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Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs

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Abstract

Long-term maintenance of captive populations followed by release of captive animals into the wild is one of many approaches to endangered species conservation. To assess captivity's effects on behavior, a simulated predator was presented and response behaviors measured in oldfield mice, *Peromyscus polionotus subgriseus*. The animals tested were from four populations collected from Ocala National Forest, Florida, and held in captivity for varying numbers of generations: 35, 14, 2, and 0 (wild caught). Results show (1) that the more generations a population has been in captivity, the less likely an individual is to take cover after seeing a predator and (2) variance in predator-response behaviors increases with generations in captivity. These results point to two ways in which captivity can compromise animal behavior and, in turn, the success of reintroduction programs. First, because individuals from populations that have been in captivity for multiple generations seek refuge less often than their wild counterparts, they might experience increased mortality in the wild due to predation. Second, increased behavioral variance could translate into decreased survivorship upon reintroduction. Therefore, more individuals will need to be released to reach the targeted wild population size.

Keywords: *Peromyscus polionotus subgriseus*; Oldfield mouse; Predator avoidance; Wildlife conservation

1. Introduction

With rapid loss of species worldwide, long-term maintenance of captive populations has become a common approach to species conservation. Since Darwin, however, scientists have recognized that captivity can drastically alter animal behavior (Darwin, 1868; Price, 1984; Lickliter and Ness, 1990; Carlstead, 1996; Price, 1998). As a result of a predictable, often unchanging environment, captive individuals may lose the range of behaviors that enable response to a variable and unpredictable environment. Behavior, like morphology and physiology, evolves in complex environments to increase an individual's survival and reproductive success in its native habitat (Reed, 1985). Captivity, however, and the selective pressures associated with it are vastly different from the environment in which species have evolved (Hediger, 1964; Price, 1970, 1998; Frankham et al., 1986; Soulé et al., 1986; Soulé, 1986; Seidensticker and Forthman, 1998). Captivity can relax existing selective pressures, change the direction of selection, or impose completely novel pressures—either intentionally or inadvertently (Price, 1970, 1998; Endler, 1986).

As a result, changes in important life history and behavioral traits may occur. Individuals from an established captive population, therefore, are often at a disadvantage when reintroduced into their native habitat. Evaluation of reintroduction programs indicates that many deaths of reintroduced animals are due to behavioral deficiencies (Kleiman, 1989; Yalden, 1993; Miller et al., 1994; Biggins et al., 1999; Britt et al., 1999). For example, during the golden lion tamarin (*Leontopithecus rosalia*) reintroduction, some individuals were unable to survive because locomotor skills were deficient; they could not orient themselves spatially; and they were not able to recognize natural foods, non-avian predators, and dangerous non-predaceous animals (Kleiman et al., 1990).

Biologists working with the oldfield mouse, *Peromyscus polionotus*, are dealing with similar issues. There are 16 recognized subspecies of *P. polionotus* found throughout the southeastern United States (Hall, 1981),

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eight of which (known as beach mice) are found along the coasts of Alabama and Florida (Humphrey, 1992). These coastal areas have experienced rapid growth in commercial and residential development. Increased building has taken up primary habitat, and a growing human population has induced an increase in domestic cats. Due to shrinking habitat and increased predation pressures, five subspecies of beach mice are listed as endangered, one as threatened, and one is considered extinct (USFWS, 2001; Wooten, 2001). All beach mouse recovery plans list captive breeding and reintroduction as goals (USFWS, 1987, 1993, 2001; Holler et al., 1989).

Oldfield mice are found in early successional sand pine scrub with dry, sandy soils (Wolfe and Summerlin, 1989; Myers and Ewel, 1990). Primary predators include domestic and feral cats, owls, and snakes (USFWS, 1987, 1993; Holler et al., 1989; Wolfe and Summerlin, 1989; Rave and Holler, 1992). *Peromyscus polionotus* are strictly nocturnal (Humphrey, 1992) and, based on home range and genetic data, presumed to be monogamous (Foltz, 1981; Millar, 1989). Their burrows, which are deeper than other *Peromyscus* species, can be as long as 180 cm, and the nest chamber is generally about 90 cm below the soil surface (Wooten, 2001; personal observation). Burrows are often located at the base of vegetative cover and include an escape tunnel that rises from the nest chamber to just below the soil surface (Ivey, 1949; Dawson et al., 1988).

Given a history of behavioral deficiencies in released individuals and the recovery plans for various *P. polionotus* subspecies, I investigated how captivity affects predator response behaviors in *P. p. subgriseus*. Four populations of this subspecies have been collected from Ocala National Forest, Florida, over a 48-year period and maintained in similar environments. This provides a unique and ideal system for answering this question. Such consistency, and the comparisons it makes possible, is rare in captive populations.

I hypothesized that captivity could change behavior in two ways. First, captivity could change the direction of selection. If this were the case, I predicted a directional change in predator response behaviors. In other words, the means of various behavioral traits would shift, but variances would either remain unchanged or possibly even decrease (Fig. 1a; Endler, 1986). In this case, there should be a correlation between the magnitude of shift in the trait and generations in captivity. Second, captivity could relax selection. In this case, the means of behavioral traits would not necessarily change, but variance would increase with generations in captivity (Fig. 1b; Endler, 1986). In other words, behavioral traits within a population could have high variance and the individuals at either extreme of the distribution would not experience reduced survivorship or reduced reproductive success. To test these hypotheses, I exposed three captive and one wild-caught population of *P. p. subgriseus* to a simulated predator, then compared behavior and variance in responsiveness among the four populations.

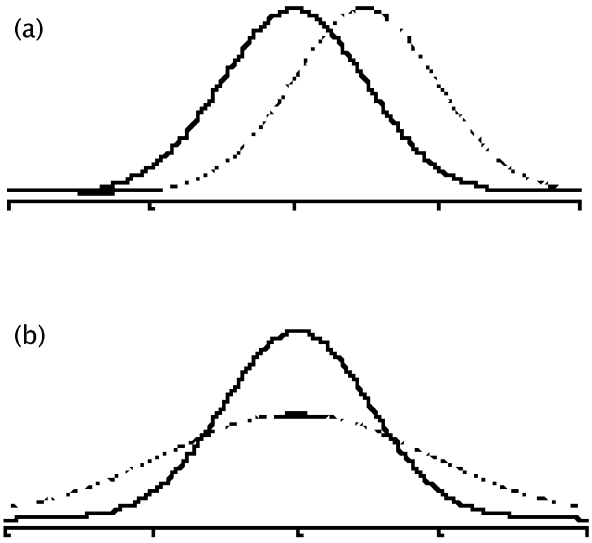

Fig. 1. Graphical depiction of directional- and relaxed-selection hypotheses. The solid curve represents the distribution of a behavioral trait in a wild population and the dashed curve represents a captive-bred population. (a) Directional selection: the mean shifts, but the shape of the distribution does not change. (b) Relaxed selection: the mean remains the same, but the distribution flattens out, including more values at either extreme.

2. Methods

2.1. Populations

Individuals used in this study were from four populations of *P. p. subgriseus*, collected from Ocala National Forest, Florida, between 1952 and 2000: GR_{35} was founded in 1952 and is 35 generations removed from the wild ($n=27$); GR_{14} was founded in 1991 and is 14 generations removed from the wild ($n=29$); GR_2 was founded in 1998 and is two generations removed from the wild ($n=28$); and the WC population (WC) was trapped in 2000 ($n=24$). All captive populations had been maintained for 35, 14 and two generations, respectively. GR_2 and GR_{14} mice were bred and housed at Brookfield Zoo, Brookfield, Illinois. The GR_{35} population was bred for one generation at Brookfield Zoo from 30 individuals purchased from the *Peromyscus* Genetic Stock Center (Columbia, South Carolina). All three captive populations were reared in very similar environments and conditions. Sex ratios for all populations were close to 1 (GR_{35} 15:12; GR_{14} 15:14; GR_2 14:14; WC 11:13).

2.2. Experimental design

All mice were housed and tested in separate rooms at Brookfield Zoo. Both rooms (housing and testing) were on a 12:12 light cycle, with the dark phase beginning at 13:00 h. During the dark phase, the rooms were illuminated with three 25-watt red lights. For housing, mice were kept solitarily in standard 18.5×29×13.5 cm cages with stainless-steel wire tops. Food and water were provided ad libitum. Testing was double blind. Prior to testing, Brookfield Zoo lab technicians randomly numbered each animal and assigned them to test groups. Each test group consisted of four individuals, one from each population. One group was tested per day.

At 17:00 h, four individuals were placed singly in one of four 55-gallon (209 l) tanks spaced approximately 150 cm apart and separated by blinds. The tanks were divided into three equal sections by strips of blue masking tape on the outside of the tank. Each tank was filled with 0.5 cup wild bird seed mixed with 19 l of corn cob bedding. A burrow was constructed from PVC piping and placed in one end of each tank. The wire lid from each animal's home cage held food and water and was placed in the other end of the tank. The substrate was approximately 75 mm deep at the burrow end of the tank and 25 mm at the feeder end.

After testing and before the next animal was placed in the tank, old bedding was removed and the tanks were sprayed with a disinfectant and allowed to sit for 10 min. Each tank was then sprayed with water, scrubbed, and dried. The burrows were disassembled and washed in high-pressure washers.

2.3. Data collection

Predator-response tests began at 13:30 h (mice had approximately 21 h to acclimatize to the tank). The mouse in tank 1 was video-taped for 10 min (Owings and Coss, 1977; Drickamer and Springer, 1998) with no stimulus (pre-exposure period). Immediately after the pre-exposure testing was complete, I presented the predator stimulus from behind a blind. The stimulus was traced from a great gray owl (*Strix nebulosa*) specimen at The Field. Museum of Natural History in Chicago, Illinois. The tracing was reduced 50% and used to create a matteboard cutout approximately 53×30 cm. At the beginning of the post-exposure period, the silhouette, mounted on a quarter-inch dowel rod, was swept about 120 cm over the tank 10 times, which took approximately 30 s. After the owl was "flown" over the tank, it was mounted above the tank in full view of the mouse. Again, the mouse was video-taped for 10 min post stimulus beginning the moment the owl appeared from behind the blind (post-exposure period). This procedure was repeated for tanks 2, 3, and 4, respectively.

All data were collected from the videotapes recorded in the lab. Videotapes were watched via an LCD projector, creating a 180 cm^2 image. For the full 10-min pre- and post-exposure periods, behavior and location were recorded at five-second intervals using instantaneous sampling (Altmann, 1974), totaling 121 observations per 10-min period. For the one-minute periods immediately pre- and post-exposure, behavior and location were recorded at two-second intervals, totaling 31 observations.

Behaviors were coded as one of the following: *vigilant*, *active*, *flight*, *grooming*, *hiding*, and *other*. *Vigilance* was measured as the number of observations in which the animal was still and alert. *Active* was the number of observations in which the animal was displaying a behavior such as locomotion or digging, excluding flight behaviors. *Flight* consisted of fast, frenetic movement and is distinguished from *active* in that the animal moved so quickly, substrate was displaced from under the individual's feet. *Grooming* behaviors included grooming, eating, or drinking. *Hiding* was any interval in which I could not see the individual. Only *vigilance* and *grooming* were considered in the analysis.

Tank location was coded as either: *in the burrow, burrow end of the tank, middle of the tank, feeder end of the tank, or refuge* (defined as any observation in which the mouse was in the preconstructed burrow, a self-constructed hole, or under the wire feeder). Only *burrow end, middle, and refuge* were considered in the analysis.

2.4. Data analysis

Even though the mice were each taped and scored for 10 min pre- and post-exposure to the silhouette, data presented here compare the 1-min periods immediately pre- and post-exposure (with the exception of *grooming* behaviors—due to limitations in data-collection methods, I compared the two minutes pre- and post-exposure). Compared with the 10-min period, the 1-min period is more biologically meaningful—in the wild, the window of survival for an oldfield mouse confronted with an aerial predator would rarely be more than 60 s. Clarke (1983) showed that under various intensities of moonlight (new, quarter, and full moon), median capture time by short-eared owls (*Asio flammeus*) of deermice (*Peromyscus maniculatus*) was always under 50 s.

I considered four metrics: (1) quantitative change in behavior between the pre- and post-exposure periods, (2) behavior after exposure to a predator, (3) time to enter the burrow after exposure, and (4) overall variance in behavior as a function of generations in captivity. To calculate quantitative change in behavior (Δ), I subtracted the mean number observations of a particular behavior in the pre-exposure period (B_0) from the mean number of observations of that behavior in the post-exposure period (B_1). Therefore, $\Delta = B_1 - B_0$. I compared

means among and between populations with the non-parametric Kruskal–Wallis test (KW; $\alpha = 0.05$). Because there were unequal variances and sample sizes, pairwise relationships were calculated with Fligner and Policello's (1981) rank procedures test. Pairs were considered significantly different if $P < 0.0083$ [α adjusted for multiple comparisons (Day and Quinn, 1989)]. Variances were compared with Levene's test (L; $\alpha = 0.05$; Sall and Lehman, 1996). Again, individual pairs of variances were considered significantly different if $P < 0.0083$.

3. Results

3.1. Change in behavior and tank use

Neither mean amount of change in behavior nor tank use after exposure to the silhouette varied as a function of captivity. Behavior change was observed in all populations. The degree to which they changed their behavior, however, did not vary as a function of generations in captivity.

3.2. Post-exposure behavior and tank use

Neither use of the burrow end of the tank nor *grooming* behaviors after exposure to a simulated predator varied significantly with generations in captivity (KW $P = 0.1378$ and $P = 0.1813$, respectively). On the other hand, vigilance (KW $P = 0.0213$), use of the middle of the tank (KW $P = 0.0240$; Fig. 2a) and use of a refuge (KW $P = 0.0309$; Fig. 2b) after exposure to an owl silhouette did vary with generations in captivity.

Post-exposure vigilance differed significantly across the four populations. Contrary to prediction, however, vigilance increased as generations in captivity increased. This result was likely due to the number of observations in which the animal was in a refuge. Therefore, I normalized for observations out of sight by considering the proportion of visible observations vigilance was observed. This difference was not significant (KW $P = 0.0703$).

Although mean number of observations in which the mouse was in the middle of the tank differed significantly by population, pairwise comparisons do not point to any specific populations that contributed most heavily to that significance. Fig. 2a indicates, however, that, on average, mice from the GR_{14} and GR_{35} populations were observed in the center of the tank more often than mice from the WC and GR_2 populations. As with use of the middle of the tank, multiple comparison analysis showed no significant pairwise differences for refuge use. Fig. 2b indicates that, on average, mice from WC and GR_2 were observed in refuges more often than mice from the GR_{14} or GR_{35} populations.

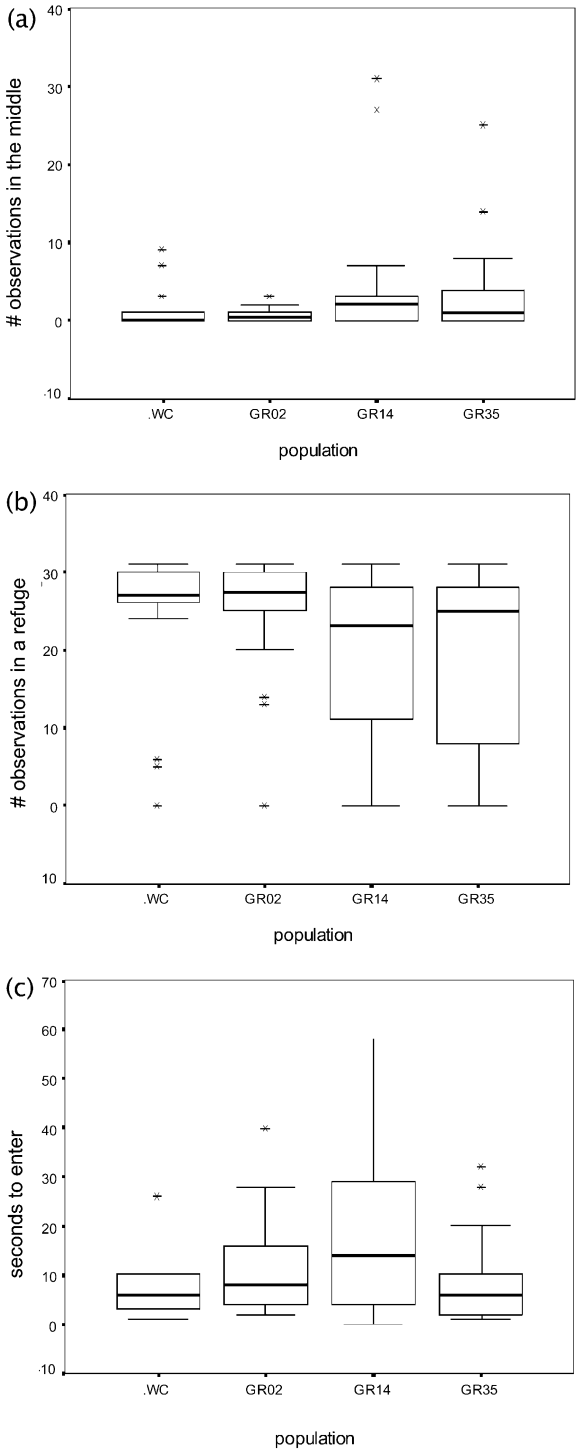

Fig. 2. (a) Number of observations in which the animals were in the middle of the tank as a function of generations in captivity (Kruskal–Wallis $P = 0.0240$; Levene's $P = 0.0056$). Mean number of observations for WC = 1.08, $GR_2 = 0.8214$, $GR_{14} = 3.621$, and $GR_{35} = 3.222$. (b) Number of observations in which the animals were in a refuge as a function of generations in captivity (Kruskal–Wallis $P = 0.0309$; Levene's $P = 0.0058$). Mean number of observations for WC = 23.875, $GR_2 = 25.3214$, $GR_{14} = 19.586$, and $GR_{35} = 18.815$. (c) Number of seconds to enter the burrow after exposure to a predator (up to one minute) as a function of generations in captivity (Kruskal–Wallis $P = 0.0628$; Levene's $P = 0.0003$). Mean number of seconds for WC = 7.1053, $GR_2 = 11.7895$, $GR_{14} = 18.8421$, and $GR_{35} = 8.1500$.

3.3. Time to enter burrow after exposure to silhouette

Of the animals that entered the burrow within the first minute after exposure ($n=77$), there is a marginally significant difference among the four populations (KW $P=0.0628$). Not surprisingly, multiple comparison analysis showed no significant pairwise differences. The trend, however, is interesting: mice from the GR_{14} population took the longest to enter the burrow, while WC mice were the quickest to enter (Fig. 2c).

3.4. Overall variance

To look at overall variance, I ranked, for each variable, the populations from one to four, with four being the population with the highest variance for that variable and one being the lowest (for variance of individual variables see Table 1). In this study, overall variance increased with time in captivity (Fig. 3). WC and GR_2 have the lowest variance and GR_{14} and GR_{35} have the highest. In 33% of the cases, the WC population was ranked either 3 or 4; GR_2 was ranked 3 or 4 in only 17% of the cases. Conversely, GR_{14} was ranked 3 or 4 67% of the time, while GR_{35} was ranked 3 or 4 83% of the time.

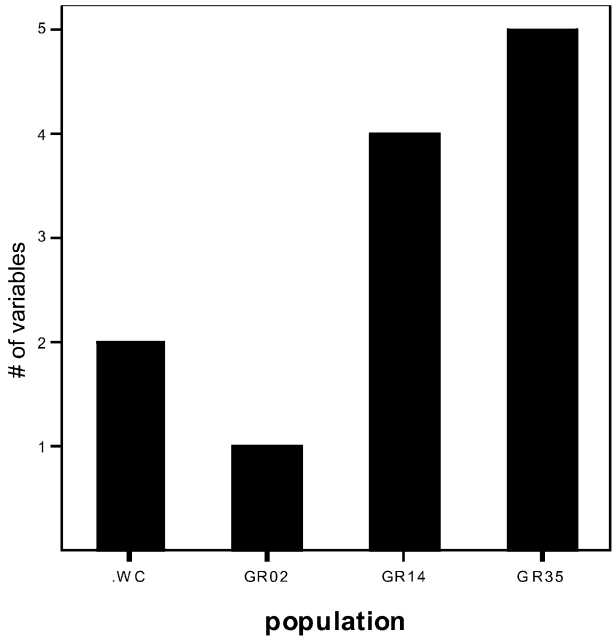

Fig. 3. The number of variables for which a population was ranked either 3 or 4 in terms of its variance. Ranking was on a scale from 1 to 4, with 4 being the population with the highest variance for a given variable.

4. Discussion

To test effects of captivity on predator-response behaviors, I measured (1) amount of change in behavior from the pre- to post-exposure treatment, (2) behavior after exposure to a predator, (3) time to enter the burrow after exposure, and (4) overall variance in behavior as a function of generations in captivity. After I analyzed quantitative changes in behavior between pre- and post-exposure periods, there seemed to be no change in behavior as a function of generations in captivity. In other words, no matter what a mouse was doing before it saw the predator, it altered its behavior to the same degree regardless of population.

In addition, mean number of seconds to get into the burrow after exposure to a predator did not differ significantly as a function of generations in captivity. The trend is worth reporting, however. As predicted under the directional selection hypothesis, the individuals from the WC population were the fastest to enter the burrow. Interestingly, however, the GR_{14} individuals took the most time to enter the burrow after seeing a predator and the GR_{35} individuals took about the same time as the WC. More work is needed to understand this result.

Comparing pre- and post-exposure behaviors reveals that GR_{14} and GR_{35} individuals were more likely to be in the center of the tank in the post-exposure period than WC and GR_2; and WC and GR_2 were more likely to be in a refuge than GR_{14} and GR_{35}. The center of the tank has no cover or protection so could be perceived as a high-risk location, especially after the animal has seen a predator. Thus, the more generations a population has been in captivity, the less likely those individuals are to take cover after exposure to a predator. Because time to enter the burrow did not differ significantly among the populations, however, the animals that spent more time in the center of the tank likely entered the burrow upon exposure to the predator and re-emerged shortly thereafter. These results support Ivey's (1949) statement that

Table 1
Variance comparison P values (Levene's test), $\alpha=0.05$[a]

Behavioural measure	P-value[a]	Pairwise relationships[b]	Standard deviation			
			WC	GR_2	GR_{14}	GR_{35}
Post-exposure behaviour						
Vigilance	**0.008**	**$GR_2 < GR_{14}$**	5.953	3.035	8.160	5.638
		$GR_2 < GR_{35}$				
Grooming	**0.006**	**$GR_2 < GR_{35}$**	15.295	15.128	5.206	1.744
Observations by burrow entrance	0.151		6.138	6.182	4.080	8.449
Use of the middle of the tank	**0.006**	**$GR_2 < GR_{14}$**	2.320	1.020	7.282	5.466
		$GR_2 < GR_{35}$				
Refuge use	**0.006**	**$GR_2 < GR_{35}$**	9.918	7.359	10.055	11.858
Time to enter burrow after exposure	**<0.000**	**$GR_2 < WC$**	5.685	10.152	17.183	8.975
		$GR_2 < GR_{35}$				

[a] Numbers in bold are significant.
[b] Pairwise relationships in bold are significant at the 0.0083 level.

captive *P. p. subgriseus* respond to "frightening" stimuli as quickly as wild individuals but are quicker to recover.

Finally, there was a significant change in overall variance in behaviors among the populations. These results support the hypothesis of relaxed selection. In the wild, small rodents are constantly trading off an investment of energy in resource acquisition and predator response (Robinson, 1980; Ludwig and Rowe, 1990; Phelan and Baker, 1992). As more energy is devoted to food acquisition, for example, less energy can go into predator response and vice versa. Behavior at either extreme of the distribution could result in mortality from predation or poor nutrition (Edmunds, 1974). In captivity, however, the selective pressures that reduce variance in that trade-off no longer exist. Thus captive mice can respond immediately or never—and their response will not affect survivorship or, ultimately, reproductive success.

In many ways, the experimental protocol used was ideal for answering this question. First, all four populations were drawn from the same location in central Florida. Such geographic consistency is rare in studies of captive-bred animals. Second, the GR_2 and GR_{14} populations were reared in identical and consistent environments at the Brookfield Zoo. The GR_{35} animals were reared in a similar environment at the *Peromyscus* Genetic Stock Center. Finally, I had good sample sizes and a model system with a short generation time that allowed comparison of populations as far removed from the wild as 35 generations. There are three caveats to these data, however. First, for the four populations used in this study, there were four separate groups of founders. Populations founded from a few individuals could have different means and variances from the beginning. Over generations, genetic drift can act on those differences causing resulting populations to be significantly different from one another (Hartl and Clark, 1997). In this case, no predictable pattern would emerge among captive populations. Second, this study is cross-sectional, not longitudinal. I did not have control over the environments in which the captive-bred animals were kept. Although the captive environments were similar, subtle and seemingly minor differences could account for some of the observed differences between populations. Third, these results are based on captive populations reared in basic conditions. The interaction between genetics and environment can affect the amount of change observed in captive animals (Price, 1998). Therefore, populations reared in more complex environments might exhibit less change than that demonstrated here. All three of these issues are common to captive breeding programs in general and not unique to this study. In this case they were unavoidable because I drew my study animals from existing colonies. The next step in this line of research is to conduct similar studies on populations drawn from the same founders and reared in the same environment.

In the context of conservation, these data point to two ways in which captivity can compromise animal behavior and, in turn, the success of reintroduction programs. First, if generations in captivity decreases an individual's proclivity to take refuge after seeing a predator, individuals from established captive populations might experience increased mortality in the wild due to predation. Second, these data show that captivity can increase variation in behavior—and increased behavioral variance could translate into increased variance in survival upon reintroduction. For biologists working with *P. polionotus* and other taxa, the results show that, due to increased variance, more individuals will be needed in the release population to reach a targeted population size (McPhee, 2002). Although this work relates specifically to *P. p. subgriseu*s, the fundamental concepts, especially that of increased variation, can inform biologists as they design reintroduction and recovery programs for other taxa as well.

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