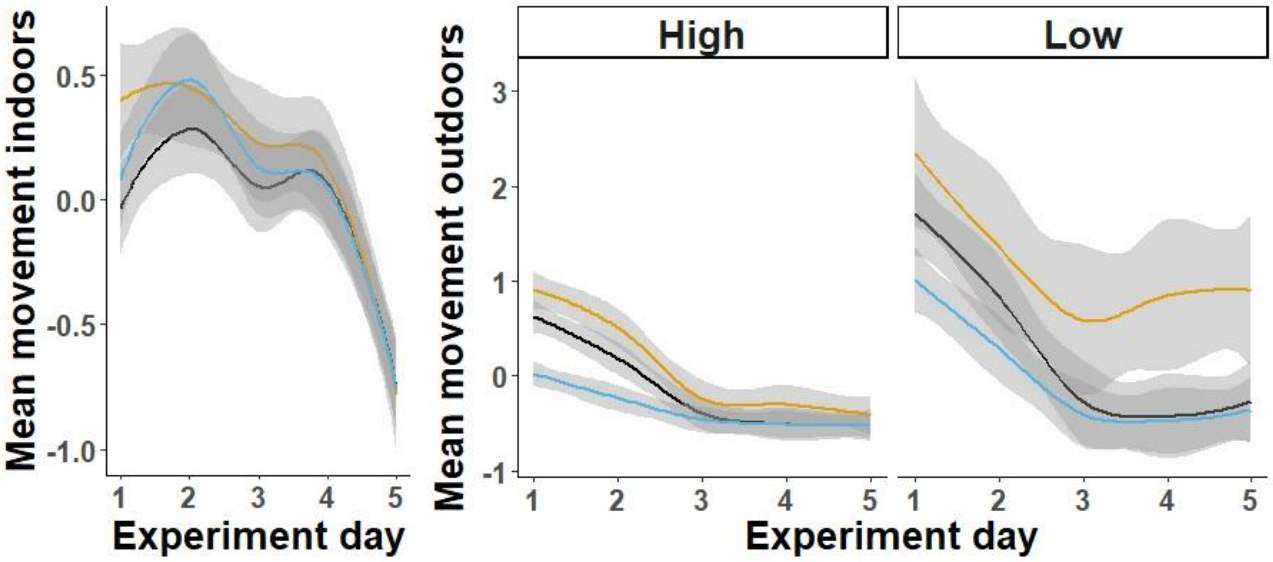

Figure 2. Loess regression curves showing strain-specific movement activity (antenna by-passes) in the indoors channels (left) and total moving activity (rounds moved in circular riffle) outdoors riffle-pools (right). Experiment day was used as a covariate and coloured lines show mean activity of strain. Grey area indicates 95% C.I.

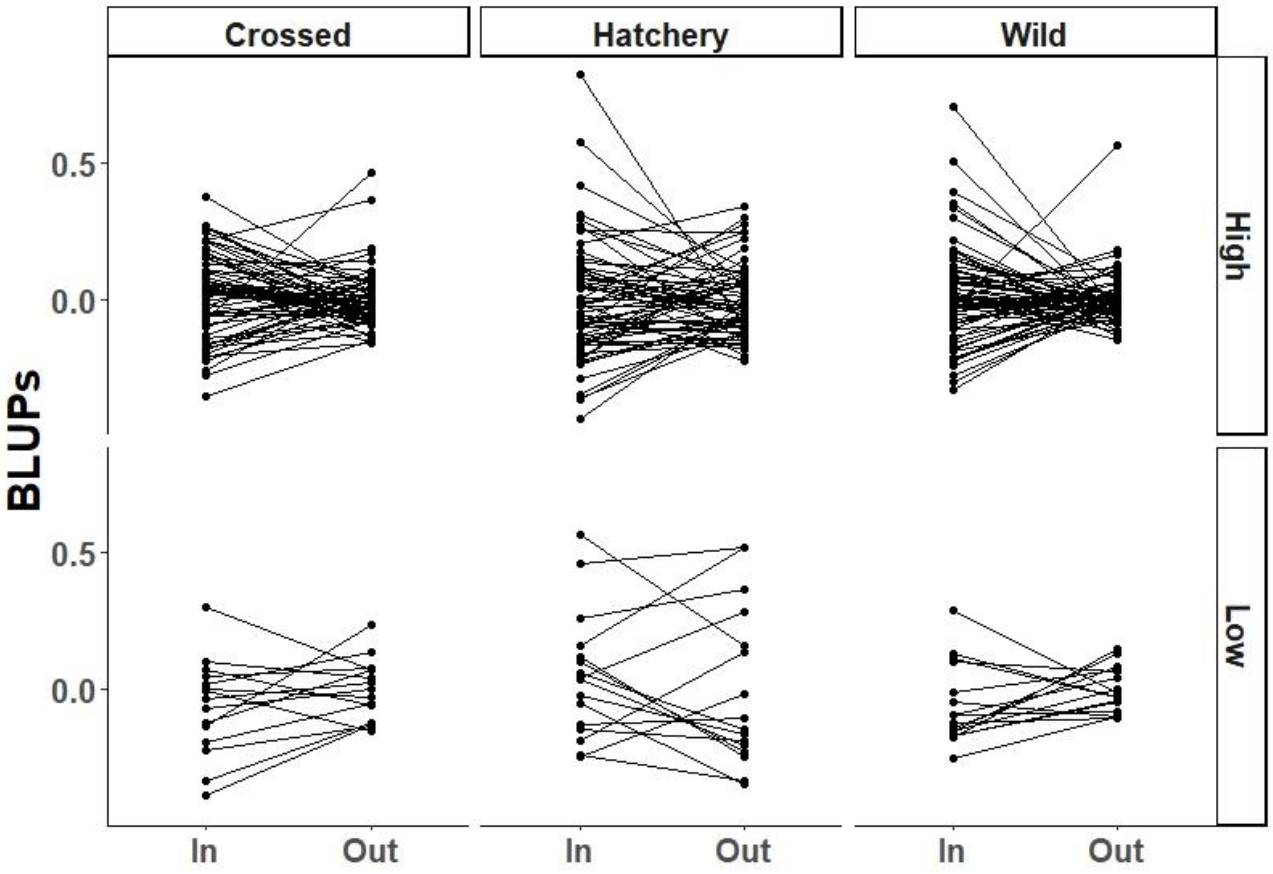

Figure 3. GLMM residuals that indicate among-individual variation in behavioural plasticity. The dots show individual means of within-individual variation of movement during five consecutive

days in both experiments (BLUPs). Single lines indicate individual reaction norm slope across the experiments, i.e. the phenotypic plasticity of post-release movement. The closer the residual value is to zero, the better individual behaviour can be estimated by the model. The smaller the slope of the line is, the more consistent the individual has been between experiments. The few deep negative or positive slopes indicates that individual has not been consistent in its behaviour between experiments but show higher behavioural plasticity than average individuals.

Table 1. Summary of linear mixed effects model of total individual movement activity based on five measurements (days) of 239 individuals in two experiments, where mean random effect and residual variances, fixed effect estimates, and confidence intervals were estimated based on 10 000 posterior simulations of β from LME model. Hybrid strain set the intercept.

Responsive variable	**Effect**		
Indoors activity	**Random**	**Mean σ^2**	**95% CI**
	Fish ID	0.186	0.159, 0.216
	Indoors channel	0.219	0.132, 0.331
	Residual	0.543	0.501, 0.588
	Fixed	**Estimate**	**95% CI**
	Intercept	0.238	-0.053, 0.528
	Experiment day	-0.216	-0.246, -0.187
	Fish length	0.013	0.006, 0.019
	Strain (hatchery)	0.183	0.011, 0.357
	Strain (wild)	0.095	-0.073, 0.265
Outdoors activity	**Random**	**Mean σ^2**	**95% CI**
	Fish ID	0.238	0.209, 0.271
	Outdoors pool	0.145	0.063, 0.268
	Residual	0.360	0.332, 0.391
	Fixed	**Estimate**	**95% CI**
	Intercept	1.183	0.741, 1.622
	Experiment day	-0.288	-0.312, -0.264
	Fish length	-0.017	-0.024, -0.011
	Indoors ID BLUP	-0.082	-0.132, -0.031
	Strain (hatchery)	0.180	-0.013, 0.376
	Strain (wild)	-0.225	-0.421, -0.033
	Density (low)	0.445	-0.175, 1.066
	Interaction (hatchery–low)	0.720	0.282, 1.171
	Interaction (wild–low)	-0.177	-0.615, 0.261

Circadian patterns

Very similar circadian activity patterns were found in both experiments and in every strain. The fish showed bimodal activity patterns, where highest peaks occurred after 5:00 in the morning and again in the afternoon between 15:00 and 20:00 (Fig. 4). In the outdoor mesocosms, fish began to be active at sunrise (Fig. 5). In the indoor streams, the only difference in activity between strains occurred

during the afternoon, when hatchery strain fish were slightly more active than hybrid and wild strain fish (Fig. 4). In the outdoor mesocosms, hatchery strain fish were more active than wild strain fish during every hour when the fish were moving (Fig. 5). Hybrid fish displayed average phenotypes compared to wild and hatchery strain fish (Fig. 5) In low density treatment, the patterns were alike to high density, but peaks were much higher indicating high overall antenna by-passes/hour-rates (Fig. 5). Individual circadian curves showed that there were no distinctly night-active individuals (Fig. S4)

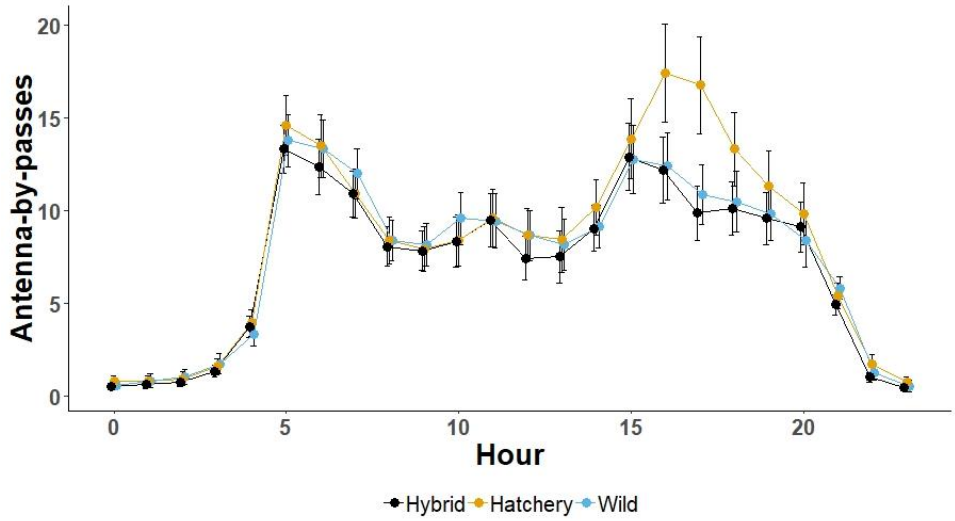

Figure 4. Mean antenna by-passes *per* clock hour over five consecutive diel cycles in the indoor channels. Whiskers indicate 95% C.I. Light were on from 5:00 to 21:00.

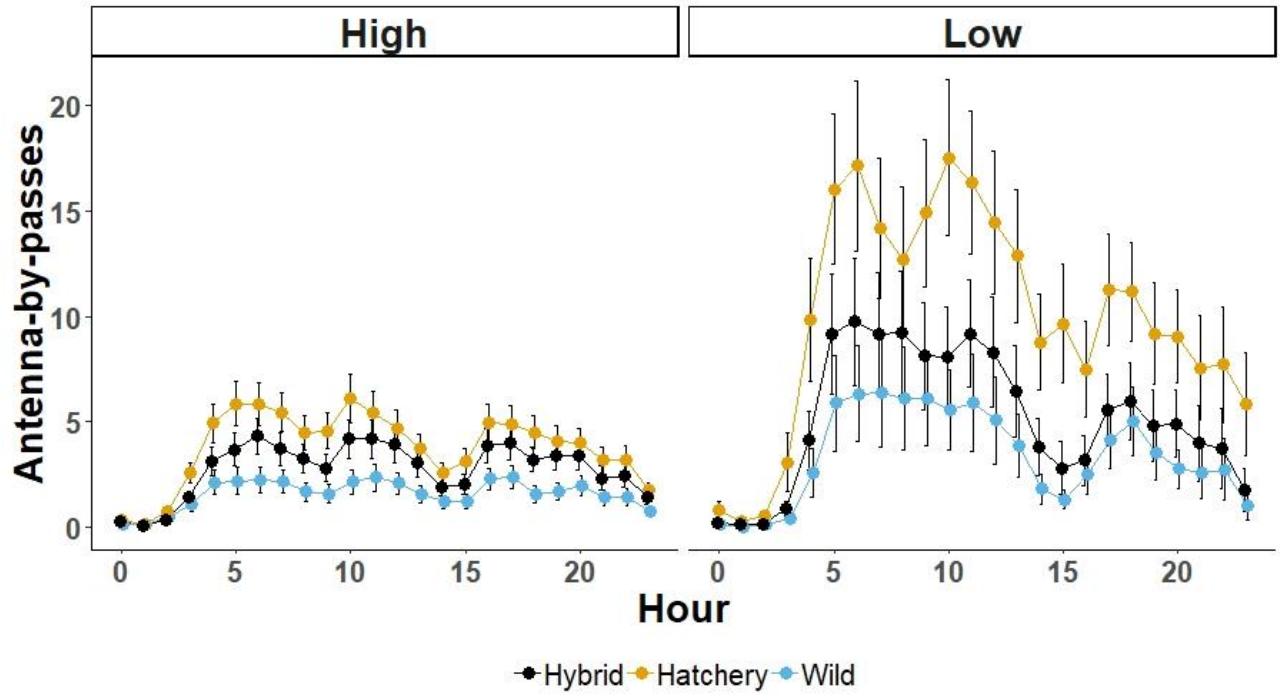

Figure 5. Mean total rounds moved *per* clock hour over five consecutive diel cycles in outdoor mesocosms. Whiskers indicate 95% C.I. Sunrise was at 2.35, and sunset at 23.50.

Discussion

Hatchery strain parr swam more downstream than other strains indicating that they will likely not stay near their stocking site but disperse rapidly. Against our expectations, low density further intensified downstream movement of hatchery strain fish in the mesocosms. The results that show parr movement occurs mainly downstream from original stocking site align with the predictions from Jørgensen and Berg (1991), and Brunsdon et al. (2017). We showed that the exploratory phase lasts at least two full diel cycles after release, but the intensity and the direction of the initial highly active movement period can be strain dependent. Indoors experiment did not reveal any strain-specific movement patterns and high individual activity in the indoors channels did not predict high movement activity in the outdoors mesocosms. Individually assessed behavioural reaction norms were found to be inconsistent indicating high variation in phenotypic responses between the experiments. Every strain obtained bimodal circadian activity patterns quickly, but hatchery strain fish showed the highest activity in both indoor and outdoor tests, as expected.

Especially hatchery strain parr moved strongly downstream immediately on the first day after release. Interestingly, low density increased hatchery strain fish dispersal tendency compared to high density, but density did not affect movement ratios of the strains. The circular mesocosm environment can increase the distance swum as fish do not reach a new habitat and hence may not know when to settle down. Even so, some of the fish were very determined in their downstream movement that it could potentially be considered as downstream (pre-smolt) migration (appr. 12 km *per* day). It could be that the stress from stocking and novel environment with running water can trigger downstream dispersal. Releasing, or translocation in general, can be considered a major human-induced environmental change and dispersal an avoidance reaction to the novel environment (Sih et al. 2011). Interestingly the wild strain fish were less downstream directed in their movement, which can indicate to-and-fro type of explorative behaviour in a novel environment (Réale et al. 2010). Whilst exploratory behaviour can be risky under natural conditions by increasing vulnerability to predation (Hulthén et al. 2017) and fishing (Biro and Post 2008, Härkönen et al. 2014), it can facilitate habituation (Adriaenssens and Johnsson 2013, McCormick et al. 2018). Introduced wild fish have less issues to habituate in their stocking site and establish their territory, whereas hatchery fish may show unnecessary aggressions towards conspecifics and have problems with finding territories (Deverill et al. 1999). Due to limited resources in enclosures, individuals are forced to continue searching downstream (Grant and Kramer 1990, Grant et al. 2017). As a result, hatchery juveniles displace themselves from their stocking site, which makes them vulnerable to predation, decreases the likelihood of finding a suitable habitat, and increases mortality in the wild (Elliott 1989). Large fish were found to move more in the indoors channels, but individual size as well as the individual behaviour in the indoors experiment had mere but significant negative effects on movement activity in the outdoors streams. This indicates that larger fish likely disperse less after releasing into the streams, probably due to their better ability to compete for available resources, and hence forcing smaller individuals to continue dispersal downstream. The nonlinear dispersal patterns of hatchery strain fish in low density suggests the idea that individuals that are unable to

occupy territory in a new habitat must continue dispersal further to seek free territory to settle. Because the density treatment did not affect movement ratios, it seems that fish prefer to disperse downstream in general. The high density potentially facilitates the settling of individuals and decreases dispersal, probably by reducing territorial behaviour of dominant individuals and/or reducing the post-release stress as they are deferred to high densities in the hatchery. If this is the case, stocked fish may later begin to redistribute if competition in the stocking site intensifies.

Hatchery, hybrid, and wild strain fish obtained a natural activity rhythm and showed bimodal circadian activity already within the first diel cycle after release in both experiments. Hence it is unlikely that adopting natural circadian rhythms could be problematic for stocked fish. Hatchery strain fish were more active than wild or hybrid strain fish in every active hour. The observed high diurnal activity rates of hatchery strain fish may associate with high energy demands, as even hatchery strain fish have been shown to start feeding within the first day after release (Rodewald et al. 2011). Changes in diel cycles can occur due to individual growth, for example, when juvenile fish increase diurnal activity as a response to high energy demands (Metcalfe et al. 1998). Indeed, individual growth rates correlate positively with diurnal activity scores in laboratory trials leading to high survival rates in the wild (Závorka et al. 2015, 2016). Despite nights are bright in Northern Finland, where the experiment took a place, in summertime, we did not observe significant night-time activity in juvenile brown trout. A longer period of resource competition might be required that inactive fish would obtain shifted circadian rhythm (Závorka et al. 2016).

Individual behavioural reaction norms showed that individual responses were inconsistent between contexts indicating phenotypic plasticity (Dingemanse et al. 2010). Personality-related behavioural responses are expected to be context dependent (Killen et al. 2016, Horváth et al. 2017, Houslay et al. 2018), thus, artificial environments may not always reveal ecologically relevant responses (Niemelä and Dingemanse 2014, Závorka et al. 2015, Näslund et al. 2015, Polverino et al. 2016). In general, small scale can restrict movements (Näslund et al. 2015), and mesocosm that mimics natural environment, is likely more stimulating than plain channels resulting in phenotypic plasticity between context (Dingemanse et al. 2010). We found clear behavioural differences between the strains in the outdoors experiment but not in the indoors. Despite behavioural development of fish is generally very plastic through gene–environment interactions, the lack of complexity of the hatchery environment and the lack of natural selection of cultured fish cause domestication in hatchery broodstocks (Lorenzen et al. 2012). Domestication may decrease fitness in the wild due to maladaptive behaviours (Johnsson et al. 2014). Our results add on the empirical evidence of behavioural differences between hatchery and wild strain fish, and endorse the importance of source population in breeding programs that aim to support reintroductions and natural reproduction (Houde et al. 2015). Our results indicate that behavioural experiments in the artificial environment are likely unable to explain individual level responses in near natural scale contexts and may fail to reveal full behavioural divergence between groups.

Conclusions

Our study provides behavioural and ecologically relevant explanation upon the

failure of stocking of captive-reared fish. We show that stocked hatchery fish can have high dispersal tendency in mesocosm streams as an avoidance towards novel environment or if they must compete for limited resources, which potentially can be related to the high mortality rates of hatchery-reared fish in the wild. High activity during afternoon hours may potentially increase the risk to predation and vulnerability to fishing. Thus, hatchery fish can be under strong natural and/or fisheries selection immediately after releasing due to behavioural differences and resulting in low success of stocking programs. Our results highlight the importance of genotype–environment interactions contributing to behaviours with fitness consequences. We propose that mixing locally adapted and naturally selected fish in the broodstock can mitigate some of the behavioural effects of hatchery selection rapidly.

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Supplementary figures

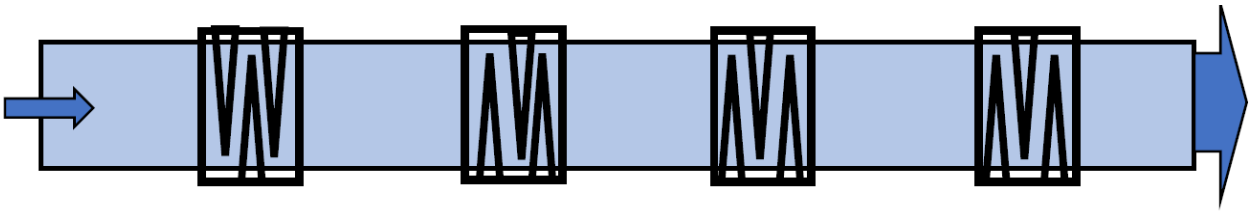

Figure S1. Artificial indoor flow-thru channels (length 6 m, width 0.4 m, depth 0.2 m, flowrate 1.60 L s-1) with added gravel (appr. grain size 50mm) in the bottom. In both ends there were a metal grid (mesh Ø=5 mm). Each channel was equipped with four PIT-antenna coils (black lined areas) covering half a metre area each. The thin blue arrow indicates the water inlet and the thick blue arrow indicates the water outlet.

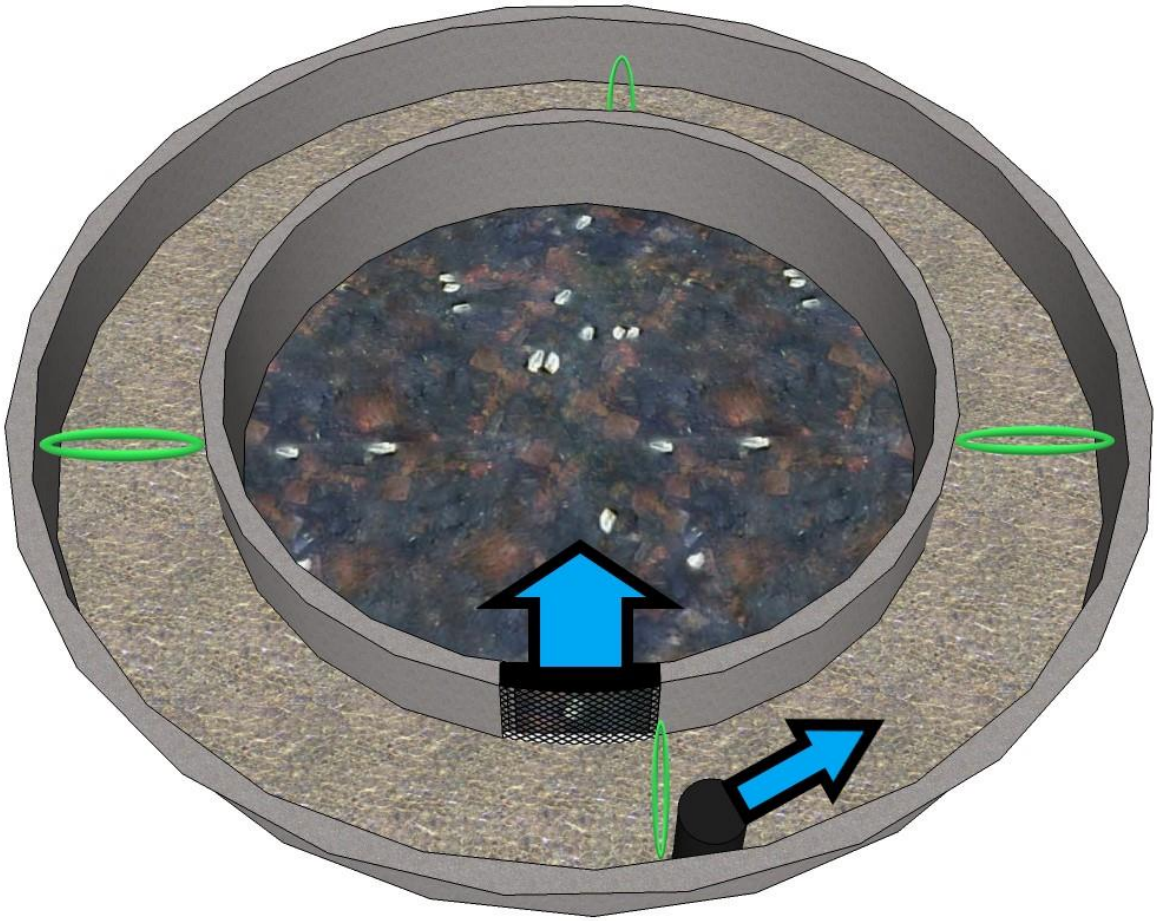

Figure S2. Outdoors riffle-pools. Riffle-pools have adjustable gravity-driven flow in the outer circle, water depth is adjustable. The circular riffle section is 26.15 m long (from the middle) and 1.5 m wide. The thin blue arrow indicates the water inlet and the thick blue arrow indicates the outlet. Metal grid (mesh size Ø = 5mm) prevents fish to escape from the riffle section to the sink which is in the middle of the pool. Green loops indicate the locations of the RFID antennas that read the HDX PIT-tagged fish, when they swim through the loop. The bottom of the riffle section is covered with gravel (appr. grain size 50mm).

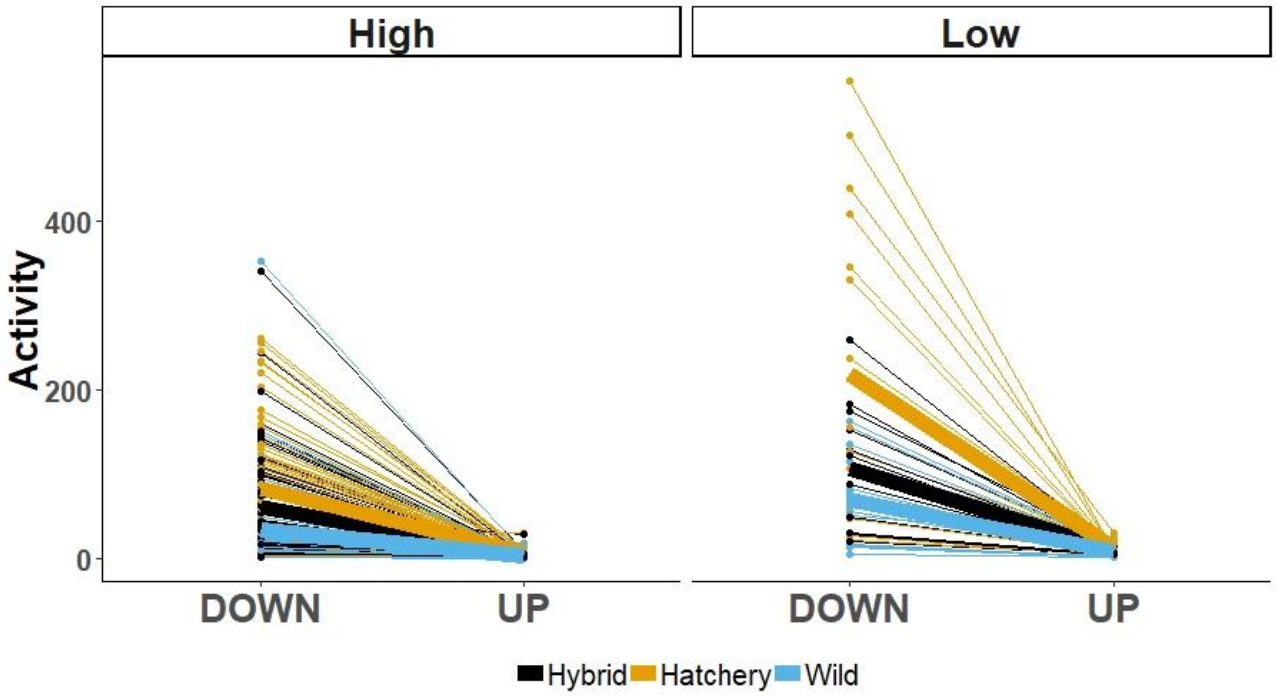

Figure S3. Direction ratios of the movement activity in the outdoors experiment. Thick lines refer strain means.

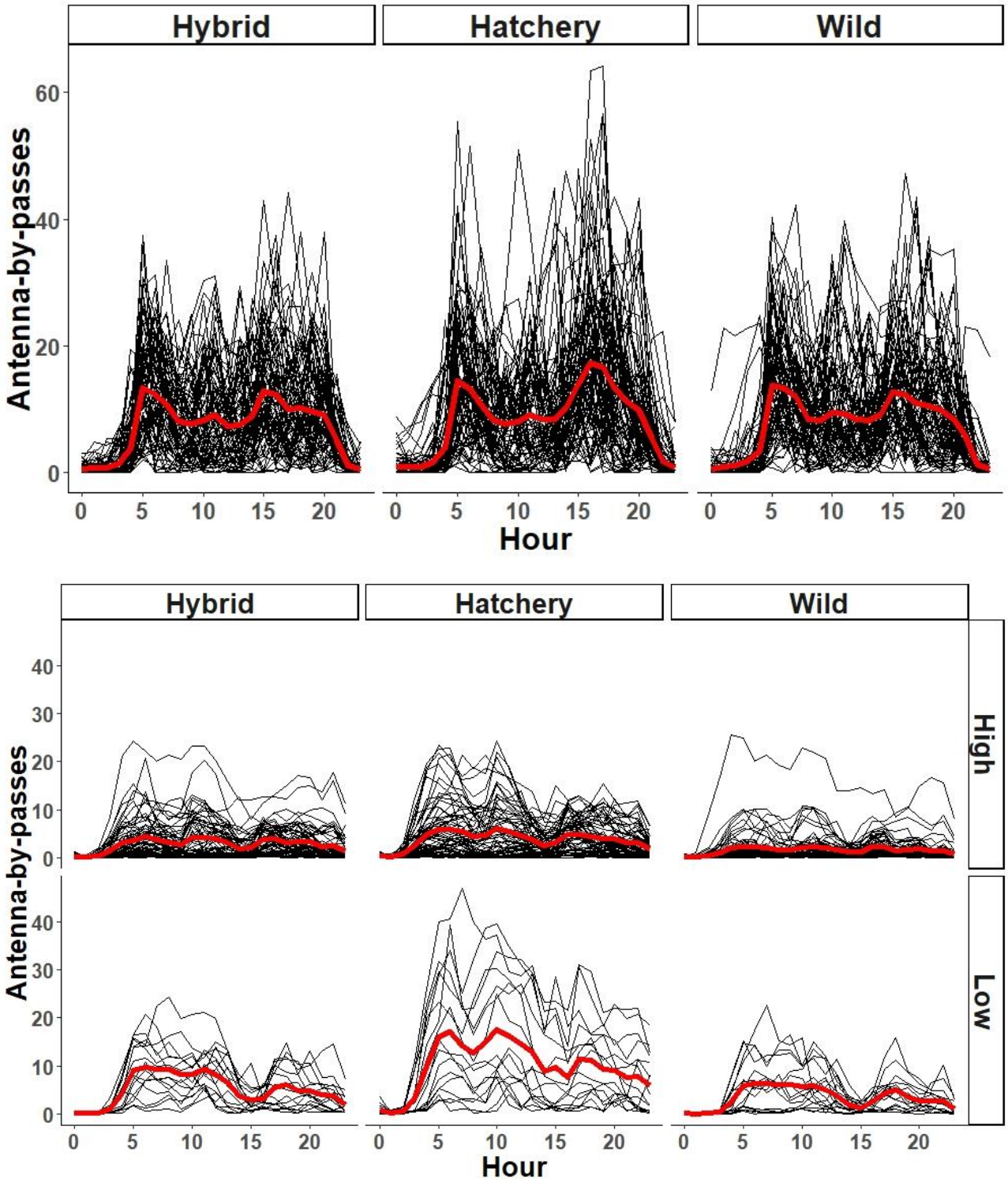

Figure S4. Individual mean diel cycles.