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Can captive-bred American bullfrogs learn to avoid a model avian predator?

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Abstract Animals that are isolated from their natural predators may lose the ability to express antipredator behavior. The aim of this study was to test whether it would be possible to train captive-bred North American bullfrogs (*Rana catesbeiana*) to avoid a model avian predator and to measure their behavioral responses to this predator. We used 18 animals divided into two groups, trained ($N=6$) and control ($N=12$); these individuals were from a line that has been bred in captivity for at least 20 generations without predator contact. The trained group was exposed, individually, to 20 sequential antipredator training sessions, during which the presence of a model avian predator was paired with an aversive stimulus. The control group was exposed, individually, once only to the same model avian predator, but without the association of the aversive stimulus. Both groups were observed for 10 min after the presentation of the avian predator, during which their behavior was recorded using instantaneous recording of behavior. The results showed that, after only two training sessions, the trained bullfrogs started to express proper antipredator behavior: diving to the bottom of the tank, lying still, and eventually, learning to cover themselves in substrate (mud). However, continued training sessions provoked a varied response to antipredator training, which was undesirable as the effectiveness of their antipredator response varied. This study has shown that captive-bred bullfrogs were capable of learning antipredator behavior, despite having been bred for many generations in captivity with no predator contact.

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Introduction

Reintroduction, which places animals back into their natural range (Beck et al. 1994; IUCN 1995), and translocations, the capture and transfer of free-ranging animals from one part of their historic geographic range to another (Kleiman 1989), are becoming increasingly important tools for population and species management (Griffith et al. 1989). Animal reintroductions and translocations are potentially important interventions to save species from extinction, but are mostly unsuccessful (i.e., animals fail to survive or establish a new population; Griffin et al. 2000). Upon reintroduction or translocation, predation is a major cause of mortality of animals subjected to these processes (Beck et al. 1994; Wolf et al. 1996; Olla et al. 1998; Griffin et al. 2000; Bremner-Harrison et al. 2004; Teixeira et al. 2007).

Antipredator training, therefore, may be a valuable addition to reintroduction programs (Maloney and McLean 1995) and could be a useful strategy to increase translocation success (Miller et al. 1990; McLean 1997; McLean et al. 2000; Teixeira et al. 2007). Presently, one common method of antipredator training is to take advantage of associative learning processes and associate a model predator with an aversive stimulus (e.g., simulated capture) (Griffin et al. 2000; Azevedo and Young 2006a; Mesquita and Young 2007)

According to Berger (1998), one effect of isolating prey from their predators is the loss of formerly adaptive antipredator behavior. If the population would later come into contact with predators, this may have adverse consequences (Blumstein et al. 2004); thus, releasing animals back to the wild without antipredator training puts them at a survival disadvantage and could be considered unethical (McLean

1997). Animals that have been ontogenetically isolated (e.g., bred in captivity) may have the capacity to express competent antipredator behavior, but this might not occur without specific experience (Griffin et al. 2000). Studies have shown that these behavioral deficits could be rectified by classical conditioning because this technique stimulates existing behavioral systems (Griffin et al. 2000). Although some antipredator behavior may persist for many thousands of years after isolation (Blumstein et al. 2004); there is, however, no adequate model to predict this response (Blumstein 2006). Prerelease antipredator training, therefore, has the potential to enhance the expression of preexisting antipredator behavior (Griffin et al. 2000, 2001; McLean et al. 2000; Blumstein et al. 2004).

Opportunities for learning about predators can arise at various stages of the predator–prey interaction, but are particularly apparent during recognition and assessment stages (Kelley and Magurran 2003). Through training, animals improve their behavioral responses to predators (Mesquita and Young 2007). These studies provide strong support for the idea that training procedures may be successful if they are designed to take advantage of a species' natural mechanisms and predispositions to learn (Griffin et al. 2000).

Teixeira et al. (2007) showed that predation possibly mediated by stress was one of the greatest causes of mortality in reintroduction and translocation projects involving species of vertebrates, and this hypothesis is compatible with the results of meta-analyses of reintroduction projects (Dodd and Segiel 1991; Beck et al. 1994). Most of the studies about antipredator training of mammals, fishes, and birds have had positive results (Miller et al. 1994; Maloney and McLean 1995; McLean 1997; Azevedo and Young 2006a; Vilhunen 2006; Mesquita and Young 2007). These experiments indicate that antipredator behavior is not solely dependent on inherited predispositions, but can be modified with experience or learning (Magurran 1990; Kieffer and Colgan 1992; Griffin et al. 2000, 2001; Blumstein 2002; Kelley and Magurran 2003; Griffin and Evans 2003). This behavioral plasticity can be explored to increase the expression of antipredator behavior of captive-born animals (Griffin et al. 2000). However, none of these studies have put their antipredator training methods to the ultimate test and measured the survival rate of trained versus untrained animals after release to the wild. Two studies that did measure survival rates of predator-trained and control animals (houbara bustards, *Chlamydotis undulata* and black-tailed prairie dogs, *Cynomys ludovicianus*) found that trained animals had a higher survival rate (van Heezik et al. 1999; Shier and Owings 2006), as has been found in some bird species (Gaudioso et al. 2011). We could find no studies that referred to antipredator training for amphibians or reptiles, despite the fact that these vertebrates also suffer from high failure rates in reintroduction programs (Dodd and Seigel 1991).

Studies carried out about antipredator training have shown that most species can learn a proper response after two or three training sessions (Chivers and Smith 1994; Maloney and McLean 1995; McLean et al. 1999; Griffin et al. 2000; Azevedo and Young 2006a; Mesquita and Young 2007). Furthermore, studies have also shown that it is possible to provide an animal with too many training sessions, in that an animal may habituate to the training protocol (Magurran 1990); that is, learn that the model predator does not represent any real threat and ignore it.

With the aim of developing an antipredator training protocol for amphibians, an experiment using North American bullfrogs as a model species was carried out in order to determine how many training sessions would be required to induce proper antipredator behavior.

Material and methods

Study subject

North American bullfrogs (*Rana catesbeiana*) are the only amphibian species native to the Nearctic region; they are found from Nova Scotia to central Florida, from the East Coast of North America to Wisconsin, and across the Great Plains to the Rockies (Conant 1958). The most important predators of the species are the great blue heron (*Ardea herodias*), raccoons (*Procyon lotor*), and garter snakes (*Nerodia* sp.) (Elliot et al. 2009).

In this study, 18 adult unsexed (due to difficulty in sexing) North American bullfrogs (*R. catesbeiana*) were divided in two groups: 6 in the trained group and 12 in the control group (C); these bullfrogs were acquired from Ranamig Froggery located in Betim, Minas Gerais, Brazil. The bullfrogs were born in captivity and come from a line that has been reproduced in captivity since 1985; therefore, they have had no contact with their possible natural predators for at least 20 generations. As bullfrogs were all tested individually, the marking of individuals was not necessary. We used a larger control group due to the fact that they would be tested only once (i.e., to increase sample size), and we used only six animals in the test group as pilot studies had shown that this sample size would be sufficient to generate a statistically detectable response.

Animal housing

This study was realized in Centro de Incentivo e Valoração do Aluno, situated at the Pontifical Catholic University of Minas Gerais (PUC Minas), Belo Horizonte, Minas Gerais, Brazil. We used three separate tanks: in the first tank, we maintained singly bullfrogs pertaining to the trained group; in the second tank, we maintained singly bullfrogs pertaining

to the control group; and the last tank was used for the antipredator training sessions. The two tanks used to maintain the animals were 80 cm in height and 125 cm in diameter. Fifty percent of these tanks' bottom had an elevated area whose floor was maintained dry to permit feeding of the bullfrogs (dead mice); the other 50 % had a 3-cm-deep layer of water. The training tank was 100 cm in diameter and 88 cm in height: being filled to a depth of 50 cm with water and the bottom had a thin layer of mud substrate.

Experimental protocol

All experimentation was conducted in compliance with international regulations and recommendation regarding the use of animals in applied animal behavior research (Sherwin et al. 2003). Before the experiments, we made 10 h of informal observations of American bullfrog behavior using nonexperimental animals. All observed behavior patterns were noted and used to elaborate an ethogram for bullfrogs' antipredator behaviors (Table 1). Pilot tests were also undertaken, with these animals, to choose which predator model (we tried a variety of bird species) and aversive stimulus (we tried a variety including simulated capture with a net) were most appropriate and also to choose the duration of each event of the training protocol (e.g., duration of the presentation of the model predator; we tried a variety of time intervals for experimental phases). Based on these observations, we chose as our avian predator model a taxidermized black-crowned night heron (*Nycticorax nycticorax*).

Due to concerns about potential carryover effects of using the same experimental protocol 20 times with each trained animal, we decided to use a control group for comparison; that is, a between-subjects rather than a within-subjects experimental design. We could have observed the trained animals before exposure to the model predator (e.g., AB design); however, we were concerned that animals could rapidly become conditioned to the experimental tank and, even before predator presentation, start to show antipredator responses (Cooper et al. 2007).

In total, the trained group was exposed, individually, to 20 antipredator training sessions, whereas the control group received only one exposure to the same predator model as the trained group. For the trained group, the following experimental protocol was used: the individual to be trained was gently and quickly caught in a net (in <30 s) and placed in the training tank where it was left to acclimatize for 10 min. During the acclimatizing period and the whole experimental protocol, the human researcher stayed out of sight of the test animal (hidden behind a wooden screen). After the acclimatizing period, the model avian predator (fixed onto the end of a 2-m-long wooden pole) was shown to the animal, from a distance of approximately 1.5 m, for 5 s (pilot studies had shown that animals always detected the model predator within this time interval) followed by 10 s of chasing of the individual with a long stick (i.e., the aversive stimulus; see Fig. 1a) (care was taken never to touch or hurt the bullfrog). The behavior of the bullfrog was then recorded for 10 min using instantaneous recording of behavior with 15-s intervals. At the end of the procedure, the trained bullfrog was placed back into the holding tank. An interval of 24 h was used between successive training sessions. The same procedure was undertaken with all individuals ($N=6$) of the trained group in all training sessions ($N=20$; i.e., a total of 120 training sessions). The protocol for the control group was identical to that of the trained group, except that the aversive stimulus (chasing with a stick in the water for 10 s) was not applied (see Fig. 1b) and they were observed for 10 min before the presentation of the model predator (generating baseline responses of untrained individuals). In total, this procedure was conducted with 12 different individuals (i.e., 12 tests).

Data analyses

In this study, individuals were the unit of study and we used a between-subjects experimental design (i.e., trained group versus control group); however, due to the fact that the trained group was learning a response, we also decided to use a within-subject comparison (comparing the first/second training sessions (1–2) with the third/fourth training sessions (3–4)). To test whether our data met the requirements for parametric statistics, we used the Anderson–Darling test, which showed that they did not fulfill the requirements, and therefore, nonparametric statistical tests were used throughout. In our data analyses, we used three principal comparisons (treatments): the mean percentage occurrence for the behaviors expressed in the first/second training sessions per individual (1–2); the mean percentage occurrence

Table 1 List of behaviors expressed by North American bullfrogs during pilot antipredator training sessions

Behavior	Description	Abbreviation
Inactive on the surface	Individual inactive on the water's surface	IS
Inactive on the bottom	Individual inactive on the bottom of the tank	IB
Swimming on the surface	Individual swimming on the water's surface	SS
Swimming on the bottom	Individual swimming on the bottom of the tank	SB
Swimming to the surface	Swimming upwards to the water's surface	STS
Swimming to the bottom	Swimming downwards to the tank's bottom	STB

Fig. 1 Schematic diagram showing the antipredator training protocol for **a** the trained group (model avian predator paired with aversive stimulus) and **b** the control group (model avian predator *not* paired with the aversive stimulus)
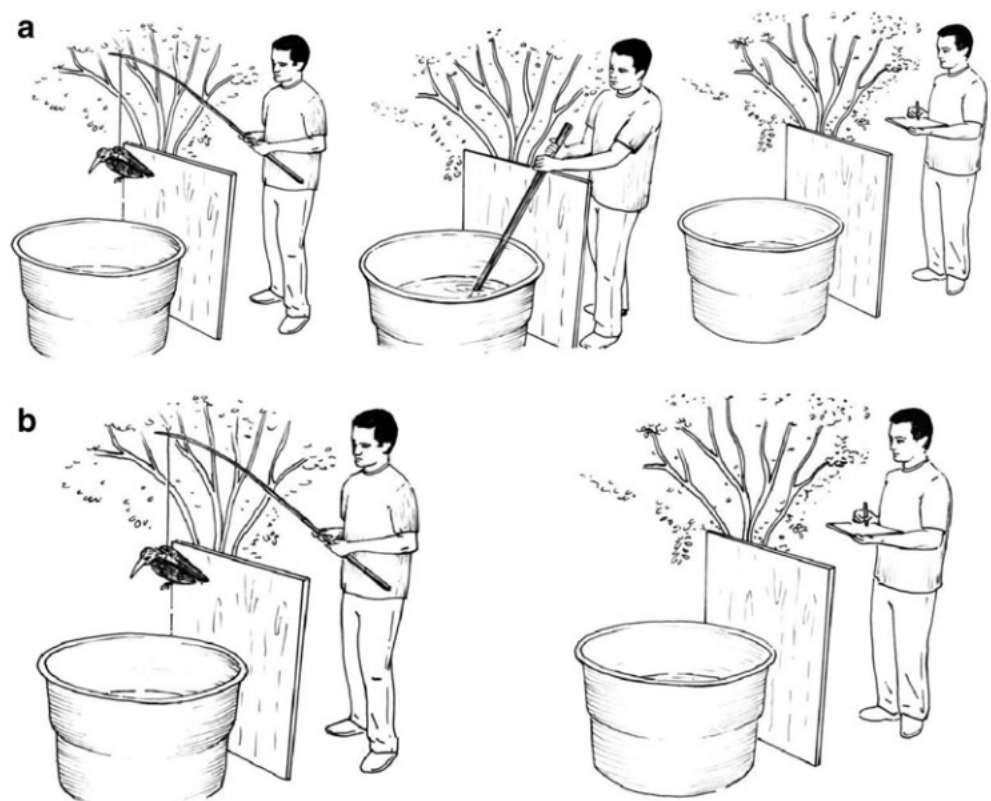
for the behaviors expressed in the third/fourth training sessions per individual (3–4); and the mean percentage occurrence of the behaviors expressed by the control group per individual. We used a Kruskal–Wallis one-way nonparametric analysis of variance to compare these three treatments rather than a Friedman nonparametric analysis of variance because a Friedman test requires equal sample sizes in treatments (in our cases, treatment sample sizes were $N=12$ for the control group and $N=6$ for the trained group) (Siegel and Castellan 1988). If a Kruskal–Wallis test was significant, we used post hoc Mann–Whitney U tests to make pairwise comparisons between treatments. More animals were used in the control group as they were "tested" only once in the experimental protocol (see the "Experimental protocol" section) and, therefore, mean values could not be calculated as per the trained group. Therefore, to minimize the effect of any potential outlier, we used more animals in the control group. We also conducted some within-subjects analyses; for example, comparing the control group's behavioral responses before and after the presentation of the predator model, with such comparisons done using Wilcoxon matched pairs tests.

Results

The behaviors, swimming to the bottom and swimming to the surface, were excluded from statistical analyses as their mean and median values were close to zero (Table 2). The mean percentage occurrence of expressing each behavioral activity by the bullfrogs in the different treatments is shown in Table 2 and the behavioral expression across training sessions is shown in Fig. 2a–c. The control group showed no significant changes when comparing their behavioral responses before and after the presentation of the predator model ($P>0.05$ in all cases).

Kruskal–Wallis analyses of the behaviors by the three treatments showed only two behaviors, inactive on the surface ($H=7.82$, $df=2$, $P<0.05$) and inactive on the bottom ($H=9.82$, $df=2$, $P<0.01$), as being significantly affected by the treatments. Mann–Whitney U tests comparing the first/second training sessions (1–2) with the combined third/fourth training sessions (3–4) showed that the behavior, inactive on the surface, significantly decreased in the third/fourth training sessions (Tables 2 and 3), whereas the behavior, inactive on the bottom, significantly increased (Tables 2 and 3). The Mann–Whitney U tests comparing the combined third/fourth training sessions (3–4) with the control group (C) showed that the behavior, inactive on the surface, was significantly more expressed by the control group (Tables 2 and 3), whereas the behavior, inactive on the bottom, was significantly less expressed by the control group (Tables 2 and 3).

After the fourth training session, the response of the bullfrogs to training sessions became highly variable (Fig. 2a–c). However, for the behavior, inactive on the

Table 2 Means (in percent), medians (in percent), and standard error of the mean (SEM) of behavioral occurrence during the first/second (1–2) training sessions, the third/fourth (3–4) training sessions, and for the control group (C) (N=6 in the cases of the trained groups; N= 12 in the case of the control group (C))

Behavior	Treatment	Mean	Median	SEM
Inactive on the surface (IS)	(1–2)	76.25	77.50	4.56
Inactive on the surface (IS)	(3–4)	27.80	42.50	11.40
Inactive on the surface (IS)	(C)	71.54	80.49	8.54
Inactive on the bottom (IB)	(1–2)	5.50	2.50	2.64
Inactive on the bottom (IB)	(3–4)	69.30	51.20	13.40
Inactive on the bottom (IB)	(C)	13.41	3.66	7.79
Swimming on the surface (SS)	(1–2)	15.50	13.75	7.89
Swimming on the surface (SS)	(3–4)	3.00	0.00	4.20
Swimming on the surface (SS)	(C)	11.79	4.88	19.31
Swimming on the bottom (SB)	(1–2)	1.25	1.25	0.88
Swimming on the bottom (SB)	(3–4)	1.00	1.25	1.05
Swimming on the bottom (SB)	(C)	2.64	2.44	2.20
Swimming to the surface (STS)	(1–2)	1.50	1.25	0.46
Swimming to the surface (STS)	(3–4)	0.25	0.00	0.25
Swimming to the surface (STS)	(C)	0.20	0.00	0.20
Swimming to the bottom (STB)	(1–2)	2.50	2.50	1.05
Swimming to the bottom (STB)	(3–4)	1.25	0.00	0.79
Swimming to the bottom (STB)	(C)	0.40	0.00	0.40

(1–2) behavior expressed during the first/second training sessions, *(3–4)* behavior expressed during the third/fourth training sessions, *(C)* behavior expressed by the control group

surface, none of the values after the second training session were as high as the values recorded in the first two training sessions (Fig. 2a). For the behavior, inactive on the bottom, none of the values after the second training session were as low as in the first two training sessions (Fig. 2a). The remaining four behaviors showed much greater variability in response in relation to the first two training periods (Fig. 2b, c).

From the 15th training session onwards, we observed bullfrogs digging on the bottom of the tank and covering themselves with mud after they had seen the model avian predator. By the last training session, all frogs were expressing this behavior.

Discussion

The antipredator training used with North American bullfrogs in this experiment proved to be effective in modifying the animals' behavioral responses to be more appropriate when confronted with an avian predator. The lack of behavioral response of the control group to the model predator showed that our study animals did not spontaneously express antipredator behavior. The trained bullfrogs responded appropriately because they avoided the tank surface when the antipredator model was shown (which had been associated with an aversive stimulus). This fact could be proved through the significant increase of the behavior, inactive on the bottom, and the significant decrease in the behavior, inactive on the surface. Furthermore, during the course of

the antipredator training sessions, all frogs started to camouflage themselves on the bottom of the tank.

The major changes in bullfrog behavior induced by antipredator training were apparent by the third/fourth training sessions. Showing that bullfrogs quickly learned the antipredator response, which is not surprising given the importance of this response to their survival. Studies with other species have also shown that the development of antipredator responses during training can develop in only a few training sessions (Chivers and Smith 1994; Maloney and McLean 1995; McLean et al. 1999; Griffin et al. 2000; Azevedo and Young 2006a; Mesquita and Young 2007). These data also confirm that, despite more than 20 generations without predator contact, it was possible to reestablish antipredator behavior in our population of bullfrogs. A similar result was also observed for a Nile tilapia (*Oreochromis niloticus*) population, which had been bred in captivity for 30–40 generations (Mesquita and Young 2007). These two studies, therefore, show that, even in explosive breeding species with short reproductive cycles, antipredator behavior is not quickly lost and may be reactivated by training procedures.

Most attempts to condition (train) animals to recognize predators in controlled conditions show that learning occurs after only one to three exposures to the paired stimuli, which is what we observed in the present study (Chivers and Smith 1994; Maloney and McLean 1995; McLean et al. 1999; Griffin et al. 2000; Azevedo and Young 2006a). It has been shown that repeated exposure to predator models may result in habituation (Magurran 1990). In the present experiment,

Fig. 2 Mean percentage of occurrence (±SEM) for behaviors expressed by antipredator trained American bullfrogs after successive training sessions with a model avian predator: **a** *IS* inactive on the surface, *IB* inactive on the bottom; **b** *SS* swimming on the surface, *SB* swimming on the bottom; **c** *STS* swimming to the surface, *STB* swimming to the bottom
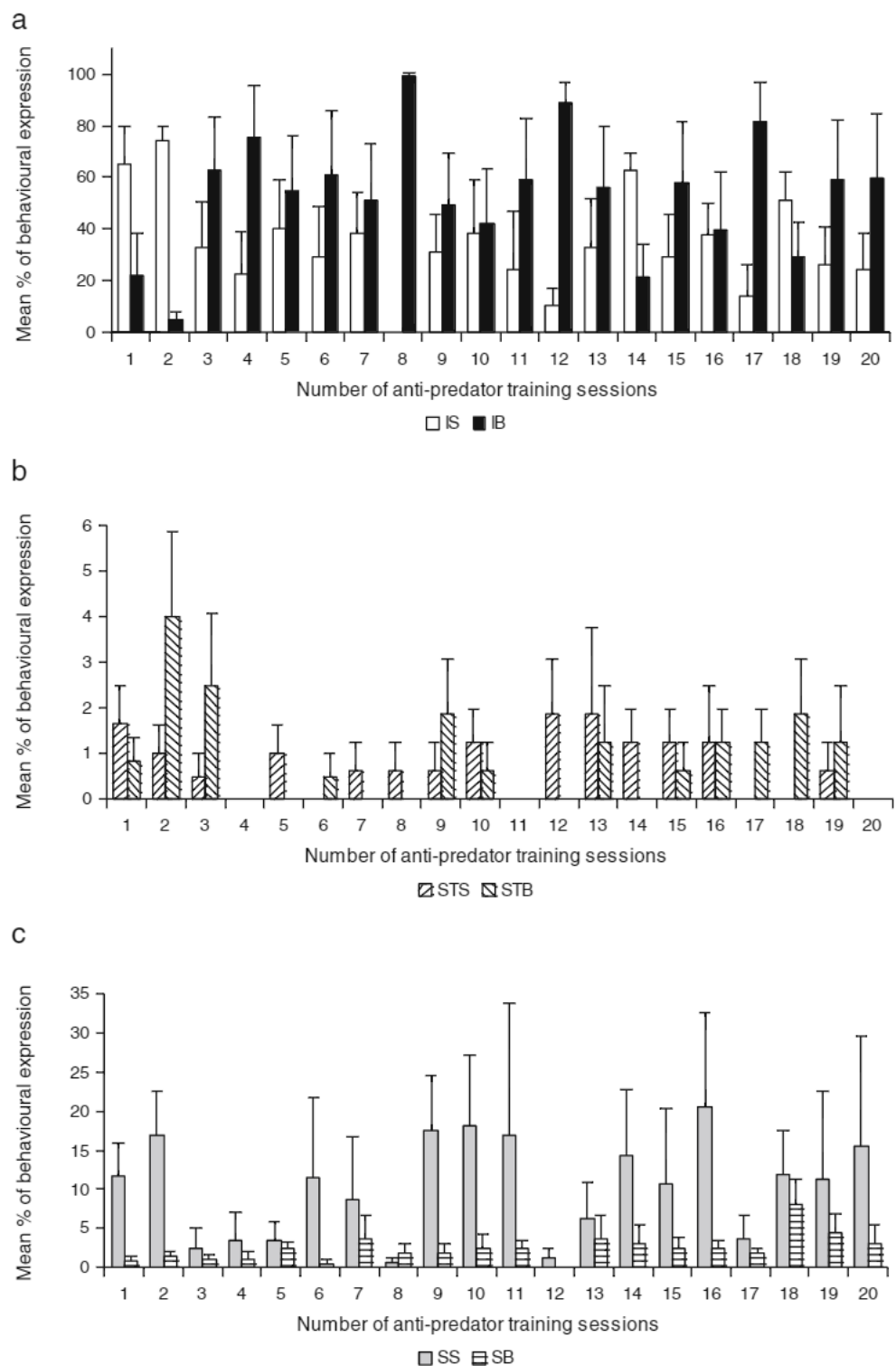
we did not observe a habituation response, but that, after five or six training sessions, behavioral responses to the model predator oscillated greatly between successive sessions (Fig. 2a–c). Thus, suggesting two important considerations: (1) that the optimal number of training sessions for the present species was three or four and (2) fear of the predator persisted beyond this optimal number, but that it

varied with some, as of yet, unidentified factor(s) of the training sessions.

This study along with others (Azevedo and Young 2006a; Mesquita and Young 2007) support the suggestion of Griffin et al. (2000) that the use of model predators as a conditioned stimulus and induction of fear as an unconditioned stimulus are adequate methods for antipredator training. Predator

Table 3 Mann–Whitney U test results comparing the behaviors expressed during the first/second training sessions with the third/fourth training sessions; the first/second training sessions with the control group; and the third/fourth training sessions with the control group ($N=6$ in the cases of the trained groups; $N=12$ in the case of the control group (C))

Behavior	Comparison	W	P
IS	(1–2)×(3–4)	151.0	<0.05
IS	(1–2)×(C)	113.0	>0.05
IS	(3–4)×(C)	75.5	<0.01
IB	(1–2)×(3–4)	89.0	<0.05
IB	(1–2)×(C)	111.5	>0.05
IB	(3–4)×(C)	148.5	<0.05

(1–2) behavior expressed during the first/second training sessions, *(3–4)* behavior expressed during the third/fourth training sessions, *(C)* behavior expressed by the control group, *IS* inactive on the surface of the water, *IB* inactive on the bottom of the tank

models are most appropriate for this kind of study because, when you are using a model predator, there is no possibility of attack; you have more control over eliciting stimuli (e.g., visual); fewer ethical concerns; and fewer logistical problems (Griffin et al. 2000).

In other research concerning antipredator training, it was observed that trained animals avoided the region where the predator model was exhibited, probably as a mechanism to increase their distance from the predator (Azevedo and Young 2006a; Vilhunen 2006; Mesquita and Young 2007). We observed this type of response in that our bullfrogs always responded, from the second training session onwards, by swimming to the bottom of the tank and then keeping still. So, what we observed was an initial escape response (swimming to the bottom), followed by a hiding response. Obviously, the physical characteristics of the tank could have affected the bullfrogs' responses—it may be in a wider tank that the bullfrogs would have swam to the bottom and then swam off in the opposite direction to where the model predator was shown.

The lack of significant effects on the behaviors, swimming on the surface or swimming on the bottom, was probably due to the low percentage of time that these behaviors were expressed. This was expected, as swimming behavior may, in nature, call the attention of predators. The behaviors, swimming to the bottom and swimming to the surface, occurred so quickly (over approximately 2 s) that (a) our behavior sampling interval did not permit us to register them and (b) even with their short duration, these behaviors were rare.

We suggest, for future antipredator training of aquatic amphibians, the inclusion of shelters. According to Brown (2003), the habitat that each population occupies plays a strong role in the development of predator avoidance. The

amphibians we trained are primarily aquatic; for this reason, we suggest that other experimental protocols should be developed for amphibians with different lifestyles, for example, for arboreal amphibians or terrestrial amphibians. Future research could also investigate how long amphibians remember their antipredator training for (see Azevedo and Young 2006b; Mesquita and Young 2007) and what effect personality has on its acquisition (Bremner-Harrison et al. 2004; Azevedo and Young 2006c).

The real test of this antipredator training technique lies in the comparison of the survival rates of trained and non-trained amphibians. Shier and Owings (2006) showed that this type of antipredator training had long-lasting effects that promoted survival among released juvenile black-tailed prairie dogs; this finding, taken together with our study and others (e.g., Azevedo and Young 2006a; Mesquita and Young 2007), shows that the principles of antipredator training are, may well be, universal across vertebrate species and that this should convert into survival benefits.

Conclusion

In conclusion, the antipredator training technique used in this study was simple, cheap, and quick to apply. The positive result of this study supports the findings of research with other vertebrates that antipredator training using classical conditioning techniques can develop an adequate response in animals, which may have survival benefits upon release to the wild.

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