

## **Effects of Captivity on Response to a Novel Environment in the Oldfield Mouse (*Peromyscus polionotus subgriseus*)**

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Long-term maintenance of captive populations and release of these animals into the wild is one approach to endangered species conservation. In this study, I used a traditional ethological technique, the open-field test, to assess captivity's effects on exploratory behavior, level of activity, and enclosure use in oldfield mice (*Peromyscus polionotus subgriseus*) upon introduction to a novel environment. The animals tested were from four populations collected from Ocala National Forest, Florida, and were held in captivity for varying numbers of generations: 35, 14, 2, and 0 (wild caught). The population 35 generations removed from the wild was behaviorally distinct from the other three populations. The mechanisms behind the differences are unclear. This study, however, is an example of how traditional behavioral methods can be applied to conservation problems. Whether captive populations are raised for lab studies or for captive breeding of endangered species, this study suggests that if they have been removed from the wild for more than 14 generations, they are likely to be significantly different from the wild counterparts of interest.

In the wild, animals need to locate resources such as food, water, and shelter while avoiding predators and other sources of mortality. Behaviors associated with resource acquisition and predator avoidance have been shaped over evolutionary time to increase reproductive success. Captivity and the selective pressures associated with it, however, are vastly different from the environment and pressures in which species have evolved (Frankham et al., 1986; Hediger, 1964; Price, 1970; Seidensticker & Forthman, 1998; Soulé et al., 1986; Soulé, 1986). Since Darwin (1868/1998), biologists have recognized that captivity can drastically alter animal behavior (Carlstead, 1996; Lickliter & Ness, 1990; Price, 1998). A captive environment can relax selective pressures, change the direction of selection, or impose completely novel pressures—either intentionally or inadvertently (Darwin, 1868/1998; Price, 1970; Endler, 1986; Lickliter & Ness, 1990; Carlstead, 1996; Price, 1998). Such changes can alter how individuals behave in a

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novel environment (Garten, 1977). Several researchers have shown that domesticated populations are less timid and inhibited than their wild progenitors (Clark & Galef, 1977; Price, 1970). If these tendencies exist for nondomesticated species held in captivity, they could help explain some of the difficulties that conservation biologists have experienced reintroducing captive individuals into natural environments.

Evaluations of reintroduction programs indicate that many deaths of reintroduced animals are due to behavioral deficiencies (Kleiman, 1989; Yalden, 1993). For example, reintroduced African wild dogs (*Lycan pictus*) were unable to capture prey, used inappropriate urbanized habitats, and were generally unable to adapt to a wild environment (Frantzen et al., 2001; Mills, 1999). Individuals in the golden lion tamarin (*Leontopithecus rosalia*) reintroductions were unable to survive because locomotor skills were deficient; they could not orient themselves spatially; and they were not able to recognize natural foods, nonavian predators, and dangerous nonpredaceous animals (Kleiman et al., 1990). In Madagascar, attempts to reintroduce the black and white ruffed lemur (*Varecia variegata variegata*) failed because released individuals could not avoid predators, find food, negotiate and locomote in a complex arboreal environment, or recognize appropriate habitat (Britt et al., 1999). Likewise, reintroduced thick-billed parrots (*Rhynchopsitta pachyrhyncha*) suffered high mortality because they did not flock appropriately and could not keep up with wild individuals. Released parrots therefore suffered high predation rates and poor nutrition even though they had been parent reared and trained prior to release (Wallace, 1994).

Biologists working with the oldfield mouse (*Peromyscus polionotus*) are currently dealing with similar issues. There are 16 recognized subspecies of *P. polionotus* found throughout the southeastern United States (Hall, 1981), 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 *P. polionotus* habitat, and a growing human population has increased the number of domestic and feral cats, which prey on this mouse. Due to shrinking habitat and increased predation pressures, five subspecies of beach mice are now listed as endangered, one is listed as threatened, and one is considered extinct (USFWS, 2001; Wooten, 2001). All beach mouse recovery plans list captive breeding and reintroduction as goals (Holler et al., 1989; USFWS, 1987, 1993, 2001).

Oldfield mice are found in early successional sand pine scrub with dry, sandy soils (Myers & Ewel, 1990). Primary predators include domestic and feral cats, raptors, and snakes (Holler et al., 1989; Wolfe & Summerlin, 1989; Rave & Holler, 1992; USFWS, 1987, 1993). *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 vertically from the nest chamber and ends just below the soil surface (Dawson et al., 1988; Ivey, 1949).

Given a history of behavioral deficiencies in captive-bred released individuals such as those described above and the current recovery plans for various *P. polionotus* subspecies, I investigated whether or not captivity modifies behavior in *P. p. subgriseus* when introduced into a novel environment. This experiment was part of a larger study that looked at predator response behaviors of *P. p. subgriseus* as a function of generations in captivity (McPhee, in press). Four populations of this subspecies have been collected from Ocala National Forest, Florida (ONF) over a 48-year period and maintained in similar captive environments. This provides a unique and ideal system for looking at behavioral differences between populations that have been in captivity for varying number of generations. Such consistency, and the comparisons it makes possible, is rare in captive populations.

Specifically, I used a traditional ethological technique, the open-field test, to examine exploration, level of activity, and enclosure use. These behaviors are commonly used in open-field tests to measure inhibition and timidity (Archer, 1973; Price, 1984). To look for differences between populations, I introduced three captive and one wild-caught population of *P. p. subgriseus* into a modified open-field environment, then compared behavioral means and variances. In this study, I show how the open-field test can be applied to a conservation problem.

## Method

### *Subjects*

Individuals used in this study were trapped in ONF between 1952 and 2000. Ocala National Forest is 383,000 acres and is managed for timber production. The areas in which mice were trapped had been cut and the debris burned within the last four years. This management practice was designed to simulate the forest's fire cycles.

The four populations of *P. p. subgriseus* used in this study were: (1) GR35, which was founded in 1952 and was 35 generations removed from the wild ( $N = 30$ ); (2) GR14, which was founded in 1991 and was 14 generations removed from the wild ( $N = 29$ ); (3) GR2, which was founded in 1998 and was two generations removed from the wild ( $N = 30$ ); and (4) WC, which was trapped in 2000 ( $N = 29$ ). Sample sizes refer to the number of individuals used in the study.

GR2 and GR14 mice were bred and housed at Brookfield Zoo, Brookfield, Illinois, under identical conditions. The GR35 population (30 individuals) was purchased in January 2000 from the *Peromyscus* Genetic Stock Center, Columbia, South Carolina. These animals were then bred at Brookfield Zoo for one generation, making them 35 generations removed from the wild. The four populations used in this study came from four separate groups of founders. For the purposes of this paper, I am assuming that all populations were samples from one, larger population. They were, however, possibly drawn from distinct populations.

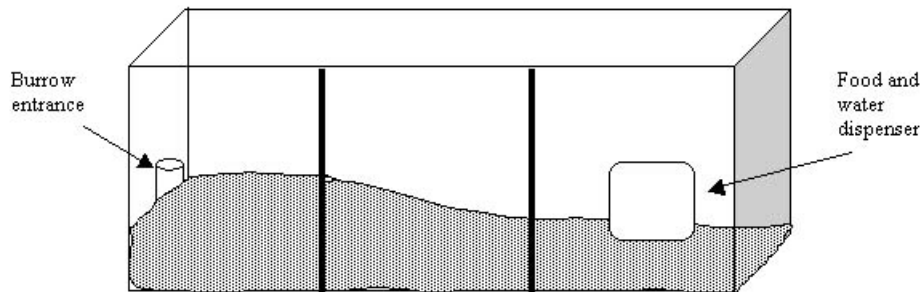
From the time of capture, all three captive populations were housed in groups of three or four in standard 18.5 x 29 x 13.5 cm plastic cages with stainless steel wire lids. During the study, animals were housed solitarily in the same types of cages. Food and water were provided *ad libitum*. Sex ratios for all samples were close to 1 (GR35 15:15; GR14 14:15; GR2 15:15; WC 14:15).

### *Apparatus and Procedure*

All mice were housed in one room and tested in another 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 25-w red lights. Testing was double blind. Prior to testing, Brookfield Zoo lab technicians randomly numbered each animal and assigned them to test

groups. All groups consisted of four individuals, one from each population (two individuals were excluded from the study due to data-collection errors). One group was tested per day. The groups controlled for any day effects that may have influenced behavior.

Glass 55-gallon (209 L) tanks were used for a modified open-field test. 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 of wild bird seed mixed with 19 L of corncob bedding. A burrow was constructed from PVC piping and placed in one end of each tank (Figure 1). The wire lid from the animal's home cage, which held food and water, 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 (Figure 1). At 17:00 h, four individuals were placed singly in the center of one of four tanks. Testing always began with tank number four, but animal identities were unknown, so they were placed randomly in the four tanks.



**Figure 1.** Representation of test arena. Burrow system extended through the entire left section of tank—only the entrance tunnel was visible; food and water dispenser was in the right section of the tank.

At the end of a day's testing, the substrate 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.

Upon introduction to the tank, each individual was video recorded for five minutes (Blackwell & Ramsey 1972; Garten 1977). All data were collected from the videotapes. These tapes were watched via an LCD projector, creating a 180 x 180 cm image. To measure open-field behavior, I considered three metrics: (1) *exploration*—number of times individual mice crossed the gridlines in the tank (e.g., Blackwell & Ramsey, 1972; Price, 1970; Rhee et al., 2001; Walsh & Cummins, 1976), (2) *activity*—number of observations in which animals were moving from one spot to another, for example, locomotion, jumping, or climbing (e.g., Walsh & Cummins, 1976), and (3) *location*—number of observations in which animals were in one of three areas of the tank (in the burrow, middle, or feeder-end of the tank) (e.g., Walsh & Cummins, 1976). Observations of activity and location were made at five-second intervals (Hanson & Coss, 1997) using instantaneous sampling (Altmann, 1974). I did not record urinations and defecations, which are common metrics in open-field studies, because video quality did not allow accurate discrimination of these behaviors.

### **Data Analysis**

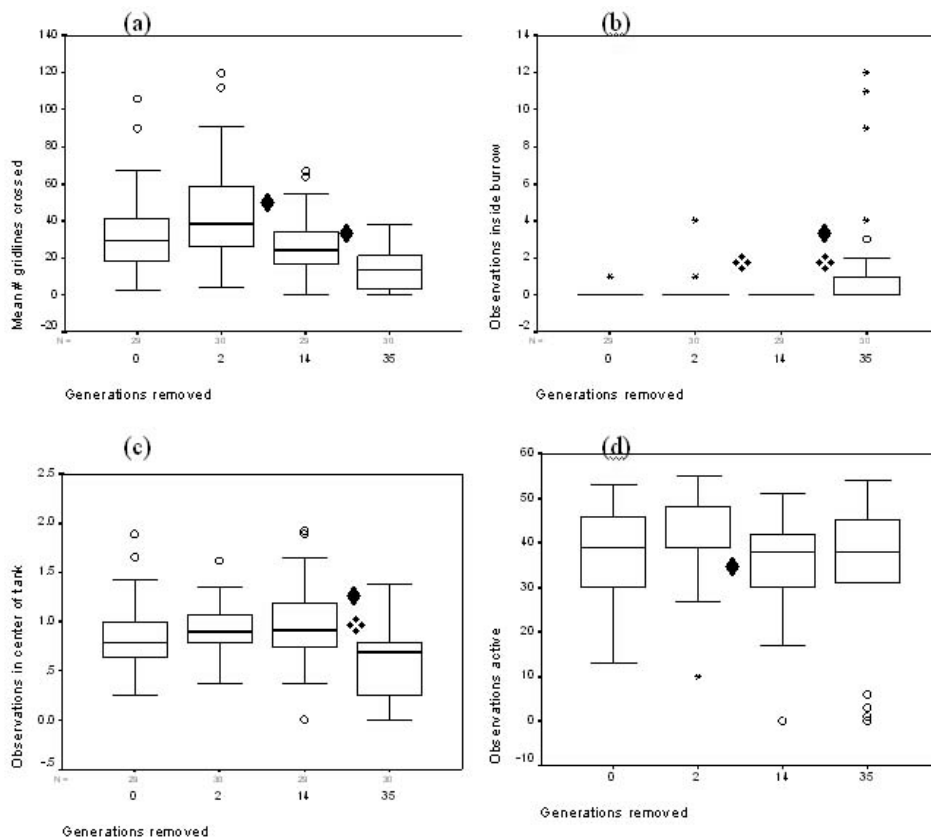
I sequentially compared means between populations with the non-parametric Kruskal-Wallis test (KW;  $\alpha = 0.05$ ). Variances were compared with Levene's test (L;  $\alpha = 0.05$ ; Sall & Lehman, 1996). Due to unequal variances and sample sizes, pairwise relationships were calculated with Fligner and Policello's (1981) rank procedures test (FP). There were three comparisons (WC – GR2, GR2 – GR14, GR14 – GR35), so means and variances of pairs were considered significantly different if  $p < 0.0167$  (Day & Quinn, 1989).

## Results

### Exploratory Behavior

Average exploratory behavior in a novel environment varied with generations in captivity (KW  $p < 0.0001$ ; Figure 2a). On average, GR35 mice were significantly less exploratory than GR14 (FP  $p = 0.0006$ ). In addition, GR14 mice were significantly less exploratory than GR2 (FP  $p = 0.0022$ ).

Variation in exploratory behavior also differed between the populations (L  $p = 0.0140$ ; Figure 2a), but multiple comparison analyses indicated the differences were not explained by comparing WC – GR2, GR2 – GR14, or GR14 – GR35.



**Figure 2.** Differences in trait occurrence and variance as a function of generations removed from the wild: (a) exploration, (b) burrow use, (c) use of the middle of the tank, and (d) level of activity as determined with Kruskal-Wallis and Levene's tests.  $\blacklozenge$  = Significant differences in occurrence;  $\blacklozenge$  = significant differences in trait variance. The horizontal line in the box indicates the median.

### ***Tank Use***

Use of the burrow and the center of the tank differed significantly as a function of generations in captivity (KW  $p = 0.0014$  and KW  $p = 0.0002$ , respectively; Figure 2b and c). GR35 mice were in the burrow for significantly more observations than GR14 (FP  $p = 0.0004$ ) and were in the center of the tank for significantly fewer observations than GR14 (FP  $p = 0.0002$ ; Figure 2b and c). Variances in burrow use and use of the center of the tank differed among the four populations (L  $p < 0.0001$  and L  $p = 0.0118$ , respectively; Figure 2b and c). GR14 had significantly less variance in burrow use than GR35 or GR2 (L  $p < 0.0001$  and  $p = 0.0163$ , respectively). The GR35 population had significantly less variance in use of the center of the tank than the GR14 (L  $p = 0.0031$ ).

### ***Activity***

In this experiment, level of activity in a novel environment varied with generations in captivity (KW  $p = 0.0113$ ; Figure 2d). GR2 mice were significantly more active than GR14 (FP  $p = 0.0002$ ).

As with exploratory behavior, variance in activity differed significantly among the four populations (L  $p = 0.0023$ ; Figure 2d) but was not explained by any of the pairwise comparisons.

## **Discussion**

As wild populations continue to dwindle, the use of reintroduction as a conservation tool increases. Scientists have long recognized, however, that captive environments can drastically alter behavior in wild mammals. For a number of species, such as the golden lion tamarin and thick-billed parrot, changes that take place in captivity can cause an increase in mortality upon reintroduction.

Cases such as these illustrate the importance of behavioral studies to conservation success. Although conservation biology is comprised of many disciplines, behavioral ecology has historically not played a major role. Examining conservation and behavior journals, both Sutherland (1998) and Clemmons and Bucholz (1997) found that behavioral papers were uncommon in conservation journals and conservation related papers were uncommon in behavior journals.

In this paper, I applied traditional ethological techniques to a complex conservation problem: the effects of captivity on behavior. To explore differences across captive-bred and wild populations, I measured behavioral responses of old-field mice to a novel environment as a function of generations in captivity. Among the four populations of *P. p. subgriseus* examined in this study (WC, GR2, GR14, and GR35), GR35 was the most behaviorally distinct. The WC population never differed from GR2 or GR14, and most of the differences in behavior and variance were seen between the GR14 and GR35 populations. Differences in exploration, burrow use, and use of the middle of the tank occurred between the GR14 and GR35 populations and level of activity differed between the GR2 and GR14 popu-

lations. Two of the behaviors, burrow use and activity level, exhibited an overall increase in variability. Exploration and use of the middle of the tank exhibited an overall decrease in variation. This pattern potentially counters Price's (1998) statement that selection in captivity is most intense during the first few generations following the transition from field to captive environments. In addition, it does not show that animals become more active and less timid with generations in captivity (cf., Clark & Galef, 1977; Price, 1970).

The mechanisms behind these patterns are unclear. There are several possible explanations. 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. Second, over generations, genetic drift can act on those differences causing populations to be significantly different from one another (Hartl & Clark, 1997). Third, 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. The interaction between genetics and environment can affect the amount of change observed in captive animals (Price, 1998).

Fourth, the GR<sub>35</sub> population was more inbred than the other captive-bred populations (mean inbreeding coefficients (F): GR<sub>35</sub> = 0.58, GR<sub>14</sub> = 0.17, GR<sub>2</sub> < 0.01). Therefore, the distinctiveness of GR<sub>35</sub> could have been due to inbreeding effects. Fifth, the behaviors in question could have been shaped by novel selective pressures associated with a captive environment. The increase in variability in burrow use and activity level suggests that the selective pressures on those behaviors were relaxed in the captive environment. If the observed differences between populations were due to selection, the behaviors measured were fairly resistant to novel pressures. This is evidenced by the similarity between the wild-caught and GR<sub>2</sub> populations and, with the exception of activity level, the similarity between GR<sub>2</sub> and GR<sub>14</sub> mice. The most likely explanation is a combination of all of these factors.

In many ways, the experimental protocol used in this study was ideal for exploring behavioral differences between wild-caught and captive-bred populations. All four populations were drawn from the same location in central Florida. Such geographic consistency is rare in studies of captive-bred animals. In addition, the GR<sub>2</sub> and GR<sub>14</sub> populations were reared in identical and consistent environments at the Brookfield Zoo. The GR<sub>35</sub> 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.

The confounding factors (e.g., nonrandom mating and separate rearing environments), 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. This would limit the number of generations available for comparison, but such work

would help determine which mechanism or mechanisms were responsible for the observed differences. Ultimately, more work is needed to determine (a) the effects of captivity on behavior in a novel environment and (b) the efficacy of open-field tests to measure base-level responses in captive-bred animals.

With most species slated for reintroduction, the release of animals 35 generations removed is not a possibility. With *P. polionotus*, a species with a short generation time and well-established husbandry techniques, the release of a GR35 population is feasible. This work suggests that releasing *P. polionotus* populations that have been in captivity for fewer than fourteen generations would increase probability of success. The specific finding that GR35 animals are distinct is not directly applicable to other taxa. These results do, however, indicate that this is an area of research, and a new application of a classic technique, that warrants more investigation for a variety of taxa including *P. polionotus*.

Whether behavioral differences among captive populations are due to specific changes in selective pressures or random changes inherent in genetic drift, biologists that take animals into captivity need to be aware that behavior has likely been modified over generations in a nonwild environment. Captive populations, whether raised for laboratory studies or captive breeding of endangered species, are likely to be significantly different from their wild counterparts. Scientists commonly use lab populations to make inferences about wild populations. The results presented in this paper suggest that such inferences need to be made with caution (see also Knight, 2001; McPhee, in press; Millar & Threadgill, 1987). Conservation biologists use captive-bred individuals to supplement or re-establish wild populations. Any behavioral trait that has been shaped by selective pressures in a captive environment could be ill-suited for the animal's native habitat. Such changes can compromise survivorship, and ultimately reproductive success, upon release.

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