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Fear in the Captive-Bred Attwater's Prairie Chicken as an Indicator of Postrelease Survival

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Releasing captive-bred Attwater's prairie chickens (APC) into an endangered wild population has successfully maintained but has not increased a small extant population. The limited success of the captive-release APC program has been largely attributed to heavy predation on the newly released birds. The poor survival rate of released birds suggests that breeding and rearing in captivity may have a detrimental effect on the expression of predator avoidance behaviors. In Experiment 1, 1- 2 week-old chicks were assessed for fear responses. Tendency to hide, as measured by the hole-in-the-wall test, correlated with postrelease survival. In Experiment 2, fear responses, including those identified as important to survival in Experiment 1, were stronger in chicks reared in a seminatural environment relative to chicks reared in an artificial environment. Implications for conservation of this endangered species are discussed.

Releasing captive-bred animals into endangered populations has shown some promise as a conservation tool over the past few decades (Beck et al., 1994). Ideally, the released animals will quickly adapt to life in the wild and eventually reproduce to increase the size and stability of the struggling population. The Attwater's prairie chicken (*Tympanuchus cupido attwateri*) is an endangered species that breeds readily in captivity so fortifying the small wild population with captive-bred animals is feasible. However, efforts to increase the free-ranging population in this manner have been largely unsuccessful. Since 1995, nearly 100 captive-bred Attwater's prairie chickens (APC) have been released each year into the small wild population on a protected refuge. Despite the large annual addition of released birds, the wild population has hovered around 45 individuals since 1996. The reintroduction program can be considered a success in one sense since, without this intervention, the wild population would almost surely be extinct today. But the program has failed to achieve its goal of increasing the extant wild population to 5,000 individuals.

The limited success of the APC reintroduction program, like many others (e.g.. Kleinman, 1989; Miller et al., 1990) is likely due to the fact that most of the released birds are not well-suited for life in the wild. Heavy predation on newly released animals is problematic in reintroduction programs (e.g., Beck et al., 1991, Short et al., 1992; Gibson, et al., 1994; Miller, et al., 1994) and has proven to be the biggest problem for reintroduced APC. Predator avoidance behaviors can be

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under-expressed in captive-bred animals (Shepherdson, 1994; Berger, 1998; Coss, 1999) making them easy targets for predators. Unlike their wild counterparts, captive-bred populations do not have the benefit of selective pressures creating a reproductive advantage for those individuals that are best able to survive in the wild. Animals that experience the least amount of stress in the captive environment are typically successful breeders whereas wary individuals are less likely to reproduce (Jones, 1997). This situation can create a population that will thrive in captivity but is not necessarily equipped for life in the wild. Despite this handicap, however, the natural variation within any population creates some individuals that may be better suited for the wild than others. Identifying and releasing individuals with the greatest potential for survival in the wild could greatly improve the success rate of reintroduction. This requires first determining which behaviors are important for survival. For the purpose of predator avoidance, fear undoubtedly plays an important role. Therefore, assessing innate fear levels prior to release may provide some indication of an individual's potential for survival.

Many behaviors, including fear responses, have a learned component (Klopfer, 1957; Knight, 1984; Conover, 1987; Thornhill; 1989) in addition to an innate component (Curio, 1975; Mueller & Parker, 1980; Hobson et al., 1988; Reichert & Hedrick, 1990). Teaching captive bred-animals to recognize and react to predators has been a common answer to the predation problem in reintroduction programs (e.g., Dill, 1974; Ellis, Dobrott, & Goddwin, 1977; Curio, 1988; Mineka & Cook, 1988; Magurran, 1989; Chivers & Smith, 1994; McLean, Lundie-Jenkins, & Jarman, 1994; Maloney & McLean, 1995; McLean et al., 2000). Some of these efforts have been successful at developing new fear responses or enhancing existing responses. However, the effectiveness of the acquired antipredator response in prolonging life in the wild has not been evaluated in most programs. Therefore, it remains to be seen whether this is a viable solution to the predation problem.

An alternative approach to teaching specific behaviors in response to specific predators is to increase the natural expression of antipredator behavior by enhancing the quality of the rearing environment. Rearing captive animals in a complex environment that shares many commonalities with their wild destination can facilitate the development of important life skills (Bronikowski, Beck, & Power, 1989) and better prepare captive animals for life in the wild. Miller et al., (1994), for example, found that Siberian ferrets reared in a seminatural environment had postrelease survival rates longer than ferrets reared in conventional breeding cages. One possible advantage of an enriched environment is increased behavioral flexibility and learning capacity (Renner, 1987), qualities that are highly adaptive for life in a dynamic environment such as the wild. A second possible advantage of enriched rearing is that it may facilitate the development and subsequent practice of specific antipredator behaviors, such as hiding, before the animal is placed in the wild where the opportunity to learn is limited by the fatality of errors. A final advantage comes from providing an opportunity to learn over a long period of time. Many animals need to learn specific skills at certain sensitive periods during their development (Bateson, 1979). Failure to identify these periods and provide the appropriate environmental stimuli may severely affect postrelease survivorship. Rearing in a seminatural environment may provide the substrates for learning antipredator behaviors throughout development thereby decreasing the chances of missing a sensitive period for learning. Furthermore, animals reared in an enriched captive environment may show a greater range of behaviors and more refined behaviors. This could include improved expression of behaviors that are consistent with predator avoidance when placed in a novel or stressful situation.

The objective of the present investigation was to determine whether the innate fear response of two-week old APC chicks could indicate potential for survival in the wild (Experiment 1) and whether the fear responses identified in Experiment 1 could be enhanced by rearing chicks in an enriched, seminatural environment (Experiment 2). The present experiments were conducted within the context of an endangered species captive breeding program. Neither investigations of behavior nor systematic evaluation of rearing protocol is a priority for the APC breeding program. Thus, sample sizes in the present experiments were limited by availability and selection of birds to be released into the wild was based on criterion other than involvement in the study. Other minor interferences related to husbandry practices are described at the appropriate point below. Despite these difficulties, however, the information gained about the effects of rearing protocol on the fear behavior and eventual survival of endangered APC is the first of its kind and could prove to be instrumental to the survival of the species.

Experiment 1

Prerelease training of survival skills has become increasingly common as a method to enhance antipredator behaviors of captive-bred animals (for review, Griffin, Blumstein, & Evans, 2000). A predator avoidance training procedure typically involves a classical conditioning paradigm: Repeatedly pairing a live or model predator with some aversive event (e.g., pursuit by the predator, McLean et al., 2000; capture by humans, Griffin, 2003; squirt of water, McLean, Lundie-Jenkins, & Jarmin, 1994). APCs are subject to predation by several different species of birds and mammals. With so many potential predators, it can be difficult for researchers to determine which antipredator behaviors need to be enhanced in a specific predation situation since appropriate avoidance responses are highly context specific (Montgomerie & Weatherhead, 1988; Cresswell, 1993). For instance, whether an APC should hide or flee probably depends on the type of predator (aerial or terrestrial), species of predator, proximity of predator, and whether the bird has been detected or not. Enhancing a tendency to flee through classical conditioning could be beneficial in some situations but prove to be a fatal mistake in other predation situations. Although the suitability of each variation of antipredator behavior depends on the situation, each potential response is the product of a common motivational state-fear.

The open field has become a standard instrument for measuring fear in animals. However, the behavior in an open field has been interpreted as representing not only level of fear, but also arousal, attention, and exploration, either separately or in combination (Ginsburg, Braud, & Taylor, 1974; Jones, Mills, & Faure, 1991; Gallup & Suarez, 1980; Jones, 1987a). Each of these behavioral constructs likely plays some role in predator avoidance and thus should provide some indication of how the bird will react, and therefore survive, in the wild. Another test, the hole-in-the-wall (HITW) test, has been used to measure fear as well (Mills & Faure, 1986). Unlike the open field test, the HITW test provides a measure of the tendency to hide, a behavior that can greatly reduce detection by predators.

In Experiment 1, several fear behaviors were measured in 1-2 week-old captive-bred APC chicks. The birds were later released onto a protected refuge when they were 4-12 months-old and were tracked via radiotelemetry. Postrelease survival was correlated with each fear behavior to determine whether the fear measures could be used to indicate which birds had the best potential for survival.

Method

Subjects. Twenty-six (17 males, 9 females) APCs bred at Fossil Rim Wildlife Center served as subjects. The subjects hatched from eggs that were collected from breeding pairs and incubated in electric incubators. Shortly after hatching, the chicks were moved to heated brooder units (122 cm wide x 56 cm deep x 61 cm high) inside a climate-controlled building (room temperature = 22° C). Subjects were housed in groups of 8-10 chicks. A salad mixture (lettuce, kale, spinach, peas, green beans, and carrots) and water available at all times. Mealworms were placed in the brooder units 2-3 times daily. Chicks were handled by caretakers 1-2 times daily in order to clean the brooder. In addition to the frequent handling, caretakers were typically visible to the chicks at least 8 h daily. The house lights were set on a 16:8 h photoperiod cycle. All chicks hatched between April and June of 2001 and were tested between 8 and 15 days of age. Four subjects were dropped from the experiment due to equipment failure (see below).

Apparatus. The open field apparatus consisted of a large box (90 cm wide x 60 cm deep x 42 cm high). Three of the walls were constructed of plywood painted white. The front wall consisted of black plastic mesh (1.27 cm^2 gauge) over a wooden frame to allow visual access into the chamber for video recording purposes. The top of the box was also covered by black mesh. The apparatus floor was lined with white butcher paper that was changed before each trial. Brightly colored string on top of the white butcher paper created a grid that divided the apparatus floor into 9 equal sections.

The hole-in-the-wall (HITW) box (25 cm^3) was constructed of plywood. The top of the box was hinged and served as service door. A guillotine-style door was located on one wall and could be opened using a pull string. Straw was placed in the bottom of the box. During hole-in-the-wall test, the HITW box was placed inside the open field apparatus, flush with and centered on one side wall. A video camera on a tripod was located 1 m directly in front of the Open Field apparatus during all open field and all hole-in-the-wall tests.

Procedure. The open field test involved placing a single chick in the open field apparatus for 5 min. Each chick was tested once and every test was video recorded. Measures of amount of time spent freezing (stereotypical crouch with no movement), latency to ambulate (first step), mobility (number of zones entered), and vocalizations were made from video recordings. Call types were difficult to distinguish by ear so all vocal activity was recorded as a general category of behavior. Vocalization data was collected for only 15 of the 22 subjects due to the installation of an air conditioning unit in the test room that masked subjects' vocalizations on the last 7 tests.

At the beginning of each hole-in-the-wall test, an individual chick was placed inside the HITW box and the lid was closed. After 1 min, the guillotine door joining the enclosure to the open field was raised and the experimenter stood out of view for 5 min. Each chick was tested only once. Every chick was video recorded during the test and its behavior was later scored for latency to leave the HITW box (when the head first emerges) and the amount of time spent outside of the HITW box.

Around 6 weeks of age, subjects were moved from indoor heated brooders to outdoor flights where they were housed in groups of 2-6 individuals. The subjects remained in outdoor group housing until they were selected for release. In order to maximize genetic variability within the APC population, the directors of the APC Release Program selected birds for release into the wild based on their genetic makeup. Nine subjects were selected for release during the Fall 2001. The remaining 17 subjects were released in the Spring 2002. Upon selection for release, the subjects were transported to the Attwater's Prairie Chicken National Wildlife Refuge, a 3,240-ha area of protected prairie and marsh habitat. Each subject was outfitted with a small, light-weight radio transmitter with a mortality sensor. Subjects were then housed in outdoor pens on the refuge during a 2-3 week acclimation period prior to release. Following release, each subject was radio-tracked several times weekly and its location noted until the mortality sensor of the individual was activated. At this time, the location of the bird was identified, death of the individual was confirmed, and the radio collar was retrieved.

Survival was defined as the number of days the bird was observed prior to activation of the mortality sensor. Four subjects were dropped from the experiment due to equipment failure during the tracking phase, leaving a total of 22 subjects.

Results and Discussion

As of January 2003, only 4 of the subjects were still alive (*Mean* days survived = 111.80; *SD* = 119.00). Initial statistical examination of the data with an independent t-test revealed a significant difference between release periods in latency to vocalize. The group released in Fall 2001 showed significantly longer latencies to vocalization in the open field test than did the Spring 2002 release group, $t(12) = 2.26$. No other measure differed significantly between release groups (see Table 1). Subjects from both release periods were pooled for further analysis.

The relationship between each fear behavior and survival in the wild was analyzed with Pearson's product moment correlation coeffecient.

Table 1

BEHAVIOR	Released Fall 01 (N = 9) Mean (SE)	Released Spring 02 (N = 13) Mean (SE)	(df) t value	p	Correlated with Postrelease Survival (df) r	p
Latency to Vocalize	66.52 (14.48)	20.08 (12.41)	(13) 2.26	< 0.05	(13) 0.19	> 0.05
Frequency of Vocalizations	54.89 (13.73)	87.17 (11.95)	(13) 1.65	> 0.05	(13) -0.38	> 0.05
Freezing	0 (0)	0 (0)	-	-	-	-
Latency to Ambulate	13.43 (11.84)	18.24 (9.62)	(20) 0.32	> 0.05	(20) -0.17	> 0.05
Mobility	17.56 (6.15)	19.77 (4.33)	(20) 0.30	> 0.05	(20) -0.09	> 0.05
Latency to Emerge from HitW Box	165.61 (43.78)	101.57 (32.85)	(20) 1.18	> 0.05	(20) 0.47	< 0.05
Time Out of HitW Box	132.53 (42.87)	178.75 (34.75)	(20) 0.83	> 0.05	(20) 0.52	< 0.01
Postrelease Surivival	127.06 (52.98)	101.23 (24.25)	(20) 0.49	> 0.05		

Open Field Test. None of the subjects were observed to freeze during the 5-min open field test so analysis was not possible on this dependent variable. There was no relationship between vocal activity and survival (see Table 1). Neither latency to vocalize after placement in the open field nor frequency of vocalization during the open field test were reliably correlated with postrelease survival. Latency to ambulate and overall mobility also failed to show significant relatedness to survival in the wild (see Table 1).

Hole-in-the-Wall Test. Analysis of the hole-in-the-wall data revealed a significant positive correlation between latency to emerge from the HITW box and survival in the wild, *r*(20) = 0.47. Time spent out of the HITW Box was also significantly correlated with postrelease survival, *r*(20) = -0.52. Chicks that were slower to leave the HITW box and spent less time in the open field tended to survive in the wild longer than chicks that showed shorter latencies to emerge from the HITW box and spent more time in the open field.

The results of Experiment 1 confirmed that fear responses present in chicks as young as two weeks old can be indicative of survival in the wild. Behavior observed during the hole-in-the-wall test was strongly related to postrelease survival. Longer latencies to emerge from the box and less time spent in the open field correlated with longer survival in the wild. This behavior may be a measure of the bird's tendency to hide, which is likely to be a good means of avoiding detection by predators.

The poor predictive value of the measures taken during the open field test was a surprising finding. Other researchers have shown that several open field responses (e.g., latency to vocalize, frequency of vocalizations, latency to ambulate, and overall locomotion) were good indicators of fear level in domestic chicks and Japanese quail (Faure, Jones, & Bessei, 1983; Jones, 1987b). Freezing, reduced vocal activity, and reduced mobility should be effective antipredator behaviors but were not related to survival in this study. None of the subjects were observed to freeze in the open field apparatus. It may be necessary to expose subjects to fear eliciting stimulus, such as the presence of a potential predator, to get a good measure of freezing. The poor predictive value of vocal activity may be due to the fact that fewer subjects were analyzed for these dependent variables (15 subjects for latency to and frequency of vocalizations versus 22 subjects for all other dependent variables). Seven subjects were not measured for vocal activity because of the installation of an air conditioning unit in the test room that masked vocalizations during testing. The air conditioning system was similar to one located in the housing area so it is unlikely that it had a significant effect on behavior during testing. More subjects need to be tested and released to convincingly rule out open field fear measures as predictors of postrelease survival.

Experiment 2

Most APCs are selected for release in the wild based on their genetic relatedness to other APCs. Every effort is made to maximize the genetic diversity in the wild population. Some candidates that are genetically ideal for release will not have the benefit of high innate fear levels and hence will be at higher risk for predation. Ideally, the fearful behaviors of these birds could be enhanced through experience prior to release so that they will not be handicapped in the wild. When reared in standard brooders, APC chicks are not provided with the substrates necessary to practice predator avoidance behaviors (e.g., hiding places), do not have the opportunity to learn behaviors from parents or model birds, and do not have experience with predation situations. Research with domestic chickens indicates these factors may be important in the development of antipredator behaviors (Palleroni, 2001). It is hypothesized that enriching the captive environment by rearing chicks with a foster hen in an outdoor pen with several hiding spots and an occasional predator soaring overhead may enhance fear behaviors relative to brooder-reared chicks.

Methods

Subjects. Fourteen captive-bred APCs served as subjects. Half of the subjects comprised a small group of chicks that were reared under a nonstandard, seminatural protocol (Seminaturally Reared, SNR). Two clutches of fertile eggs were taken from APC hens prior to onset of incubation and placed under two broody domestic hens. The domestic hens carried out incubation of the eggs till the time of hatching then brooded the APC chicks in a large outdoor pen (5.5 m x 7.4 m) that had several small enclosures (2 nest boxes, 1 enclosure with mesh walls and top, 2 enclosures with mesh walls and solid top, 1 plastic barrel cut in half lengthwise, and 1 plastic lean-to). SNR chicks were provided with salad and water at all times plus mealworms twice daily. The SNR chicks were not handled by caretakers until they were moved to the indoor facility at the time they were becoming independent from the hen (8-10 days of age). At that time, the SNR chicks were placed in a heated brooder with feeding, handling, and light conditions identical to that described above. SNR chicks were tested after at least 24-h habituation to the indoor environment.

Seven additional subjects were selected from the APC chicks were reared under the standard, artificial protocol (Artificially Reared, AR) described for Experiment 1. These subjects were matched with the SNR subjects for hatch date and age at testing. All of the subjects hatched between May 9 and May 16, 2001, and were tested between 8 and 11 days of age.

Apparatus. The open field apparatus and hole-in-the-wall box that were used in Experiment 1 were also used in Experiment 2. A hawk silhouette (27.9 cm beak to tail; 74.9 cm wingspan) was constructed of black foam board and modeled after a Northern Harrier (*Circus cyaneus*), a common predator of APC. The silhouette was located 110 cm above the floor of the open field apparatus and was operated via a pulley system. The silhouette track was 4.5 m long with the open field apparatus located directly under the center point. A curtain of shredded cloth strips concealed the silhouette when in the starting position and end position. Duration of “flight” from the start to the end position was approximately 10 s.

Procedure. An open field trial began when a chick was gently placed in the center of the open field apparatus. After 5 min in the open field, the flyover test took place. While the subject was still in the open field apparatus, the hawk silhouette was flown over the top of the open field apparatus by the experimenter pulling on a rope attached to the pulley system. The chick remained in the open field for 2 min after the silhouette reached the end position. Each chick was tested once. All trials were recorded by a video camera on a tripod located 1 m directly in front of the open field apparatus. Data were obtained from videotapes at a later time. The effects of the flyover test were evaluated by comparing behavior during a 2-min period prior to the presentation of the hawk (min 2-4 of the open field test) with the two min period following the hawk. The amount of time spent freezing (stereotypical crouch with no movement), vocalizations, latency to ambulate (first step), and mobility (number of zones entered) were measured.

The hole-in-the-wall test was conducted in a manner identical to that described in Experiment 1. The HITW box was located inside the open field apparatus, flush and centered on one side wall. A single chick was place in the HITW box and allowed 1 min to acclimate before the experimenter raised the guillotine-style door. The chick was then free to move between the HITW box and the open field environment for 5 min. All tests were video recorded and later scored for each chick’s latency to emerge from the HITW box and the amount of time spent outside of the HITW box during the 5-min test period.

Results and Discussion

Open Field Test. Fear behaviors measured during the 5-min open field test were analyzed using independent *t*-tests. Analysis revealed that rearing environment had a significant effect on vocal activity in APC chicks. AR chicks vocalized sooner, $t(12) = 2.55$, and more often, $t(12) = 3.63$, than did SNR chicks. In contrast, latency to ambulate and overall mobility were similar in both groups, *t*s(12) = 1.03 and 1.66, respectively.

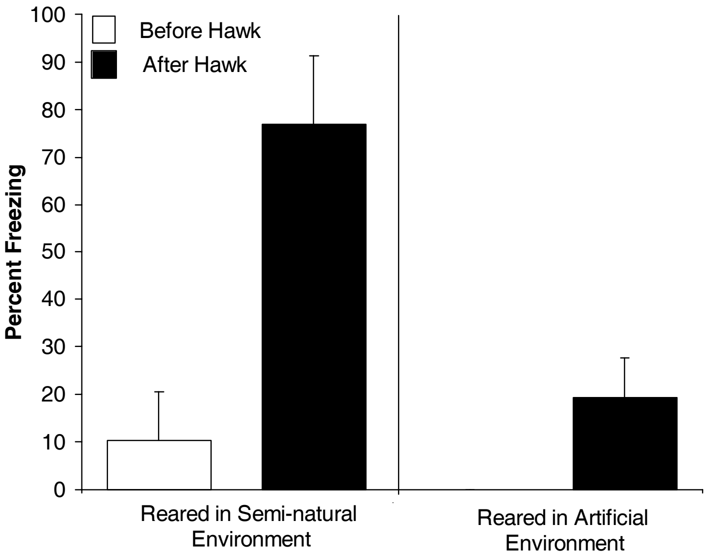

Figure 1. Mean percent of trial spent freezing (+*SE*) before and after presentation of hawk silhouette (left panel) during fly-over tests for chicks reared in a seminatural environment (*n* = 7) and chicks reared in an artificial environment (*n* = 7).

Flyover Test. Flyover data was analyzed with a mixed-model analysis of variance with Rearing Environment (seminatural vs. artificial) as a between group variable and Test Phase (before hawk vs. after hawk) as a within group variable. Freezing data was converted into percentage time spent freezing during a 2 min period prior to the hawk presentation and 2 min after the hawk presentation. Both groups spent more time freezing after the hawk was presented than before, (main effect of Test Phase, *F*(1, 12) = 23.89) but Group SNR showed a substantially stronger response following the hawk than did Group AR (Figure 1). This was confirmed by a significant Test Phase x Rearing Environment interaction, *F*(1, 12) = 7.31.

Group SNR showed longer latencies to vocalize than Group AR (Figure 2, top panel). The main effect of Rearing Environment was significant, *F*(1, 12) = 16.19. Neither the main effect of Test Phase nor the Test Phase x Rearing Environment interaction were significant, *F*s < 1.35. Frequency of vocalization differed between groups as well (Figure 2, bottom panel). SNR vocalized less often than AR chicks, *F*(1, 12) = 18.74, but the appearance of the hawk decreased vocalizations in both groups, *F*(1, 12) = 15.03. The interaction of Test Phase and Rearing was not reliable, *F* < 1.

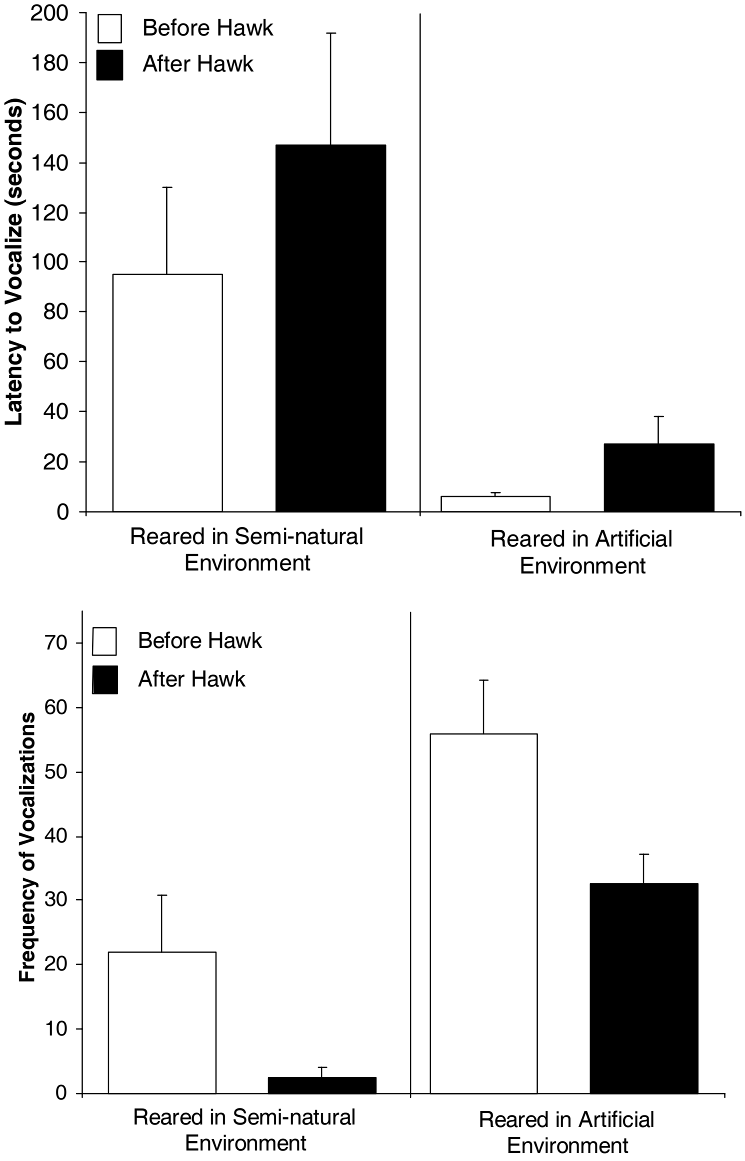

Figure 2. Mean latency to vocalize (top panel) and frequency of vocalizations (bottom panel) (+*SE*) before and after the presentation of the hawk silhouette during the fly-over test for chicks reared in a seminatural environment ($n = 7$) and chicks reared in an artificial environment ($n = 7$).

There was a tendency for both groups to show longer latencies to ambulate after the hawk than before, $F(1, 12) = 11.26$ (Figure 3, top panel). But this tendency did not vary as a function of Rearing Environment (main effect of Rearing Environment $F(1, 12) = 1.74$, Rearing Environment x Test Phase interaction $F < 1$). Overall mobility was similar for both groups and during both phases of the test, main effect of Rearing Environment $F(1, 12) = 1.85$; main effect of Test Phase and Rearing Environment x Test Phase interaction, *F*s < 1 (Figure 3, bottom panel).

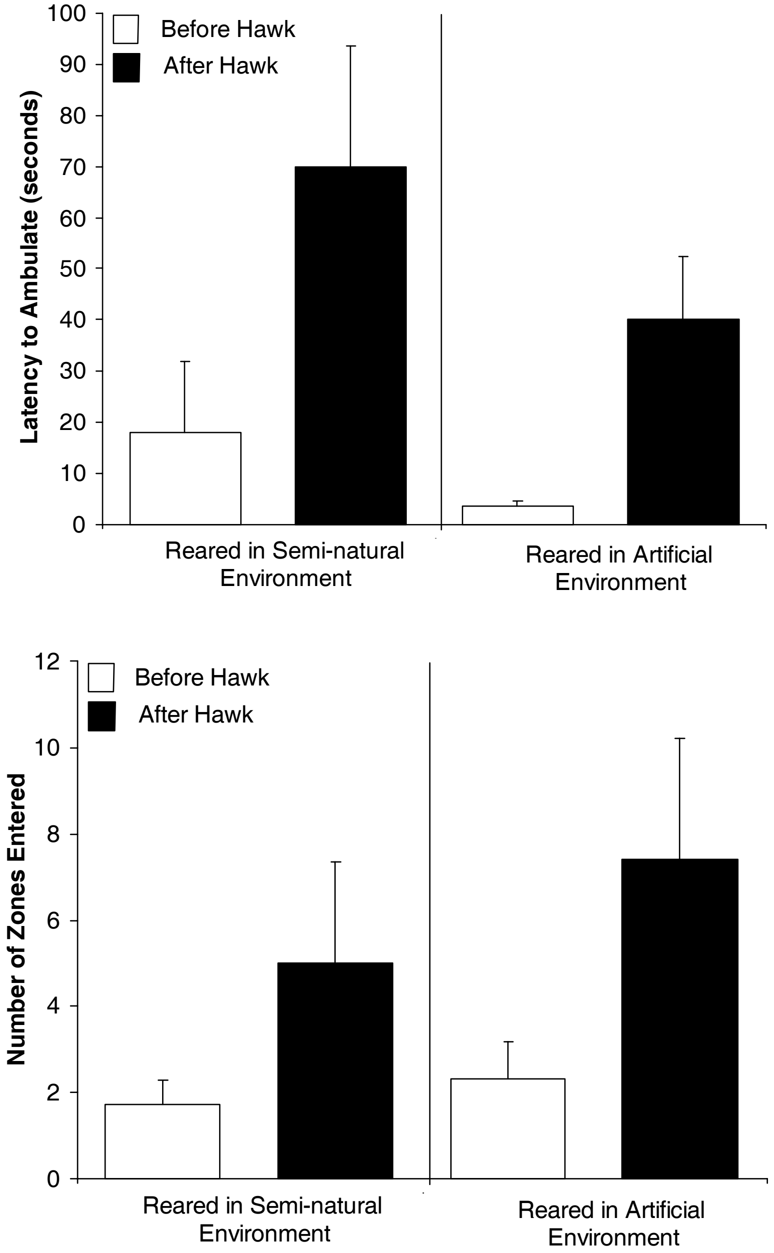

Figure 3. Mean latency to ambulate (top panel) and mobility (bottom panel) (+*SE*) before and after the presentation of the hawk silhouette during the fly-over tests for chicks reared in a seminatural environment (*n* = 7) and chicks reared in an artificial environment (*n* = 7).

Hole-in-the-Wall Test. Independent t-test revealed that SNR chicks were significantly slower to emerge from the HITW box than AR chicks, *t*(12) = 4.52 (Figure 4). Furthermore, SNR chicks spent less time outside of the HITW Box, in the open field, than AR chicks, *t*(12) = 3.73 (Figure 4).

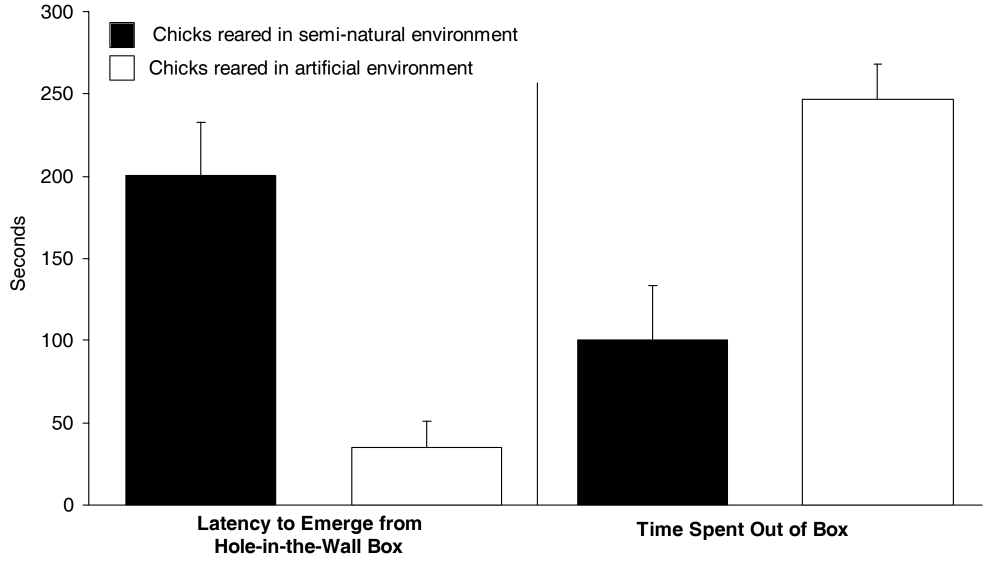

Figure 4. Mean latency to emerge from Hole-in-the-Wall box (left panel) and time spent outside of Hole-in-the-Wall box (right panel) (+*SE*) for chicks reared in a seminatural environment (n = 7) and chicks reared in an artificial environment (n = 7).

The results of Experiment 2 provide evidence that rearing under seminatural conditions enhanced several fear behaviors of 8-11 day-old chicks. APC chicks reared in the seminatural environment were slower to vocalize and vocalized less frequently in an open field and during the flyover test than chicks reared in an artificial environment. SNR chicks also reacted to a hawk silhouette passing overhead with more freezing than AR chicks. In the hole-in-the-wall test, SNR chicks were slower to emerge from an enclosure and spent less time in the open field.

These results cannot be explained by differential sensitivity to the presence of the experimenter. Both groups had repeated pairings of humans with food (positive reinforcement) and were occasionally handled by the caretakers (habituation). Both of these events are known to decrease fear of humans in domestic chicks (Jones, 1995a, 1995b). Unlike SNR, AR chicks had substantial visual exposure to caretakers as well (8+ h/day). While visual exposure is also known to reduce fear of humans (Jones, 1994), the effect of the experimenter's presence was minimized by the experimenter remaining visually concealed during the tests.

The subdued behavior and the tendency to hide seen in the SNR chicks is likely to reduce chances of detection by predators and may prolong postrelease survival. The results from Experiment 1 support this hypothesis. However, the effects of rearing protocol on survival in the wild can only be tested by documenting the postrelease survival of SNR birds. Unfortunately, only one SNR bird from Experiment 2 was selected for release onto the APC refuge. The remaining SNR birds were maintained in captivity for breeding purposes. The released SNR bird was observed for 7 days before the trackers lost contact with it. Loss of contact is likely due to either equipment failure (a dead battery on radio collar) or because the bird moved far out of the normal population range. As of January 2003, it was unknown whether or not the bird was still alive. Although the results of Experiment 2 are encouraging, they do not directly address the question of how early experiences affect survival in the wild. To fully test the effects of rearing environment on postrelease survival, it will be necessary to compare the postrelease survival of several SNR birds to AR birds. Future research will focus on this comparison.

General Discussion

As the number of endangered species continues to increase (IUCN, 2000), the need for effective conservation tools is growing dire. Breeding threatened and endangered species in the safety of captivity then releasing groups into the wild is one possible solution to this problem. However, past efforts to bolster failing populations with captive-bred individuals have only had moderate success, partly due to heavy predation on newly released animals. Individuals that are born and reared in captivity are not necessarily prepared for the unpredictable and dangerous environment in the wild. Postrelease survival may be increased by identifying which behaviors are important for survival then selectively releasing individuals that express these behaviors.

Experiment 1 suggests that an inherent tendency towards fearfulness provides a survival advantage in the wild. Specifically, hiding behavior (latency to emerge and time spent outside hole-in-the-wall box) was most closely linked with postrelease survival. Chicks that had a natural tendency to seek cover and avoid open spaces at 1-2 weeks of age showed the longest survival when released into the wild several months later. Fearfulness has a genetic basis (Mills & Faure, 1991; Mills et al., 1994) so selective breeding based on fear behavior characteristics could produce a captive population that is more suited for life in the wild. However, this approach could create management problems within the captive breeding program. Fearful birds are less likely to breed in captivity, are more difficult to handle, and are prone to injury and illness (for review see Jones, 2003). Alternatively, high fear birds produced by the natural variation within the population could be identified as young as 8 days of age and selected for release into the wild population.

Experiment 2 showed that fear responses, which are associated with antipredator behavior (suppressed vocal activity and mobility, increased hiding), can be augmented by rearing chicks in a seminatural environment. Chicks reared under seminatural conditions showed enhanced fear responses relative to chicks reared under highly artificial conditions (standard brooders). Most importantly, latency to emerge from the hole-in-the-wall box and amount of time spent inside of the hole-in-the-wall box, behaviors that were predicative of postrelease survival in Experiment 1, were both enhanced by the seminatural rearing protocol described in Experiment 2. These results suggest that augmenting fear behaviors through rearing in a seminatural environment may increase the postrelease survival in chicks that do not have inherently high fear. This method of creating high fear birds may be more feasible than selective breeding for fear from a management perspective since it would allow breeding program organizers to heighten the fear response of only the birds that have been selected for release based on other criterion such as genetic relatedness. Birds kept in captivity for breeding purpose could be reared under the artificial protocol (standard brooders) that frequently pairs humans with pleasant or innocuous events, hence reducing fear.

Before a seminatural rearing protocol is instated as a predator avoidance training program, further tests of the nature of the acquired antipredator responses seen in Experiment 2 are necessary. While rearing in a seminatural environment enhanced fear responses, it is unknown whether these acquired fear responses will translate into a survival advantage. The nature of the fear seen in the seminatural chicks of Experiment 2 may be inherently different than the fear observed in the high responders of Experiment 1. The tendency of birds in Experiment 1 to react fearfully reflects an inherent, unlearned quality of the individual. In contrast, the fear of seminatural chicks may be either inherent or may be learned from experience in the seminatural environment during the first week of life. It is possible that fear that is learned in the seminatural environment may be subsequently reduced through habituation and positive reinforcement associated with humans when the chick is moved from the outdoor enclosure into the artificial environment during week 2, as is the standard procedure. If the learned fear behaviors are retained until the time of release, it remains to be seen whether learned antipredator behaviors are as effective as innate responses. A full assessment of the efficacy of the seminatural rearing program as a means of increasing predator avoidance behavior in APC will requires releasing SNR birds into the wild and comparing their survival with the AR birds.

When considered together, the results of Experiment 1 and Experiment 2 suggest a 2-prong approach to the captive rearing of endangered APC destined for release in the wild. The first prong is to identify the individuals that are genetically predisposed to show strong fear responses with a 5-min hole-in-the-wall test. Chicks that show the strongest tendency to hide should be given priority as candidates for release. If these individuals do breed in the wild, they will pass this beneficial predisposition on to the next generation, thereby increasing the stability of the wild population. The second prong is enhancement of the antipredator behavior via rearing in a seminatural environment. Individuals that have been targeted for release based on their innate hiding tendencies could then be reared under a seminatural protocol designed to enhance antipredator behaviors until the time of release into the wild. By utilizing both aspects (innate and learned) of predator avoidance behavior this 2-prong strategy provides the most comprehensive approach to addressing the problem of behavioral deficits in captive-bred animals destined for release into the wild.

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