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Article

Balancing past and present: how experience influences boldness over time in Eurasian perch

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Abstract

Adapting to fluctuating predation conditions is a challenge for prey. By learning through experience, animals may adjust their anti-predator behavior to better reflect current predation risk. Although many studies show experience of predation to alter prey behavior, little is known about how prey rely on such experience over time. By comparing boldness over different temporal scales between individuals of Eurasian perch, either experienced or naïve of predators, we examine how risk is traded based on past and present experience. Differences in predator exposure during the first year of life were found to lead to differences in risk-taking behavior, even after the perch been kept in a predator-free environment for 9 months. However, the response to a potential predator was quickly readjusted after increased experience of current conditions. The results highlight how prey have to balance past experiences of predators against current threat levels.

Key words: behavior, fish, learning, personality, predation, risk-taking.

Prey animals frequently have to trade fitness-related behaviors, such as foraging, against the risk of predation (Lima 1998). Theory suggests adaptive anti-predator responses to reflect the intensity, duration, and variability of the predation risk (Helfman 1989; Lima and Bednekoff 1999), with the prey adjusting behavior on the basis of a reliable risk assessment (Bouskila and Blumstein 1992). Flexibility in anti-predation response can hence be advantageous, allowing prey to continually fine-tune behavior to match the experience of current predation condition.

Changing behavior based on experience requires the ability to learn from events and situations, and to be able to act on gained knowledge for a certain amount of time (Shettleworth 2010). Depending on context, the time span an animal is affected by past experience may have adaptive significance (Kramer and Golding 1997; Ferrari 2010a). In fluctuating environments, acting on the most recent information is likely more relevant than relying on old information recalled from prior experience. For example, rapid and unpredictable spatial change in food distribution may disfavor foraging individuals restrained by past experience, and favor individuals more guided by current experience (Cuthill et al. 1990; Warburton 2006). Likewise, knowledge that has relevance during extended periods should be retained by the animal for longer time. For example, in salmon, information related to homing is obtained at a young age and then remembered throughout the entire life without the need for reinforcements (Dittman et al. 1996).

Little is known about how prey depend on learned anti-predator behavior over time (Kelly and Magurran 2006; Ferrari et al. 2010a). One may argue that learned anti-predator responses should be retained for longer time than, for example, learned knowledge regarding food-patch profitability, as failing to respond correctly to a predator may lead to death of the prey (Ferrari et al. 2010a). However, for most prey, predation risk varies greatly over time and space (Lima and Bednekoff 1999), as well as changes as prey gets larger and more experienced with age (Lundvall et al. 1999; Magnhagen and Borcherding 2008). Under such conditions, being too guided by prior predation experiences may result in suboptimal anti-predator responses and in the end potential loss of fitness, for example, by being too risk-averse the time spent foraging may decrease (Godin and Smith 1988; Lima and Dill 1990; Sih 1992).

In fish, a general response to predation risk has been thought largely innate, allowing even young fish to correctly avoid predation without any need of prior experience (Kelly and Magurran 2003). Today, we know that fish also learn to recognize and respond to predators, either via direct experience, or through associative or social learning (Brown and Laland 2003; Kelly and Magurran 2006). One can assume that a constant revision of learned anti-predator behavior would be adaptive for a prey, making it able to adjust the intensity of the response to reflect the most recent learning experience (Ferrari et al. 2010a).

In this study, we investigate the influence of past and current experience on risk-taking behavior in Eurasian perch *Perca fluviatilis*. We are using perch from the same population that had either been living in its natural environment, with a high density of cannibalistic perch, or been raised from hatching in a pond without predators. The perch are tested for boldness immediately after capture or after spending 9 months in tanks. Short-term behavioral change occurring during observations and between repeated runs was also monitored and compared.

Materials and Methods

Background

The study was conducted on Eurasian perch collected from lake Fisksjön, a 0.75-ha mesotrophic lake close to Umeå (63°47′ N; 20°17′ E), Sweden. Fisksjön has a dense population of small perch with stunted growth, which creates a high cannibalistic predation pressure on the young-of-the-year (YOY) juvenile perch in the lake (Persson et al. 2003; Magnhagen 2006; Magnhagen and Borcherding 2008). Earlier studies, investigating Fisksjön and other lakes, have correlated predation pressure with perch behavior, and concluded that YOY perch from Fisksjön are less bold compared with perch from lakes with lower cannibalistic predation pressure (Magnhagen 2006; Magnhagen and Borcherding 2008). Magnhagen and Borcherding (2008) also concluded that such behavioral differences are not likely a consequence of selective predation mortality, but of fish adjusting behavior based on current predation conditions. Using a common garden approach, Hellström and Magnhagen (2011) found Fisksjön perch reared in predator-free environment to be significantly bolder than wild perch, indicating that boldness phenotype in these perch to a large extent is shaped by experience, rather than being inherited. This was further reinforced by Magnhagen et al. (2012) who reported inter-annual difference in risk-taking behavior in Fisksjön perch to be correlated with inter-annual predation pressure, hence concluding that variation in risk-taking reflected direct phenotypic responses to recent experience of predation risk, rather than divergent selection caused by differences in predation pressure.

Data collection

In May 2007, immediately after the spawning of perch in lake Fisksjön, approximately 2,500 eggs from 10 distinct egg clutches were collected in the littoral zone and stocked into a nearby seminatural pond. The pond lacked other fish and the fry were hence able to hatch and grow in the absence of piscivores (40 × 8 m). Macroinvertebrates and zooplankton, the natural food of young perch, were available in the pond. During the first week of September, YOY perch were collected from both the pond and from the lake by beach-seining.

The fish were transported to Umeå Marine Research Centre, and lake and pond reared fish were kept separated in 2 identical tanks (tank dimension 1 × 1 × 1 m) with continuously running water. The fish were fed at least twice a week with frozen chiromonids *ad libitum*. Light conditions were set to follow the natural cycle of the season, and the tanks had artificial vegetation to use as shelter. Water temperature in the tanks fluctuated with natural temperatures, between 0 and 11°C, (see Appendix 1 for the range of water temperatures in the tanks during the whole study period). See also Hellström and Magnhagen (2011) for a detailed account of fish collection and rearing.

Behavioral tests

Behavioral tests were conducted in September 2007 and June 2008, thus, either immediately after capture or after the perch had spent 9 months in the laboratory storage tanks. The timing was adjusted so that natural water temperatures was the same during both test periods, because temperature has been found to affect personality traits, such as boldness (see, e.g., Zhao and Feng 2015). The fish were tested in groups of 4, and different individuals were used in September 2007 and June 2008. Groups consisted of perch of the same ecotype. Under natural conditions, young perch form schools and by testing them in social groups, we were expected to obtain a more natural behavior (see also Magnhagen 2012). Immediately before being transferred from the rearing tanks to the test aquaria, the fish was anaesthetized (MS222) and tagged by alcian blue on their caudal fin to enable individual identification within group. The fish were then allowed to acclimatize in the aquaria for 48 h before tests begun. The aquaria (170 L, 95 × 41 × 44 cm) were divided in 3 equally sized sections. The predator section contained a large perch (18–22 cm long). The vegetated section contained green sling bands, simulating dense vegetation. Between the predator section and the vegetated section was an open area. The small perch could move freely between the vegetated section and the open area, but a plastic net (mesh size 5 mm) restricted access to the predator section. An opaque screen was set to cover the plastic net to hinder the small perch from seeing the predator. The behavioral test started by moving the screen so that the group of perch was enclosed in the vegetated area. Thereafter, approximately 60 chironomid larvae were poured into the open area, between the plastic net and the opaque screen. After the larvae had settled at the bottom, the screen was lifted and the behavioral observations started. The perch now had the choice to enter the open area to forage in front of the predator, or remain in the vegetated area, further away from the predator. The observer, sitting in front of the aquarium, recorded the position (in open area/not in open area) of each perch during 10 min, entering the data in real time into a computer program (Magnhagen and Borcherding 2008). In the subsequent statistical analysis, the data were set to a resolution of 5 s, that is, only observations every 5 s were used. After each observation period, the opaque screen was put back next to the net. Three observation periods, 1 per day for 3 consecutive days, were conducted on each group. In total, 12 groups of lake perch and 10 groups of pond perch tested in September 2007 and 8 groups for lake and pond perch, respectively, in June 2008. Before each test period in September and June, perch were weighed using a Satrorius digital scale (± 0.1 g) and total length was measured to the nearest mm. Water temperature was 11°C during both test periods.

Analysis

Probability of residing in the open area (hereafter defined as boldness) was modelled as a function of origin using a generalized linear mixed model (GLMM) with binomial error and a logit link function (Bates et al. 2011). Origin was treated as a 2-level nominal variable (Lake/Pond). Individual length was added as a continuous fixed effect. To avoid pseudo-replication due to correlations between repeated measures on individuals within groups, a random effect structure with individual nested in group was added to the model. Models were fitted with the Laplace method. As the response data were binary (in open / not in open), overdispersion was not corrected for. Separate models, but with identical structure, were set up for September and June. Optimization of the model structure was done on both the random and fixed component of the model, using AIC-based model selection (Burnham and Andersson 2002) following the protocol outlined by Zuur et al. (2009). The most parsimonious model in both September and June included only origin as a fixed effect and were of the form:

$$\operatorname{logit}(p_{ijk}) = \alpha + \beta \times Origin_{ijk} + a_k + a_{j|k}$$

where p is the probability of residing in the open area at observation i in individual j of group k, and a represent a random intercept where a_k allows for variation between groups (k) and $a_{j|k}$ for the variation between individuals (j) within the same group (k). The best models had considerable support in the data (ΔAIC to the next best model = 45.6 in September and 32.8 in June), indicating low model selection uncertainty. Significance of Origin was determined by a log-likelihood ratio test comparing models with and without the term, assuming chi-squared distribution of the ratio statistic.

To investigate the difference between lake and pond fish in boldness over time during an observation session, for each of the 3 runs in September, boldness was modelled as a function of origin and time using a generalized additive mixed effect model (GAMM) with binomial error and a logit link function (Wood 2011). Origin was treated as a 2-level nominal variable (Lake/Pond) and Time as a smothered continuous variable with cubic regression splines as smoothers. The amount of smoothing was determined by automated cross-validation (Wood 2006). An interaction term between time and origin (using the "by" command in the R package "gamm4") was also included. Individual nested in group was added as a random effect structure. The full model hence looked like:

$$\operatorname{logit}(p_{ijk}) = \alpha + f(Time_{ijk}) : Origin_{ijk} + a_k + a_{j|k}$$

where p is the probability of residing in the open area at observation i in individual j of group k, α is the intercept, and a represent a random intercept where a_k allows for variation between groups and $a_{j|k}$ for the variation between individuals within the same group. $f()$ denotes that time is modeled as a smoothing function, and $f(\mathrm{Time}_{ijk})$:Origin_{ijk} denote that 1 smoother is used for each origin. A separate model for each run was used to avoid a 3-way interaction term (i.e., time:factor(origin):factor(run)), which is not supported in the R packages used ("gamm4"; Wood 2011). Model optimization strongly supported the full model structure for the first 2 runs (ΔAIC to the next best model = 34.3 for Run 1 and 26.4 for Run 2); however, for Run 3, a model without the interaction term was judged almost as good as the full model (ΔAIC = 3). Statistical inference and parameter estimates were derived from the full models in all 3 runs. A list of all candidate models tested can be found in Appendix 2.

Difference in length between lake and pond perch, as well as between perch in 2007 and 2008, was tested by a 2-way factorial ANOVA. All analyzes were done in the statistical program R, using packages "lme4" (Bates et al. 2011) and "gamm4" (Wood 2011).

Methodological considerations

Generalized additive models provide a flexible way to model nonlinear relationships between response data and continuous variables. It allows for a dynamic visualization of change in behavior over time and may hence reveal potentially important structures otherwise missed if only "the average behavior over time" is considered, as is common in behavior studies. Smoother curves visualized in this study were based on data from several groups. Small irregularities in the curves are hence likely to lack any meaningful biological interpretations. However, broad trends and differences in the shape of smoothers are likely to reflect true dynamics in behavior. Although within-subject correlations were accounted for by applying a random effect structure, our models did not correct for possible temporal autocorrelation resulting from repeated measure over time. Temporal autocorrelation may lead to inflated P values. Wood (2004; the "mgcv" package) allows for incorporation of temporal correlation structures on binary data in a generalized additive model framework. In our case though, a model with an autoregressive correlation structure of order 1 (AR1) applied on the level of individual time series still concluded as strong significances for all fixed effect terms as the model we used in the analysis (i.e., a model with a nested random effect structure). The experiments in this study comply with the current laws of Sweden and were approved by the local ethics committee of the Swedish National Board for Laboratory Animals (CFN, license no. A-94-06).

Results

Long-term comparisons

There was a significant difference in average boldness between lake and pond fish in both September and June, with the pond fish having a higher probability of residing in the open area than lake fish in both months ($\chi^2_1 = 99.7$, $P < 0.01$ in 2007; $\chi^2_1 = 148.5$, $P < 0.01$ in 2008; Figure 1). Inclusion of size did not improve model performance, indicating little effect of size on boldness in our study. Still, perch from the pond were significantly larger than lake fish in both 2007 (mean ± standard deviation (SD): 67.9 mm ± 6.2 vs. 61.5 mm ± 5.1; $F_{1,62} = 20.4$; $P < 0.01$) and 2008 (71.8 mm ± 7.8 vs. 66.2 mm ± 3.82; $F_{1,61} = 13.1$; $P < 0.01$). Overall, perch in 2008 fish

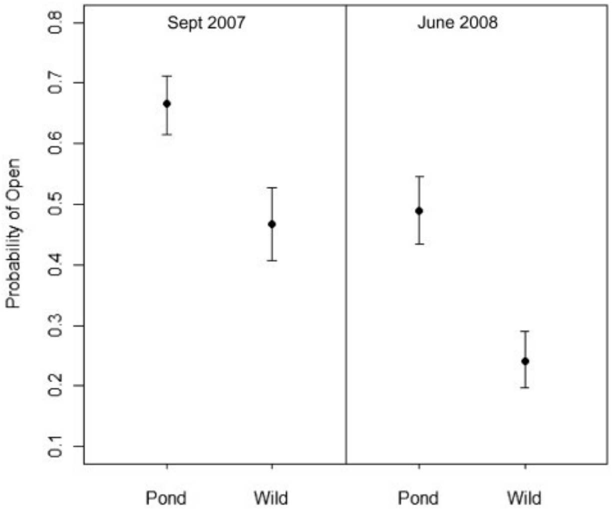

Figure 1. Probability of residing in the open area (i.e., boldness) for pond-reared and lake Eurasian perch in September 2007 and June 2008. The data are calculated from the means of 3 observational runs. The perch tested in June 2008 had been kept in tanks under identical, predator-free conditions since September 2007. In both September and June, pond fish were significantly bolder than lake fish.

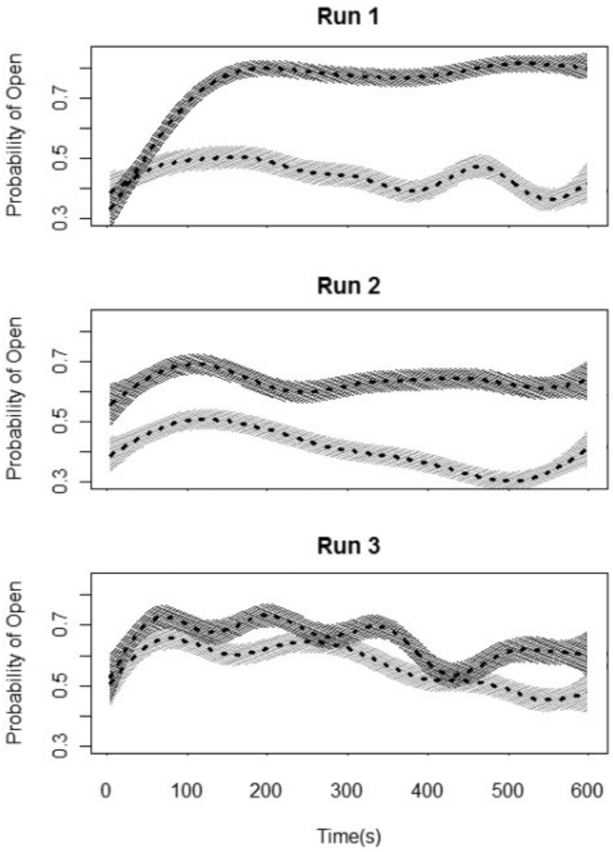

Figure 2. Probability profiles of time residing in the open area (boldness) over time for Lake and Pond fish in 3 runs. The dotted lines are the fitted values from a generalized additive mixed effect model with binomial errors, and represent averages of multiple groups per ecotype. Lines are embedded with 95% confidence shades (dark = Pond; light = Lake).

were larger than perch in 2007 (69.0 mm ± 6.7 vs. 64.9 mm ± 6.5; $F_{1,123} = 16.7$; $P < 0.01$).

Short-term changes

There was a non-linear relationship between boldness and time for both lake and pond fish in all 3 runs (Figure 2). The most parsimonious model included an interaction term indicating that the effect of time differed by origin in all 3 runs. Time had significant effect on boldness for both ecotypes and all runs (Table 1)

Discussion

Experience of predation shapes risk-taking behavior in young perch, and individuals exposed to predation are less bold than predator naïve individuals (Hellström and Magnhagen 2011). The current study concludes that such predator-induced behavioral differences can persist for up to 9 months, even after predator-exposed and naïve fish were contained under identical, predator-free conditions without any reinforcing stimuli. Additionally, perch adjusted boldness during the behavioral tests, and the difference between exposed and naïve fish decreased after 3 repeated runs.

The fact that the difference in risk-taking was still present 9 months after the last exposure to predation, and that the predator sympatric perch continued to display the most risk-averse behavior when confronted with a predator, indicate that experience of predation has long lasting effects on behavior in fish. Few studies have investigated how fish retain and depend on learned anti-predator behavior over time. An indication is given by studies investigating memory retention of short-term predator exposure. Such studies often proceed by first conditioning the fish to recognize a novel predator by simultaneously pairing Schreckstoff (an alarm substance generating a panic response in the fish) with the odor of the predator, and then measure for how long the fish still respond to only the predator odor. Commonly the intensity of the learned anti-predator response decreases with time elapsed since last exposure to predation (Chivers and Smith 1994; Brown and Smith 1998; Bereijikan et al. 1999; Mirza and Chivers 2000; Ferrari et al. 2010b; Brown et al. 2011). Chivers and Smith (1994) found fathead minnows *Pimephales promelas* to maintain a learned anti-predator response to northern pike *Esox Lucius* for at least 2 months, without reinforcing stimuli. Bereijikan et al. (1999), however, showed that juvenile Chinook salmon *Oncorhynchus tshawytscha*, conditioned to cutthroat trout as predator, no longer recognized the predator after 10 days without re-exposure. Rainbow trout *Oncorhynchus mykiss* are able to retain a learned anti-predator response for at least 8 days to 3 weeks (Brown and Smith 1998; Brown et al. 2011), after 1 single learning event. Memory formation is influenced by the strength and duration of the stimuli to be learned (Shettleworth 2010). In all of the aforementioned studies, the time the fish were given to learn about the predator was short, from a few days to only 1 h. The lake-caught perch in our study lived sympatric with predators from hatching until capture (approx. 4 months), hence having sufficient time and opportunity to learn and form anti-predator behavior. It is possible that the long-lasting effects of prior experience seen in this study are a result of a long period of continuous reinforcement (Brown and Chivers 2005).

Table 1. Effect of time on boldness

	df	χ^2	*P*
Lake fish			
Run 1	8.82	40.7	<0.001
Run 2	6.25	104.9	<0.001
Run 3	7.76	107.6	<0.001
Pond fish			
Run 1	5.41	284.4	<0.001
Run 2	5.99	18.5	0.015
Run 3	8.60	73.16	<0.001

P values represent significance of smooth terms from generalized additive mixed effect models.

In an environment such as the laboratory tanks, the absence of predators gets more probable and predictable as time passes. Thus, maintaining a learned anti-predator response long after the last exposure to predation risk may seem maladaptive. Recent theory predicts the retention time of learned anti-predator behavior to reflect the most current predation conditions. However, knowledge about predators may still have an adaptive value even when the predator is not present, in contrast to, for example, information of food distribution (Ferrari et al. 2010a). Hence, even though the likelihood of predation is very small, the potential prey should still retain anti-predator responses to predators that would pose a threat if encountered, as failing to do so may be lethal. Further, the retention time should also reflect the level of threat posed by the predator. Experience of high-risk predators had longer lasting behavioral effects than experience of low-risk predators in rainbow trout (Ferrari et al. 2010b), indicating a threat-sensitive dimension in how prey rely on predator experience over time. In our study, the large perch used as a predator in the aquarium studies are also the main predators on the small perch in the lake (Persson et al. 2000; Magnhagen 2006). All prey used were also small enough for the predator not to be limited by gape size (Lundvall et al. 1999). There is hence strong motivation for the small perch to still recognize the large perch as a potential threat, as the knowledge would again be relevant should they encounter the predator.

Experiences early in life may have long-lasting effects on behavior. In both humans and animals, many studies have shown personality dimensions such as boldness and exploration behavior to be shaped by experiences early in life (McCrae et al. 2000; Figueredo et al. 2005, Chapman et al. 2010, but see Stamps and Groothuis 2010). Also, mate and food preferences, as well as homing cues, are established in young age, and retained during most of the life (Dittman et al. 1996; Witte 2006; Schausberger et al. 2010). In fish, innate predispositions such as predator recognition could be further reinforced and more strongly expressed, after "predator training" during critical periods in juvenile stages (Berejikian et al. 2003; Hawkins et al. 2008). In our study, the exposure to predation during the fry or juvenile stage may have established a robust risk-averse phenotype in the predator-sympatric perch, causing them to trade-off risk differently than predator-naïve perch.

Although the difference in boldness between lake and pond fish was maintained after 9 months in the tank environment, overall boldness was lower in the post-tank tests compared with pre-tank tests for both ecotypes. We have no good explanation for this. Life in the tanks was almost completely free from any major disturbances, possibly making it harder for the fish to quickly adapt to the abrupt transition when moved to the experimental aquaria. Also, as fish were fed ad libitum in the tanks, foraging competition may not have served as a mechanism promoting bold behavior. We do not believe that the decrease in boldness reflect ontogenetic changes in behavior, as wild Fisksjön perch of similar age and size as the ones tested in this study, has been found to be bolder than YOY perch (i.e., increasing, instead of decreasing their boldness with age; Magnhagen and Borcherding 2008).

Although reinforcement may extend the time a learned behavior is retained, repeated exposure may also habituate the prey, causing it to decrease its response to the stimuli (Shettleworth 2010). Leussis and Boliver (2006), discussing habituation in rodents, differentiate between within and between session habituation, where the former refers to a continuous behavioral diminution over time as individuals gradually get familiar with the stimulus environment, and the latter to behavioral adjustments occurring in steps, after individuals recalling prior sessions. In our study, the difference between predator experienced and predator naïve fish decreased after repeated trials, indicating that the perch took into account memory of prior trials in their risk assessment. It seems like fish from ponds decrease boldness as the runs progress, and fish from the lake increase boldness. For pond fish, it is the first time they perceive a predator around that they can see and smell, and may get increasingly more cautious if the predator moves and attempt attacks. The lake fish—who have always known that predators are around—may perceive the predator to be less dangerous than previously perceived given that, in previous runs, predators did not chase or pursue prey despite close proximity. Perch also made continuous behavioral adjustments within trials, and both lake and pond fish tended to peak in risk-taking shortly after the trials begun, after which risk-taking remained constant or declined. Assuming that fish constantly assess risk and that there is a positive relationship between amount of acquired knowledge and time, one might have expected boldness to gradually increase with time as fish got more accustomed to the environment. Still, fish may have been getting satiated, or food may have become depleted, resulting in fish being gradually less motivated to take risk to obtain food (Milinski 1993). The within-trial decline in boldness was more pronounced in lake fish than pond fish, possibly suggesting lake fish to be more responsive to fine-scale changes in the trade-off conditions between predation and growth.

Other factors besides predation may generate phenotypic diversity in animals, and influence how experience mediates behavior. Habitat stability has been shown to affect how sticklebacks act on experience, with fish originating from more stable conditions retaining information for shorter time than fish from less stable habitats (Brydges et al. 2008). This result seems, however, counterintuitive and the authors also state that it opposes their initial predictions. Experience of unpredictability in food supply early in life shaped boldness in guppies, and generated phenotypes that could not be adjusted to match recent experience (Chapman et al. 2010). In this study, we argue that predation indeed is the underlying driver of the differentiation in boldness seen between lake and pond perch. Correlation between predation pressure and boldness phenotype in Fisksjön perch has by now been established in several studies, using varying comparative approaches such as multi-lake comparisons (Magnhagen 2006), inter-cohort comparisons (Magnhagen and Borcherding 2008), common garden experiments (Hellström and Magnhagen 2011), and multi-year comparisons (Magnhagen et al. 2012).

In conclusion, this study contributes to the understanding of the role of experience in shaping behavior. The study reports that prior experience of predation can influence behavior in perch long after the last exposure to predators occurred. It also shows that although anti-predator behavior was retained for considerable time, behavior could quickly be adjusted after learning of current conditions. The results highlight how prey has to balance past experiences of predators against current threat levels. We encourage more studies to explore the use of the analytical approaches presented here to investigate continuous behavioral adjustments over time.

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