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To cite this article: Janelle R. Sloychuk, Douglas P. Chivers & Maud C. O. Ferrari (2016) Juvenile Lake Sturgeon Go To School: Life-Skills Training for Hatchery Fish, Transactions of the American Fisheries Society, 145:2, 287-294, DOI: 10.1080/00028487.2015.1123183

To link to this article: http://dx.doi.org/10.1080/00028487.2015.1123183

Published online: 26 Feb 2016.

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Juvenile Lake Sturgeon Go To School: Life-Skills Training for Hatchery Fish

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Abstract
Hatchery supplementation of declining fish populations is commonly employed to try to increase year-class strength. However, the success of such programs is often hampered from low postrelease survival as a result of the failure of hatchery fish to appropriately recognize predation threats. Not surprisingly, there has been considerable effort to train prey to recognize predators prior to release. The objective of our current work was to characterize the antipredator response of hatchery-reared, predator-naive young-of-the-year Lake Sturgeon *Acipenser fulvescens* (an endangered species) to alarm cues from injured conspecífics and test whether these alarm cues could be used to train sturgeon to recognize unknown predators. We found that skin-derived alarm cues elicited an antipredator response without learning and that learning required cues coming from whole-body grinds, presumably because they represent a much more reliable indicator of risk. When the experiment was repeated with older sturgeon from Wolf River (Wisconsin), training with cues from whole-body grinds did not enhance the response. Subjecting the fish to several training sessions (six over 3 d) led to some alteration in behavior. Our results provide insights into how ontogenetic changes (size, scute growth) could explain the different learning outcomes from the larger fish as related to hatcheries and conservation programs.

Of the 27 species of paddlefish and sturgeons recognized worldwide, most are currently viewed as extinct, endangered, or threatened (Birstein 1993). Harvesting bans on caviar and meat fisheries, in addition to sport-fishing bans, have been imposed in many regions to protect populations. However, these management actions have often been futile in slowing population declines. The life history attributes of sturgeon present a particular challenge to conservation managers. Traits such as late age at maturity, infrequent periodic reproduction, and long life expectancy make population assessment and management challenging (Birstein et al. 1997). Moreover, population-level management strategies become difficult in highly migratory sturgeon populations because certain populations may migrate as much as 500 km over their lifetime (Auer 1999; DeVore et al. 1999).

Development of culture methods for conservation stocking has rapidly expanded around the globe. Hatchery-produced sturgeon can survive to adulthood (Secor et al. 2002); however, to our knowledge, there has not been a thorough investigation of the success of sturgeon stocking programs. The success of most fish stocking programs is thought to be hampered by low postrelease survival resulting from the failure of the released fish to recognize predators (Suboski and Templeton 1989; Brown and Smith 1998; Brown et al. 2013a). As a
result, there has been considerable effort to train fish to recognize predators prior to release. One common method used to train fish to recognize predators is to expose them to the sight or odor of a novel predator paired with chemical alarm cues released from injured conspecifics. This is a highly efficient form of learning in many species of fishes, as well as other aquatic organisms (Chivers and Smith 1994; Ferrari et al. 2010). The effectiveness of such life-skills training in promoting increased survival of predator-naive fish has not been consistent (Brown et al. 2013a). Yellow Perch *Perca flavescens* and Atlantic Salmon *Salmo salar*, which were conditioned to recognize Northern Pike *Esox lucius*, did not show improved survival when stocked into lakes with pike (Wisenden et al. 2004; Hawkins et al. 2007). In contrast, juvenile Chinook Salmon *Oncorhynchus tshawytscha*, that were raised in enriched hatchery environments and then trained to recognize a predatory Cutthroat Trout *Oncorhynchus clarkii*, had higher survival upon release into natural rivers than those that did not undergo the training (Berejikian et al. 1999). Similarly, Brook Trout *Salvelinus fontinalis* stocked into stream enclosures with Chain Pickerel *Esox niger* had higher survival if they underwent predator training. Such increase in survival following prereleased predator training has also been found in White Seabream *Diplodus sargus* by D’Anna et al. (2012), Murray Cod *Maccullochella peeli* by Hutchison et al. (2012) and two species of larval damselfish (*Pomacentrus*) by Lonnstedt et al. 2012b; Ferrari et al. (2015).

Recently, Wishingrad et al. (2014a, 2014b) documented that young-of-the-year (age-0) Lake Sturgeon *Acipenser fulvescens*, possess chemical alarm cues and suggested that they would appear to be a good candidate for life-skills training, particularly given their well-developed olfactory systems. In addition, juvenile Lake Sturgeon show strong site fidelity; in one study, Barth et al. (2011) showed that more than 90% of fish captured in the Winnipeg River moved less than 2 km over a 30-month period. High site fidelity means that predator training can be tailored to the local predator fauna.

We investigated the potential for life skills training for Lake Sturgeon. First, we characterized the antipredator response of age-0 sturgeon to a variety of chemical cues, including feeding and alarm cues and then tested whether the fish could be trained to recognize a common predator through training with alarm cues released from the skin of damaged conspecifics. Surprisingly, we did not find evidence that sturgeon could learn based on this common learning paradigm. This result contrasts dozens of studies in a variety of fishes, larval amphibians and aquatic invertebrates (Chivers and Smith 1998; Ferrari et al. 2010). However, given that age-0 sturgeon spend time moving in interstitial spaces of rocky substrates or potentially abrasive sandy substrates, we hypothesized that the detection of injured skin cues may not always indicate that a predation event has occurred. However, whole-body extract, or the cues released from badly injured conspecifics, would provide prey with a more accurate indicator of predation. Consequently, we repeated the learning experiment using whole body grinds on two different populations of sturgeon. In our final experiment, we examined the effect of multiple conditioning on acquired predator recognition in one of the populations.

**METHODS**

**Source of sturgeon.—** Age-0 Lake Sturgeon used in experiments 1 and 2 were obtained as larval sturgeon from Sustainable Sturgeon in Emo, Ontario, in May 2012 and originated from broodfish from Rainy River, Ontario. Sturgeon were kept in 70-L tanks as larvae and moved to a 650-L circular water-flow-through tank once they were free-swimming. Larvae were fed to satiation every 4 h with brine shrimp, and older sturgeon were fed frozen blood worms (Polychaeta) twice daily. The temperature of the holding and test tanks ranged from 15°C to 19°C, and the photoperiod was constant at 14 h light and 10 h dark. Age-0 fish used in experiments 3 and 4 were obtained from the sturgeon stocking program out of the Genoa National Fish Hatchery in Genoa, Wisconsin, the fish originating from the Wolf River in Wisconsin. These fish were held under the same conditions as the Rainy River fish.

**Collection of predator odors and alarm cues.—** The predator odor used for all experiments was collected from five Northern Pike (mean = 20.8 cm TL, SD = 10.3) that were captured (seine nets) in June 2013 from Pike Lake, Saskatchewan. Northern Pike are natural predators of age-0 sturgeon. The pike were housed in a 6000-L flow-through circular tank at 12°C (SD = 1) and were fed ad libitum with live Fathead Minnows *Pimephales promelas*. However, the predators were fasted in their holding tank for 7 d prior to stimulus collection. Individual predators were placed into a clean tank containing 30 L of water and left undisturbed for 24 h after which time the stimulus water was frozen in 60-mL aliquots until it was needed.

Skin-derived chemical alarm cue was prepared following established protocols from Wishingrad et al. (2014a, 2014b). For experiment 1, we removed 3.2 g of skin fillets from six age-0 sturgeon (mean = 6.4 cm TL, SD = 0.4). The skin was homogenized using a Polytron homogenizer (Brinkman Instruments, Rexdale, Ontario) and then diluted in 1 L of distilled water. The solution was then filtered through glass wool and frozen in 50-mL aliquots at −20°C until required. For experiments 2, 3, and 4, we prepared alarm cues from whole body grinds rather than skin extracts. For experiment 2, we used five age-0 Rainy River Lake Sturgeon (mean = 6.5 cm TL, SD = 0.4), and for experiment 3 and 4 we used five Wolf River sturgeon (13.9 cm TL, 0.4). Sturgeon were killed by cervical dislocation (in accordance with the Canadian Council on Animal Care), and the whole sturgeon was placed in distilled water. The tissue was homogenized then filtered through glass wool to remove remaining tissue. The solutions were diluted to a tissue concentration of about 3.2 g/L of distilled water to make the concentrations comparable to experiment 1. Bloodworm extract was
prepared from thawed bloodworms and minnow extract was prepared from six Fathead Minnows (3.5 cm TL, SD = 0.3) following the same procedure as for the whole body grind. Again, the solution was diluted to a concentration of 3.2 g/L.

We conducted four experiments to examine the potential for life-skills training in age-0 Lake Sturgeon. In experiment 1, we characterized the antipredator response of sturgeon (Rainy River population) to alarm cues from conspecifics and a variety of other odors and then tried to teach them to recognize the odor of Northern Pike as a predator. We hypothesized that the sturgeon would learn to display an antipredator response following the alarm-cue conditioning, while the water controls would not. Due to the results from experiment 1, we repeated the learning experiment on additional Rainy River sturgeon in experiment 2, this time using alarm cues from whole body grinds instead of skin-derived alarm cues. We hypothesized that whole-body grinds would represent a much more reliable indicator of risk and, hence, should mediate learning. Experiment 3 was identical to experiment 2 but used fish from another population, Wolf River. Finally, in light of the results of experiment 3, we increased the number of conditionings of the Wolf River fish (six times over 3 d) during experiment 4 and tested for the occurrence of any learned response.

Experiment 1.—This experiment consisted of two phases, conditioning trials followed by recognition trials. During conditioning trials, sturgeon were exposed to one of four cues:

1. Skin-derived sturgeon alarm cue paired with pike odor. This is a commonly used technique used to train prey to recognize predator odor in many fish species (Ferrari et al. 2010).
2. Skin-derived minnow alarm cues paired with pike odor. Skin cues from distantly related heterospecifics should not induce a learned response and, hence, was used as a negative control (Ferrari et al. 2010).
3. Bloodworm extract paired with pike odor. This allowed us to compare the behavioral response to a risk cue (sturgeon alarm cues) to that from a feeding cue (bloodworm).
4. Distilled water paired with pike odor. This controlled for the possibility of innate recognition of the pike odor.

Recognition trials were completed the day following the conditioning trials. During recognition trials, we exposed the sturgeon to pike odor alone, to assess whether they would display a learned antipredator response to the pike cue. Experiment 1 was carried out from October 15 to November 5, 2012, when the fish were between 140 and 161 d posthatch (7.1 cm TL, SD = 0.7).

Groups of three sturgeon were placed in 37-L tanks and were left to acclimate for a 24-h period prior to conditioning. The tanks contained a sand substrate and an air stone and were filled with dechlorinated tap water. Each tank had a grid (8.5 × 11 cm) with the side divided into three rows and six columns, which was drawn on the front of the tank to facilitate measuring activity, while the sides and back of the tank were covered in black plastic sheets to block visual disturbance from adjacent tanks. To inject test stimuli into the tanks, we used a 2-m long piece of plastic tubing attached near the air stone, which aided in distribution of the stimuli.

All trials were conducted between 1000 and 2200 hours. Observations consisted of an 8-min prestimulus and an 8-min poststimulus injection period. Prior to the prestimulus period, we withdrew and discarded 60 mL of water from the injection tubes (to remove any stagnant water) and then withdrew and retained an additional 60 mL of water for slowly flushing the stimulus into the tank after injection. Following the prestimulus period, we injected one of the four stimuli (20 mL of sturgeon extract, minnow extract, bloodworm extract, or distilled water paired with 20 mL of pike odor). Once the stimuli were fully injected, we began the poststimulus observation period.

When a benthic fish detects a potential threat, it has a variety of behavioral options. Often, fish stop moving, thereby increasing their crypsis and avoiding detection by the predator (Lima and Dill 1990). In contrast, they could exhibit dashing behavior and flee away from the predator. Wishingrad et al. (2014b) documented that age-0 Lake Sturgeon exhibit a dramatic increase in activity in response to alarm cues from conspecifics, but there are no published papers on responses of sturgeon to predator odors. For fishes that typically live in flowing water, fleeing into the water column could help them to escape benthic predators, and indeed Kynard et al. (2010) reported on the swim-up behavior of disturbed age-0 Lake Sturgeon. We used a well-established procedure for testing the antipredator response of fishes (Chivers and Smith 1998; Ferrari et al. 2010). We recorded the vertical-use index of a focal fish (randomly chosen but consistent for the duration of the trial) every 15 s (1 = fish on the bottom row of the tank, 2 = fish in the middle row of the tank, 3 = fish in the top row of the tank). The number of line crosses (using the three by six grid pattern drawn on the front of the tank) was also recorded for one randomly selected sturgeon of the three; the selected fish was observed until the end of the conditioning period. All trials were performed blind and the order of stimulus injection was randomized.

One hour after the end of the conditioning trials, the fish were moved to identical 37-L tanks filled with clean dechlorinated tap water and the recognition trials were performed 24 h later. Following the prestimulus period, we injected 20 mL of pike odor into the tank and immediately began the poststimulus observation period. All trials were performed blind, and the order of testing was randomized. We tested 80 sturgeon (mean = 6.4 cm TL, SD = 0.4) in total, or 20/treatment.

For both the conditioning and recognition trials, we performed a one-way ANOVA to compare prestimulus activity level and vertical area use among the four treatments. Given that there was no difference in prestimulus data, we analyzed the data using the difference (poststimulus score minus prestimulus score) in activity and vertical area use using the same statistical approach.
Experiment 2.—This experiment also consisted of conditioning trials followed by recognition trials. During conditioning, sturgeon from Rainy River were exposed to one of two treatments, alarm cues derived from the whole-body grind of sturgeon paired with pike odor or distilled water paired with pike odor. During the testing phase, the fish were exposed to either pike odor to test whether they had learned to respond to pike odor or a distilled water control. The testing protocol was identical to experiment 1. Data collection was carried out from August 23 to December 17, 2012, when the sturgeon were between 87 and 203 d posthatch (5.7 cm TL, SD = 0.4). We tested a total of 77 fish (19–20/treatment). All trials were performed blind, and the order of stimulus injection was randomized. Using a two-way ANOVA, we tested the effect of conditioning cue (alarm cue versus water) and testing cue (pike odor versus water) on the prestimulus value and change in behavior. All data followed parametric assumptions.

Experiment 3.—This experiment was identical to experiment 2, except that we used fish from Wolf River. Data collection was carried out from October 1 to December 20, 2012, when the fish were between 168 and 248 d posthatch (mean at the time of testing = 11.1 cm TL, SD = 1.4). We tested a total of 74 fish (18–19/treatment). The analyses were identical to those performed for experiment 2. All data followed parametric assumptions.

Experiment 4.—This experiment followed the same protocol as experiment 3, except that the fish were conditioned a total of six times over a 3-d period. Conditioning occurred at 1030 hours and 1530 hours each day. The experiment was carried out from April 15 to April 20, 2013, when the Wolf River sturgeon were between 364 and 369 d posthatch. We tested a total of 64 fish (19–20/treatment). All trials were performed blind, and the order of stimulus injection was randomized. Once again, we ran a two-way ANOVA on both prestimulus and change in behavior. Prestimulus data for line crosses were log-transformed to meet assumptions. For line crosses, we ran a nonparametric two-way ANOVA on ranked data, using the Scheirer–Ray–Hare extension of the Kruskal–Wallis $H$-test (Sokal and Rohlf 1995).

RESULTS

Experiment 1

Conditioning trials.—Conditioning cue did not have any significant effect on prestimulus values for line crosses (one-way ANOVA: $F_{3, 78} = 0.1, P = 0.9$) or vertical use ($F_{3, 78} = 0.5, P = 0.7$). Treatment differences were found for change in activity (one-way ANOVA: $F_{3, 78} = 19.8, P < 0.001$) but not for vertical use ($F_{3, 78} = 0.7, P = 0.5$). Post hoc comparisons (Tukey HSD tests) indicated that the mean change in line crosses for fish conditioned with alarm cue paired with predator odor was significantly different than all other stimuli, but the other treatments did not differ from each other (Figure 1).

Recognition trials.—The results of the one-way ANOVA indicated that there was no significant effect of conditioning cue on prestimulus values for line crosses ($F_{3, 77} = 0.1, P = 0.9$) or vertical use ($F_{3, 77} = 0.7, P = 0.5$). When we consider change from the prestimulus baseline, we found no effect of conditioning treatment on either line crosses ($F_{3, 77} = 0.9, P = 0.4$) or change in vertical use ($F_{3, 77} = 0.9, P = 0.4$).

Experiment 2

Prestimulus data for line crosses were not affected by conditioning cue (two-way ANOVA: $F_{1, 73} < 0.1, P = 0.9$), testing cue ($F_{1, 73} = 1.2, P = 0.2$) or any interaction between the two factors ($F_{1, 73} = 0.7, P = 0.4$). However, vertical use was affected by an interaction between conditioning and testing cues ($F_{1, 73} = 4.6, P = 0.036$). We thus used percent change from the prestimulus baseline ([(post − pre) / pre] as the response variable in the analysis for this variable only, allowing us to compare the different groups to each other.

A marginally significant interaction between conditioning and testing cues was found for line crosses (two-way ANOVA: $F_{1, 73} = 4.0, P = 0.049$, Figure 2). Sturgeon pseudo-conditioned with water paired with pike odor did not differ in their response to water and pike odor ($P > 0.9$). However, sturgeon conditioned with body-derived alarm cues significantly decreased their activity compared with water ($P = 0.024$), indicating that Rainy River sturgeon have learned to recognize pike odor as a threat when conditioned with body-derived alarm cues. However, for vertical use we failed to find an effect of conditioning ($F_{1, 73} < 0.1, P = 0.9$), testing ($F_{1, 73} < 0.1, P = 0.9$), or any interaction ($F_{1, 73} = 1.2, P = 0.3$).
Experiment 3

Prestimulus data were not affected (two-way ANOVA) by conditioning cue (line crosses: $F_{1, 70} = 1.2$, $P = 0.5$; vertical use: $F_{1, 70} = 1.2$, $P = 0.5$), testing cue (line crosses: $F_{1, 70} = 0.1$, $P = 0.9$; vertical use: $F_{1, 70} = 0.7$, $P = 0.6$), or any interaction between the two factors (line crosses: $F_{1, 70} = 0.42$, $P = 0.5$; vertical use: $F_{1, 70} = 3.9$, $P = 0.053$).

Two-way ANOVA showed that testing cue ($F_{1, 70} = 14.0$, $P < 0.001$), but not conditioning ($F_{1, 70} = 3.5$, $P = 0.06$) or conditioning × testing ($F_{1, 70} = 0.3$, $P = 0.6$), had an effect on change in line crosses. Sturgeon decreased activity when exposed to pike odor but not when exposed to water, regardless of conditioning treatment (Figure 3). For change in vertical use, we failed to find an effect of conditioning (two-way ANOVA: $F_{1, 70} = 0.9$, $P = 0.3$), testing ($F_{1, 70} = 2.6$, $P = 0.1$) or any interaction between the two factors ($F_{1, 70} = 1.3$, $P = 0.3$).

Experiment 4

Prestimulus data for line crosses and vertical use (respectively) was not affected by conditioning (two-way ANOVA: $F_{1, 60} = 3.3$, $P = 0.07$; $F_{1, 60} = 0.2$, $P = 0.6$), testing cue ($F_{1, 60} = 0.19$, $P = 0.7$; $F_{1, 60} = 1.3$, $P = 0.26$) or any interaction between the two factors ($F_{1, 60} = 0.01$, $P = 0.9$; $F_{1, 60} = 2.6$, $P = 0.11$). Change in line crosses was affected by conditioning cue (two-way Kruskal–Wallis $H_{1, 60} = 5.4$, $P = 0.035$) and testing cue ($H_{1, 60} = 5.4$, $P = 0.023$) but there was no interaction ($H_{1, 60} = 0.6$, $P = 0.5$). The average change in activity was greater for conditioned than pseudo-conditioned fish, and this change tended to be greater in response to water than in response to pike odor (Figure 4).

For vertical use, a significant interaction between conditioning and testing cue was found (two-way ANOVA: $F_{1, 60} = 5.0$, $P = 0.029$). Namely, fish that were pseudo-conditioned with water did not differ in their response to water and pike odor (Tukey post hoc test: $P = 0.78$). However, those sturgeon that underwent the multiple conditioning procedure did increase vertical use significantly more in response to pike odor than water (Tukey post hoc test: $P = 0.011$; Figure 4).

DISCUSSION

Our experiments highlight that life-skills training holds considerable promise to enhance survival of hatchery-reared Lake Sturgeon. In our first experiment, we documented a rather dramatic increase in activity in response to alarm cues released from injured age-0 Lake Sturgeon. The response was an antipredator response rather than a feeding response as the fish do not show the same behavioral response to food cues. These results are in accordance with the findings of Wishngrad et al. (2014a, 2014b). Interestingly, the fish failed to learn the odor of northern pike that was presented in conjunction with the alarm cues. This is a rather surprising finding because this mechanism of learning has been documented many dozens of times in a diversity of taxa (Ferrari et al. 2010) ranging from flatworms (Wisenden and Millard 2001), through insects (Wisenden et al. 1997), mollusks (Rochette et al. 1998) fishes (Chivers et al. 1995; Ferrari et al. 2005), and amphibians (Mirza et al. 2006; Ferrari and Chivers 2009). We speculated that the lack of learning may indicate that alarm cues released from age-0 Lake Sturgeon may not always be associated with a high level of predation risk. Sturgeon are benthic fish that spend time moving in interstitial spaces of rocky and sandy
substrates and as such may frequently rub their skin against abrasive surfaces and cause epidermal damage. We do not know whether sturgeon have tough skin, but we do know that alarm cells of many fishes are contained outside of the dermal scales (Smith 1992), and hence, little damage may be needed for the cues to be released. If sturgeon are often exposed to small amounts of skin-derived alarm cues, then they should avoid learning to associate new odors with damage because this would result in incorrect learning of odors as dangerous. We hypothesized that greater damage may be necessary to indicate that a predation event has occurred. In accordance with this hypothesis, when we used cues released from badly injured conspecifics (i.e., whole-body extracts) we saw that the Rainy River fish were able to learn to recognize the predator based on a single conditioning event. We were very careful to match the concentration of cues used in each of these experiments. Rather than concentration being the factor driving differences in learning, it is likely that differences in the source of the damaged tissue causes the difference in learning.

When we attempted to condition Wolf River fish to recognize pike odor using whole-body grinds (experiment 3), we had a rather surprising result. We observed an antipredator response to predator odor, regardless of whether the fish were conditioned or not. The reduction in activity was comparable in magnitude to that of the learned recognition by Rainy River fish and suggests the possibility of innate recognition of pike by this population of sturgeon. Regardless of whether there was innate recognition, our single conditioning trial did not influence the intensity of the antipredator response the fish exhibited upon exposure to pike odor. It is possible that multiple instances of conditioning could enhance innate predator recognition or could trigger learning. Therefore, in our last experiment, we conditioned fish multiple times and looked for responses to pike odor. In this experiment, we had no evidence that Wolf River fish exhibit innate predator recognition, but we were able to show that multiple conditioning resulted in learned predator recognition. Fish conditioned multiple times fled into the water column in response to pike odor, while those that were pseudo-conditioned did not. Future work needs to consider whether Wolf River sturgeon or other populations of sturgeon have innate recognition of predators. If some populations have innate recognition of predators, and others do not, then fish from populations with innate recognition may be preferentially stocked. Experiment 3 suggests that Wolf River have innate recognition of predators, while experiment 4 suggests they do not. One obvious difference is that age and size of the fish tested between the experiments. Fish were between 168 and 248 d posthatch in experiment 3 but were 364 and 369 d posthatch in experiment 4. Any consideration of differences in responses to predators through ontogeny needs to consider the development of morphological defenses. Sturgeon develop scutes during the larval stage at approximately 25 mm TL (Gadomski and Parsley 2005). As sturgeon grow, their scutes become very sharp and form prominent apical hooks (Scott and Crossman 1985). A reduction in antipredator behavior with age is not particularly surprising given that morphological defenses are much more developed. Hence, size and age might indeed drive the different response patterns seen between the two populations. Given that the two hatcheries did not offer fish the same size, we could not formally test this hypothesis, but there is a wealth of literature with regards to ontogenetic shift in antipredator responses (Golub and Brown 2003; Jones et al. 2003; Marcus and Brown 2003; Harvey and Brown 2004). Likewise, there is considerable literature documenting population differences in fish antipredator behavior (Mathis et al. 1993; Brown et al. 2013b), but to our knowledge, this does not include studies on alarm cues.

Our results suggest that life-skills training holds considerable potential for use in sturgeon management plans. However, life-skills training will probably need some considerable development. Unlike most fishes that learn based on skin-derived alarm cues, sturgeon need to be conditioned with whole-body
grinds. Attention needs to be given to potential population effects in training programs. In one population, we had no evidence of innate recognition of predators, while in another population we had some evidence of innate recognition. Additional studies need to consider the time of training and release. Wishingrad et al. (2014b) documented a complex relationship between behavior and morphology in sturgeon. There was particular good evidence for trait codependence between escape responses and body size, where larger fish were able to show stronger escape responses. Perhaps this explains why the largest fish we tested exhibited a response whereby they fled into the water column in response to risk. Small fish on the other hand responded to predators by dramatically reducing activity. It is rather fascinating that small Rainy River fish respond to alarm cues by fleeing, but their learned responses to predators consists of reducing activity. Fleeing in response alarm cues may be beneficial if alarm cues attract additional predators (Chivers et al. 1996; Wisenden and Thiel 2002; Lonnstedt et al. 2012a). Fleeing in response to a known predator may be less desirable than reducing activity, unless the exact location of the predator is known or the prey are of sufficient body size to quickly escape (Wishingrad et al. 2014b).

ACKNOWLEDGMENTS

This work was support by a Canadian Wildlife Federation Grant to D.P.C. and Natural Sciences and Engineering Research Discovery Grants to D.P.C. and M.C.O.F. We thank V. Wishingrad for help with fish care. All research herein was conducted under animal use protocol 20120045 issued by the University of Saskatchewan.

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