Title

Influences on Foraging Preferences of the Endangered Pacific Pocket Mouse (Perognathus longimembris pacificus): Implications for a Novel Conservation Strategy

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Influences on Foraging Preferences of the Endangered Pacific Pocket Mouse (*Perognathus longimembris pacificus*): Implications for a Novel Conservation Strategy

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requirements for the degree Master of Science

in Biology

by

Brigit Danae Harvey

2018

ABSTRACT OF THE THESIS

Influences on Foraging Preferences of the
Endangered Pacific Pocket Mouse (*Perognathus longimembris pacificus*):
Implications for a Novel Conservation Strategy

by

Brigit Danae Harvey
Master of Science in Biology
University of California, Los Angeles, 2018
Professor Gregory F Grether, Chair

One approach to combating the threat of invasive species replacing the native food sources of captive-bred endangered animals from conservation breeding and reintroduction programs is to expand the foraging options of these animals to include palatable invasive species. Utilizing the conservation breeding program for the endangered Pacific Pocket Mouse (*Perognathus longimembris pacificus*, PPM), we experimentally determined how seed origin, exposure during crucial developmental periods, and nutritional quality influence PPM's willingness to consume invasive food types. Preferences were tested using the Cafeteria Method design and nutritional characteristics were determined with near infrared-reflectance spectroscopy. Captive-born PPM preferred commercial seeds, which contain higher levels of moisture and starch, to native and invasive seeds. However, exposure to invasive seeds during pre-weaning increased PPM's

willingness to forage for invasive seeds. This study, the first of its kind, has the potential to improve PPM reintroduction efforts and provides insights to other management programs facing similar concerns.

The thesis of Brigit Danae Harvey is approved.

Peter Nicholas Nonacs

Thomas Bates Smith

Debra Marie Shier Grether

Gregory F Grether, Committee Chair

University of California, Los Angeles

2018

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You all have been the sails to help me fly and the anchors to keep me grounded.

Influences on Foraging Preferences of the Endangered Pacific Pocket Mouse (*Perognathus longimembris pacificus*): Implications for a Novel Conservation Strategy

INTRODUCTION

Conservation breeding and reintroduction programs have become a globally renowned form of species recovery and currently incorporate hundreds of species from across vertebrates and invertebrates (Kleiman 1989, Seddon et al. 2007; Soorae et al. 2018). Although the success rates of these recovery programs have been on the rise since their inception in the 1970s (Taylor et al. 2017), introductions utilizing captive-bred animals continue to show lower rates of successful establishment than translocations of wild animals (Letty et al. 2007; Rummel et al. 2016). It has been long acknowledged that captive-bred animals suffer high post-release mortality rates due to the development of ineffective behavioral responses, including predator detection and avoidance, social interaction, and foraging, as a result of living in captive conditions (Kleiman 1989; Synder et al. 1996; Mathews et al. 2005; Moehrenschalger et al. 2013). Adaptive management, such as research-based methodology changes and decision-making, has improved post-release survivorship in many recovery programs (Schreiber et al. 2004; Seddon & Armstrong 2016; Taylor et al. 2017), especially with regards to improving antipredator behavioral response training (Griffen et al. 2000, Shier 2016). However, starvation is still a leading cause of mortality in some introduced taxa (Jules et al. 2008). Thus, research on foraging behaviors and dietary preference development is also needed to identify ways to reduce post-release mortality.

Foraging includes the ability to locate, identify, manipulate, consume, and process natural food sources (Alberts 2007). Foraging skills and dietary preferences can form through

coexistence with a food type over evolutionary time (Peters et al. 2003), exposure during crucial developmental periods (Provenza and Balph 1987, 1988), and necessary nutritional requirements (Pearson et al. 2011; Bonachie et al. 2017). Unfortunately, many conservation breeding and reintroduction programs have very limited knowledge about how a target species' foraging skills and dietary preferences develop, and, due to extensive program costs, resort to providing a standardized commercial diet that meets the target species' minimum nutritional needs. As a result, captive-bred animals can develop unintentional dietary preferences for the commercialized diet over their native diet, thus decreasing their foraging efficiency and post-release survivorship (Ortega-Reyes and Provenza 1993; Brown et al. 2003; Kasparian and Millar 2004; Whiteside et al. 2015). As seen in reintroduced captive-bred Golden lion tamarins (*Leontopithecus rosalia*), these effects can be counteracted with foraging training and experience with native food sources during captive upbringing (Stoinski et al. 2003; Stoinski and Beck 2004). Foraging exposure and training have also been beneficial for other captive-released vertebrates (Sherrod et al. 1981; Brown et al. 2003; Whiteside et al. 2015).

In addition to ensuring that captive animals slated for release have been given an appropriate diet and experiences to develop effective foraging skills, conservation breeding and reintroduction programs also need to consider incorporating methodologies that prepare captive-bred animals for release into a human-modified ecosystem (Schreiber et al. 2004; Seddon 2010). Exotic invasive species, many of which have contributed to numerous ecological shifts and species declines through predation, competition, and replacement of native food sources, are globally pervasive (Mack and D'Antonio 1998; Mooney and Cleland 2001; Clavero and García-Berthou 2005; Seddon et al. 2007; Bøhn et al. 2008; Soorae 2018). Many wild taxa do not preferentially forage for invasive species as an alternative food source (Hackerott et al. 2013;

Wilcox and Fletcher 2016; Cuthbert et al. 2018; Soorae 2018). One possible explanation for this lack of preference is that generalist and specialist foragers may prefer food types that they have coevolved with (Keane and Crawley 2002; Lucero 2018). Another explanation is that invasive species may have lower nutritional quality when compared to native food types (Cattau et al. 2010; Wilcox and Fletcher 2016; Christianen et al. 2018). Regardless of the reason, the enemy release hypothesis predicts that preferential foraging for native food types frees exotic invasive congeners from predation, thus allowing invasive species, to continue to persist and spread (Elton 1958; Keane and Crawley 2002; Lucero 2018). This spread can enhance the pressure for native consumers to compete for an increasingly limited native prey species (Maron and Vilà 2001; Orrock et al. 2008). Therefore, even with improved foraging training and a native diet, captive-bred animals may suffer from fewer foraging options following release in regions where invasive species are challenging to remove and threaten to replace their native food sources.

Empirical studies show that animals can learn to consume novel food sources if exposed to them during a period in which their foraging preferences are developing (Provenza and Balph 1988, 1989; Nolte and Provenza 1992; Bilko et al. 1994). Researchers that work with conservation breeding programs have the unique opportunity to manipulate the rearing environment of a target species to identify how and when foraging preferences develop. Equipped with this knowledge, breeding program managers could raise animals that consume both native and palatable invasive food types, thereby expanding the foraging options of captive-bred animals post-release. In this study, I apply this approach to a captive-bred endangered species of pocket mouse in Southern California.

Study Species and System

The Pacific pocket mouse (*Perognathus longimembris pacificus*) is a federally endangered subspecies of the little pocket mouse (*P. longimembris*) in the family Heteromyidae. Pacific Pocket mice (PPM) have been part of a conservation breeding and reintroduction program at the San Diego Zoo Institute for Conservation Research since 2012 and were first reintroduced to Laguna Coast Wilderness Park in 2016 (Shier et al. 2016). Because PPM are bred and released as part of a research-based reintroduction program, they are an ideal species to pursue questions related to the development and expansion of foraging preferences.

Due to limited knowledge regarding the dietary preferences of PPM and the nutritional composition of native seeds at the onset of the conservation breeding program, captive PPM have been provided a primarily subsistence diet comprised of commercial finch seed mixes. These mixes were supplemented weekly with multiple native plant seed types as enrichment. To determine which native seed species PPM preferred and whether there was a preference between native seed types and the commercial diet, a series of cafeteria (food choice) experiments were conducted on both captive-born and wild-caught individuals (Shier et al. 2016). Wild-caught mice preferred native seeds over finch mix seeds, but captive-born mice had the reverse preference. These results suggested that rearing environment and early exposure might play a significant role on seed preference development in PPM.

Although PPM are indigenous to the coastal chaparral of southern California, the spread of invasive plant species is changing the landscape and distribution of PPM's native food sources. Invasive forb and grass species, such as *Erodium* and *Bromus* spp., have explosive dispersal rates and a competitive seeding period, making them resistant to removal efforts in California (Minnich and Dezzani 1998; Dukes and Mooney 2004; Martin 2013). Invasive plant

species also are linked to increased fire frequency and rate of post-fire recovery (Keeley et al. 2005; Pec and Carlton 2014). By decreasing the ability of native woody species to grow, these invasive plant species are shifting many chaparral ecosystems into grasslands (Minnich 2008; Pec and Carlton 2014). This landscape shift will likely affect the distribution and abundance of historic food sources of PPM. Fecal pellets analyzed using genetic barcode sequencing suggest that wild PPM consume invasive *Erodium* and *Bromus* spp., among other invasive species found along the southern California coastline (Iwanowicz et al. 2016). *Bromus* spp. have also been found in the caches and burrows of other heteromyid species (Longland et al. 1996; McMurray et al. 1997).

In this study, we aimed to determine (1) whether captive-bred PPM prefer native over non-native seeds, (2) whether the dietary preferences of PPM can be predicted from nutritional characteristics of the seeds, and (3) whether exposure to different species of seeds during a critical period affects the development of dietary preferences. To the best of our knowledge, this is the first experimental test of whether exposure to novel invasive food types in captivity can induce a willingness to consume, or a dietary preference for, invasive species in a captive-bred endangered species.

MATERIALS & METHODS

Animals and Housing

All experiments were conducted in the Pacific Pocket Mouse Captive Breeding Facility at the San Diego Zoo Institute for Conservation Research, Escondido, California. Mice were housed in

clear acrylic boxes (30 x 12 x 30 cm) that were filled approximately 8 cm with sand, contained a nesting cup, and a 'T'-tube made from PVC pipe to simulate a burrow.

Mice were fed a daily diet comprised of a finch seed mix (commercial non-native seeds) provided by Leach Grain & Milling, Downey, CA, USA. The mix contains roughly equivalent quantities of small white and red millet (*Panicum miliaceum*), canary seed (*Phalaris canariensis*), nyger seed (*Guizotia abyssinica*), rapeseed (*Brassica napus*), oat groats (*Avena sativa*), and flax seed (*Linum usitatissimum*) with a guaranteed analysis of at least 12.30% crude protein and 5.25% crude fat (source: Leach & Grain Milling). Mice were also provided a mixture of California native seed species as supplements to their daily commercial diet every other day of the week. Native seeds were acquired from two suppliers: S&S Seeds Inc, Carpinteria, CA, USA, and Stover Seed Co, Sun Valley, CA, USA. The most frequently purchased native seeds from these suppliers are California sagebrush (*Artemisia californica*), California croton (*Croton californicus*), California buckwheat (*Eriogonum fasciculatum*), White sage (*Salvia apiana*), Black sage (*Salvia mellifera*), and Purple needlegrass (*Stipa pulchra*).

We tested the influences of seed origin, early exposure, and nutritional content on the foraging preferences of $n = 50$ captive born PPM in 2 separate experiments. All mice used in these experiments were adults ranging from 70 to 1487 days of age and body masses ranging from 4.68 to 8.08 g. All preference trials were performed between June and October in 2017 and June and July in 2018. All animal testing, handling, and treatment followed IACUC protocol approval (project number: 15-005) at the San Diego Zoo Institute for Conservation Research.

Experiment 1: Effect of Seed Origin on Foraging Preferences

We tested the influence of seed origin on the foraging preferences of 20 captive born adult PPM (*n* = 10 males, *n* = 10 females). We used a standard 'Cafeteria Experiment' set-up to test individual mouse seed preferences in which each mouse is presented with all food options simultaneously. This method has been determined to accurately represent the food habits of small mammals (Drozdz 1966). We presented mice with two native seed species, *Croton californicus* and *Stipa pulchra* (a forb and a grass, respectively), and two non-native seed species, *Avena sativa* and *Panicum miliaceum* (a forb and a grass, respectively) that are found within the commercial finch seed diet. All mice had experience consuming all four of these seed species prior to testing.

To ensure that the mice were motivated to collect seeds, each focal mouse was placed into a holding cage without food. The holding cage was filled with approximately 3 cm of sand and a 'T'-shaped PVC pipe from the focal mouse's home cage for shelter. Focal mice remained in the holding cage for no longer than 120 min.

Preference trials occurred in a clear, acrylic cage (60 x12 x 60 cm), divided into two, separate arenas (30 x 12 x 30 cm each) by an opaque barrier; the floor of which was filled with approximately 8 cm of sand. Prior to each trial, the top layer of sand was sifted to remove any seeds or debris. Four seed cups were then placed equidistant from each other in the center of each arena and filled with 1.00 g of seed (See Figure 1-1). The location of the seed species was randomized between trials. Two mice were tested simultaneously, one in each adjacent arena. An additional empty seed cup was placed at the center of each cage to mark the mouse's starting position for the trial and prevent placement bias. Preference trials were 90 min in duration and occurred after dusk (beginning approximately at 21:00). All trials were recorded from above using a wall-mounted video camera.

Upon termination of the trial, each focal mouse was returned to its home cage and uneaten seed or plant material was collected, sorted by species, and reweighed.

We identified and recorded 7 primary behaviors for the duration of each trial: exploring the arena, near seed cup, investigating seed cup, caching, jumping, sand bathing, and digging (See Ethogram of behaviors; Table 1-1) and quantified behavior using Behavioral Observation Research Interactive Software (BORIS 2018). A behavior had to occur consistently for at least 2 seconds before being recorded.

Seed Collection

All commercial non-native seeds used in this experiment were taken from the finch seed mix provided by Leach Grain & Milling. Both *Avena sativa* and the white variant of *Panicum miliaceum* were chosen for the preference experiments because they were the most readily consumed by mice at the facility when provided (personal observation). Similarly, both *Croton californicus* and *Stipa pulchra* were chosen for the preference experiment because they were the most readily consumed of the native species when provided in the enrichment mix (personal observation). *C. californicus* and *S. pulchra* are perennial plants found across coastal sage scrub and chaparral regions in Orange and San Diego Counties and their seeds constitute part of the natural diet of PPM (Shier et al. 2016).

In order to remain consistent with protocol utilized by the breeding facility, the seed-bearing pericarps were not removed from the native or non-native seeds provided. Native seeds were sterilized in an autoclave prior to placement within PPM enclosures. Autoclave sterilization is used by many breeding facilities to decrease the risk of spreading any potential bacteria or

pathogens that may be present in the feed (National Research Council Subcommittee on Laboratory Animal Nutrition, 1995).

Nutritional Assessment

Near infrared-reflectance spectroscopy (NIRS) is widely used as an efficient method for seed nutritional characteristic analysis in small seed sample sizes of 3 to 4 grams (Hom et al. 2007). Using the NIRS system (model DS2500) at the San Diego Zoo Institute for Conservation Research, we analyzed samples of the seeds presented in the preference experiment (*Avena sativa*, *Panicum miliaceum*, *Croton californicus*, and *Stipa pulchra*) for the following characteristics: percent crude protein, percent crude fat, percent moisture, percent crude fiber, percent starch, percent ash, and percent nitrogen content. These are commonly measured characteristics of seeds utilized in preference experiments and diet assessment (Kerley and Erasmus 1991; Kasparian and Millar 2004; Ríos et al. 2012; Bonacchi et al. 2017). None of the seeds analyzed for nutritional content were autoclaved.

To aide with replacing the commercial captive diet into a fully native diet (and therefore preventing future unintentional dietary preferences for the commercial captive diet), we also analyzed the samples of the other native species that were provided to PPM as enrichment, but not utilized in this experiment (*Artemeisia californica*, *Eriogonum fasciculatum*, *Salvia apiana*, and *Salvia mellifera*), for the same nutritional characteristics.

Prior to analysis, seed samples were husked because PPM have not been observed consuming pericarps, similar to other heteromyids (Jenkins 1988; Jenkins and Ascanio 1993). Seed samples were then ground in a Kniftec mill (model KN295). Ground samples were placed within the NIRS sample holder (3 cm diameter round cell) until one-half to three-fourths full. To

create a calibration for each seed type's nutrient and characteristic profile, approximately 30 ground samples were analyzed per native species and 3 – 7 ground samples per non-native species. Samples were then sent to the DairyOne Forage Lab, Ithaca, NY, USA for chemical analysis.

Statistical Analyses

All data analyses were carried out using SAS software, Version 9.4 (SAS Institute Inc., Cary, NC, USA).

To identify the influences of PPM seed foraging preferences between native and commercial non-native seed species, we calculated the quantity of seeds foraged, time investigating seed cup, first seed type investigated, and frequency of investigations of seed cups by both species and origin. Quantity of seeds foraged was calculated as 1 – the giving up density (GUD; the remaining quantity of seeds within the seed cup). Due to the limitations of the video observations, true consumption activity could not be accurately identified; therefore 'foraging' in the context of this paper refers to the quantity of seeds in grams that were removed from the seed cup by the focal mouse for consumption or caching. Other preference studies utilizing the Cafeteria Method have defined preference with the Rodger's Index in which tests of food choice account for the order, consumption rate, and total amount of each food type eaten (Rodgers 1990). However, the protocol restrictions at the conservation breeding facility prevented the calculation of consumption rate, and therefore it was not feasible to use Rodger's Index in this study. Preference was indicated instead by the highest quantity of seed type foraged and the frequency of visits to the seed cup.

The quantity of seeds (g) foraged and total time investigating (s) were analyzed using general linear mixed models (Proc GLIMMIX; SAS 9.4). We entered body mass as a continuous covariate, sex, seed species, seed origin and relevant interactions as fixed effects, and individual mouse ID as a random effect.

Principal component analysis (PCA) was used to reduce the dimensionality of the data and identify the primary axes of variation in seed nutritional characteristics of the four seed species used in this experiment (Proc FACTOR; SAS 9.4). The variables included in the PCA were (in percentages): crude protein, crude fat, moisture, crude fiber, starch, ash, and nitrogen content. Scores from principal components with eigenvalues of $\lambda \geq 1.0$ were used to compare the characteristics of native and non-native (commercial) seeds were compared in nonparametric Wilcoxon two-sample tests (Proc NPAR1WAY; SAS 9.4).

Experiment 2: Effect of Exposure During Development on Foraging Preferences

We tested the effect of exposure to invasive non-native seed types on the foraging preferences of $n = 30$ captive born adult PPM ($n = 15$ males, $n = 15$ females). We separated pups into two groups: (1) Control (no exposure to invasive non-native seeds prior to trial, $n = 10$ mice) and (2) Exposure (exposure to invasive non-native seeds prior to trial, $n = 20$ mice). To determine if there was a sensitive period during development that influenced dietary preference formation, we further divided the Exposure group into two treatments: (1) Pre-weaned (early exposure to invasive non-native seeds, $n = 10$ mice) and (2) Weaned (late exposure to invasive non-native seeds, $n = 10$ mice). All mice were exposed to commercial non-native seed species found within the daily finch mix diet in accordance with dietary protocol at the facility.

The Pre-weaned treatment group consisted of PPM adults that were exposed to invasive non-native seeds during early development (prenatal – 30 days of age). Female PPM have a total gestation period of 22 – 23 days and are unable to be identified as being pregnant until at least 19 days post-mating. Therefore, once females were identified as being pregnant between 19 – 21 days post-mating, they were presented with 1.25 ml of a 50/50 mixture of the invasive non-native seeds in addition to their regularly provided captive diet mix 3 times a week for the rest of the duration of their pregnancy (resulting in 2 – 3 servings before birth of pups). Once the pups were born, we continued to provide the invasive non-native mix 3 times a week until the pups were 30 days old (13 days total over a 30-day period). The Weaned treatment group consisted of PPM adults that were not exposed to the invasive non-native seeds until after weaning (30 – 60 days of age). Similar to the Pre-weaned group, these mice were provided 1.25 ml of the invasive non-native seed mix 3 times a week over a 30-day exposure period (13 days total). After 30 d of age, neither treatment group was exposed to the invasive non-native seed mix until the preference trial.

Similar to Experiment 1, we simultaneously presented the focal mice with four foraging options using the Cafeteria Method (Drozdz 1966). Mice were provided two commercial non-native seed species found in their daily captive diet, *Avena sativa* and *Panicum miliaceum* (a forb and a grass, respectively), and two invasive non-native seed species, *Erodium botrys* and *Bromus madritensis rubens* (a forb and a grass, respectively). Both invasive species are abundant throughout the current range of PPM.

The remainder of the preference trial design, methodology, and data collection is identical to Experiment 1.

Seed Collection

Similar to Experiment 1, commercial non-native *Avena sativa* and *Panicum miliaceum* were acquired from the finch seed mix provided by Leach Grain & Milling. The invasive non-native seed species utilized in this study were collected near the PPM release site at the Laguna Coast Wilderness Park (Lat/Long: 33.565, -117.786 and other San Diego County Parks (Buena Vista Lagoon (Lat/Long: 33.168,-117.358), Mission Trails Park (Lat/Long: 32.846,-117.037), San Onofre State Beach (Lat/Long: 33.376,-117.569)). We collected *Erodium botrys* and *Bromus rubens* during May and June of 2017 and 2018.

Collected seeds were stored in 1-gallon plastic bags and mixed together by species to prevent potential bias in preferences for source population. The seeds were then autoclaved to decrease the risk of spreading bacteria or pathogens that may be present in the seed exteriors.

To remain consistent with the breeding facility protocol, the seed-bearing carpels were not removed from the invasive non-native seeds provided; however, all other outer structures were removed, such as the spiral-shaped style or awn on *Erodium botrys* seeds.

Nutritional Assessment

Using the San Diego Zoo Institute for Conservation Research NIRS system, we analyzed samples of the invasive non-native seeds presented in this preference experiment (*Erodium botrys* and *Bromus rubens*) for the same characteristics as in Experiment 1. All seed preparations were identical to Experiment 1.

Statistical Analyses

To identify the influences of PPM seed foraging preferences for wild non-native seed species by exposure during different developmental periods, we calculated the amount of seeds foraged, time investigating seed cup, first seed type investigated, and frequency of investigations of seed cups by both species and origin (identical to Experiment 1).

The quantity of seeds (g) foraged and total time investigating (s) were analyzed using general linear mixed models (Proc GLIMMIX; SAS 9.4). We entered body mass as a continuous covariate, sex, seed species, seed origin, and relevant interactions as fixed effects, and individual mouse ID as a random effect.

As in Experiment 1, principal component analysis (PCA) was used to reduce the nutritional characteristics of the four seed species used in this experiment to a smaller number of orthogonal variables (Proc FACTOR; SAS 9.4). Scores from PCs with $\lambda \geq 1.0$ were used to compare the nutritional characteristics of native, non-native (invasive) and non-native (commercial) seeds in nonparametric Wilcoxon two-sample tests (Proc NPAR1WAY; SAS 9.4).

RESULTS

Experiment 1: Effect of Seed Origin on Foraging Preferences

PPM foraged significantly more on commercial non-native seeds (mean foraged 0.414 ± 0.105 g) than native seeds (mean foraged 0.041 ± 0.010 g), indicating an overall preference for commercial non-native seed types ($F_{1,58} = 398.93$, t = -19.97, $n = 20$, $p < 0.01$; Table 1-2a; Figure 1-2). Non-native seeds, *Panicum miliaceum* and *Avena sativa*, comprised 48.35% and 42.64% of all seeds foraged and native seeds, *Stipa pulchra* and *Croton californicus*, comprised 6.26% and

2.74%. PPM foraged on *Panicum miliaceum* only marginally more than *Avena sativa* ($t = -1.81$, $p = 0.08$), but significantly more than both of the native seeds, *Stipa pulchra* ($t = -14.52$, $p < 0.01$) and *Croton californicus* ($t = -13.95$, $p < 0.01$). *Stipa pulchra* was the preferred native seed type ($t = 3.44$, $p < 0.01$). Neither sex ($F_{1,58} = 0.39$, $t = 0.62$, $n = 20$, $p = 0.54$) nor weight ($F_{1,58} = 3.60$, $t = 1.90$, $n = 20$, $p = 0.06$) influenced PPM foraging behavior.

PPM investigated non-native seeds first 80% of the time and for significantly longer (mean duration of 198.3 ± 57.7 s or 71.73% of total time) than native seeds (mean duration of 78.2 ± 22.8 s; $F_{1,58} = 972.09$, $n = 20$, $p < 0.01$; Table 1-2b; Figure 1-3). *Avena sativa* was investigated first 50% of the time, *Panicum miliaceum* 30% of the time, *Stipa pulchra* 15% of the time, and *Croton californicus* 5% of the time. *Avena sativa* was investigated longer (mean duration of 124.2 ± 57.7 s or 44.91% of total time) than *Panicum miliaceum* ($t = -15.70$, $p < 0.01$), *Stipa pulchra* ($t = -24.77$, $p < 0.01$), and *Croton californicus* ($t = -31.38$, $p < 0.01$). *Stipa pulchra* was the most investigated native seed species (mean duration of 48.7 ± 15.6 s or 17.59% of total time; $t = -9.59$, $p < 0.01$). Neither sex ($F_{1,58} = 3.01$, $t = 1.74$, $n = 20$, $p = 0.09$) nor weight ($F_{1,58} = 0.30$, $t = -0.55$, $n = 20$, $p = 0.59$) influenced time PPM spent investigating seed types.

The PCA of nutritional composition variation between 8 different characteristics resulted in three principal components with eigenvalues ≥ 1 that together accounted for 98.12% of the variance among the four seed species (Table 1-3). The nutrient pattern described by component one separates seeds that are high in fat, protein, nitrogen, ash, and fiber from those that are high in starch. Component 2 mainly separates seeds by moisture content. Component 3 shows a smaller separation of seeds by protein and nitrogen content. Because subjects in Experiment 1 foraged on *Avena sativa* more than any other seed type, PPM may prefer seed types that are relatively higher in starch and moisture, but lower in protein, nitrogen, ash, fat, and fiber (Table

1-4). Non-native commercial and native seeds were significantly separated by each of the 3 components (component 1: $z = -3.890$, $n = 45$, $p < 0.01$, component 2: $z = 3.289$, $n = 45$, $p < 0.01$, component 3: $z = -3.489$, $n = 45$, $p < 0.01$). Non-native commercial seeds showed higher levels of starch and moisture, with relatively lower levels of the remaining nutrients (Table 1-4; Figures 1-4a, 1-4b).

Experiment 2: Effect of Exposure During Development on Foraging Preferences

PPM showed a foraging preference for non-native commercial seeds (mean foraged 0.273 ± 0.052 g) over non-native invasive seeds (mean foraged 0.031 ± 0.006 g; $F_{1,88} = 15.15$, $n = 20$, $p < 0.01$; Table 2-1a; Figure 1-5), regardless of previous exposure to non-native invasive seeds (exposed: $t = 17.92$, $n = 10$, $p < 0.01$; not exposed: $t = 6.76$, $n = 20$, $p < 0.01$). Nevertheless, PPM previously exposed to non-native invasive seeds foraged significantly more on these seed types (0.045 ± 0.008 g) than PPM that were not exposed to non-native invasives (0.003 ± 0.002 g; $t = -3.94$, $p < 0.01$). *Panicum miliaceum* was the most overall foraged seed species, and *Erodium botrys* was the most foraged non-native invasive seed species (Table 2-1b). Regardless of previous exposure to non-native invasive seed types, PPM in both exposure groups investigated non-native commercial seed types first only 3% of the time but for a longer duration than non-native invasive seed types ($F_{1,33} = 14.68$, $t = -1.46$, $p = 0.15$; Table 2-2a; Figure 2-1). PPM that were previously exposed to invasive seed types investigated these seeds for significantly longer (91.6 ± 21.9 s) than mice that were not exposed to these seed types (18.7 ± 12.0 s; $t = -6.03$, $p < 0.01$).

The developmental period of exposure influenced PPM foraging decisions with non-native invasive seeds ($F_{2,87} = 7.58$, $n = 30$, $p < 0.01$; Table 2-1b; Figure 2-2). Control treatment mice foraged significantly on less *Erodium botrys* (0.002 ± 0.002 g) than Pre-Weaned treatment mice (0.038 ± 0.008 g; t = 3.58, p = 0.01), but not Weaned treatment mice (0.008 ± 0.003 g; t = 1.65, p = 1.03). Control mice also foraged on significantly less *Bromus rubens* (0.001 ± 0.001 g) than both Pre-Weaned mice (0.022 ± 0.005 g; t = 2.83, p = 0.01) and Weaned mice (0.015 ± 0.008 g; t = 2.53, p = 0.01). Pre-Weaned mice foraged for significantly more *Erodium botrys* (t = -2.75, p = 0.01) but not *Bromus rubens* (t = -0.66, p = 0.513) when compared with mice in the Weaned treatment. Neither sex ($F_{1,88} = 0.13$, t = -0.36, $n = 30$, p = 0.72) nor weight ($F_{1,88} = 0.21$, t = 0.45, $n = 30$, p = 0.65) influenced PPM foraging decisions.

Overall, time PPM spent investigating different seed species was influenced by exposure to non-native invasive seed types during different periods of development ($F_{2,87} = 6.96$, $n = 30$, $p < 0.01$; Table 2-2b; Figure 2-4). Of all seed types provided, Control treatment mice investigated non-native invasive seeds first 3% of the time (including both *Bromus rubens* and *Erodium botrys*), Pre-weaned mice 3% of the time (only *Erodium botrys*), and Weaned mice did not explore non-native invasive seeds before non-native commercial seeds. However, Control treatment mice spent significantly less time investigating non-native invasive seeds types (18.7 ± 12.0 s) than non-native commercial seed types (122.8 ± 31.2 s; t = 2.35, p < 0.01). Pre-weaned treatment mice investigated non-native invasive seed types (148.7 ± 31.9 s) significantly more than mice in the Weaned treatment (34.4 ± 16.6 s; t = -4.58, p < 0.01). Control treatment mice spent significantly less time investigating *Erodium botrys* (6.9 ± 4.4 s) than Pre-weaned mice (117.2 ± 24.5 s; t = 9.16, p < 0.01) and Weaned mice (27.3 ± 13.4 s; t = 4.57, p < 0.01), but did not investigate *Bromus rubens* (11.8 ± 11.6 s) more or less than Pre-weaned treatment (13.8 ±

4.2 s; t = 1.18, p = 0.24) and Weaned treatment mice (7.1 ± 3.3 s; t = -1.17, p = 0.25). Pre-weaned mice spent more time investigating both *Erodium botrys* (t = -4.89, p < 0.01) and *Bromus rubens* (t = -2.26, p = 0.03) than Weaned treatment mice. Neither sex ($F_{1,90}$ = 0.16, t = 0.41, *n* = 30, p = 0.69) nor weight ($F_{1,90}$ = 0.31, t = 0.55, *n* = 30, p = 0.58) influenced the amount of time PPM investigated different seed species.

The PCA of nutritional composition variation resulted in two principal components with eigenvalues ≥ 1 that together accounted for 93.35% of the variance among the four different seed species (Table 2-3). The nutrient pattern described by component one separated seeds that are high in protein/nitrogen, ash, and fat. Component two separated seeds that are high in moisture and starch but low in fiber. Because subjects in Experiment 2 foraged on *Panicum miliaceum* more than any other seed type, PPM may prefer seed types that are relatively high in starch and moisture, but low in protein, fat, and fiber (Table 2-4). These characteristics are also descriptive of *Avena sativa*, which was preferentially foraged for by subjects in Experiment 1. Non-native invasive seeds showed higher levels of protein, nitrogen, fat, ash, but relatively lower levels of the moisture and starch when compared with non-native commercial seeds (component 1: z = -3.138, p < 0.01; component 2: z = 3.044, p < 0.01; Figure 2-5).

The nutritional composition variation of these same characteristics of the native seeds from Experiment 1 and the invasive seeds from Experiment 2 were compared using a PCA. The PCA yielded 3 principal components with eigenvalues ≥ 1 that together accounted for 93.75% of the variance among the four seed species (Table 2-5). Component one separated seeds that are high in ash, protein, nitrogen, and fat, but low in fat. Component two separated seeds by moisture content. Component three separated seeds that are high in starch, protein and nitrogen. When compared with native seeds, non-native invasive seeds showed higher levels of protein,

nitrogen, fat, fiber, and ash, but lower levels of starch (component 1: $z = 3.386$, $p < 0.01$; component 3: $z = -1.987$, $p = 0.05$; Figure 2-6b). Both non-native invasive and native seeds showed similar levels of moisture (component 2: $z = 1.055$, $p = 0.29$; Figure 2-6a).

DISCUSSION

Conservation breeding and reintroduction programs are faced with many management decisions in order to prevent captive conditions from forming ineffective behavioral responses in released animals (Snyder et al. 1996; Mathews et al. 2005; Stoinski and Beck 2004). These animals are often being released into habitats that are rapidly changing due to spread of invasive species (Seddon et al. 2007; Soorae 2018). As a way to combat the replacement of native food sources by invasive species, recovery programs can prepare captive-bred animals by incorporating palatable invasive prey species into the captive diet. Therefore, reintroduced animals will not be limited in foraging options and will be more likely to survive long-term. The results of this study shed light on the importance of understanding how foraging skills and dietary preferences develop in a captive-bred endangered heteromyid, and whether captive-bred animals can be induced to consume a palatable invasive species.

Regardless of how much time they spend investigating different seeds, PPM prefer non-native commercial seed species, *Avena sativa* and *Panicum miliaceum*, over native seed species, *Croton californicus* and *Stipa pulchra*. This finding suggests that, even with exposure to native seeds in captivity, captive-bred PPM continue to prefer non-native commercial seeds, consistent with the preliminary foraging preference study (Shier et al. 2016). Although it is considered uncommon for specialists, like PPM, to preferentially forage for non-native food types (Keane

and Crawley 2002), granivorous rodents frequently choose non-native seeds found in commercial finch mixes over native seeds (Price 1983; Kelrick et al. 1986; Longland and Bateman 1998). Therefore, factors other than evolutionary history with a food source likely influence PPM foraging preferences. Seed size is typically an important limiting factor in the seed choices of granivorous rodents, as larger seeds are associated with increased handling time (Kerley and Erasmus 1991; Jenkins and Ascanio 1993; Muñoz and Bonal 2008). PPM do not appear to make foraging decisions based only on seed size, as they preferred the larger of the two non-native seed species (*Avena sativa*) but the smaller of the two native species (*Stipa pulchra*). *Perognathus spp.* pocket mice, unlike larger heteromyids, do not have inflated auditory bullae or the associated smaller maximum gape from reduced jaw muscles. As a result, pocket mice are more capable of consuming larger seeds than other heteromyids (Nikolai and Bramble 1983; Jenkins and Ascanio 1993). Therefore, PPM foraging preferences are likely dictated by other factors, such as exposure to the food type during a crucial developmental period, or nutritional characteristics.

Our results indicate that there is a sensitive period of development during which PPM develop diet preferences. Mice that were previously exposed to non-native invasive seeds during the Pre-Weaned stage of development foraged for significantly more non-native invasive seeds than mice from other treatment groups. Similar to the results of Experiment 1, the time that PPM spent investigating different seed species did not influence food choices. Because mice in the Pre-Weaned treatment group foraged for invasive seed types the most, it is likely that there is some component of the rearing environment that influences foraging preference development in PPM. In lab rats (*Rattus spp.*), food preferences are thought to be formed by sampling their mother's feces, consuming or smelling particles of food that cling to their mother's fur, or from

the flavor or odor of the mother's diet that is incorporated into her milk (Galef and Henderson 1972). Although mother's milk is the most influential factor in forming rat pup foraging preferences for both palatable and unpalatable food types (Galef and Henderson 1972), dietary preferences in rabbits (*Oryctolagus cuniculus*) are influenced in part by both pup exposure to maternal feces and milk (Bilko et al. 1994). Some granivore dietary choices are also influenced by parental demonstration or social interaction with siblings during the pre-weaning stage (Galef and Clark 1972; Rymer et al. 2008). Because very little is known about the rearing environment, the role of odor, the influence of mother's milk, and/or the dynamics of social interactions between siblings and mothers in heteromyids as a whole, further research is needed to in order to determine the mechanism by which foraging preferences form.

Although mice in the Pre-Weaned treatment foraged most for invasive seeds, some individuals from the Weaned and Control treatments did forage for invasive seeds as well. This suggests that there is an influence from factors outside of the rearing environment, such as the nutritional composition of the food type. When comparing the variation in nutritional composition of non-native commercial seeds and native seeds, non-native commercial seeds show high levels of moisture and starch with relatively low levels of all other nutrients. Native seeds show the reverse, with higher nutritional variation with relatively low levels of moisture and starch. Because PPM preferred *Avena sativa* and *Panicum miliaceum* over other seed species across both experiments, PPM likely prefer seeds that have high levels of moisture and starch. PPM and other heteromyids are typically located in water-limited habitats. Heteromyids do not drink free water, rather they acquire water from preformed water present in their diet and through the oxidation of food (Schmidt-Nielsen 1964, 1972). When choosing between seeds that have a different range of nutritional characteristics, heteromyids prefer seeds that yield the most

metabolic water gain (Frank 1988). Because PPM were not water-stressed during the preference trials, they are expected to prefer seeds that show high carbohydrate, high lipid, and moderate protein levels (Frank 1988), which is consistent with our findings. Therefore, despite the co-evolutionary history of PPM with native grasses and forbs, the nutritional composition of commercial non-native seeds were more consistent with anticipated metabolic requirements. Additionally, non-native commercial seeds are distinct from non-native invasive seeds in that they have lower values of different nutritional components (such as protein, fat, and crude fiber), but higher levels of moisture. *Erodium botrys,* the most preferred of the invasive species, had comparatively higher levels of protein, fat, and crude fiber when compared with non-native commercial seeds. Future food choice experiments should incorporate nutritional composition to determine which nutritional factors are most influential in PPM foraging preferences as there has been much contradictory research on the topic in other heteromyids (Frank 1988; Schmidt-Nielsen 1964; Henderson 1990). Additionally, the impacts of different diets on the composition of the gut microbiome in PPM should be investigated as these diets may affect PPM's ability to process necessary nutrients post-release (Allan et al. 2018).

Based on the results of this study, incorporating invasive seeds as an alternative food source into an otherwise fully native seed diet will be beneficial, rather than harmful, for reintroduced populations of PPM. Generally, native species that consume invasive food types are at risk of further population decline by 1) creating an evolutionary trap if they are preferentially foraging for a nutritionally inferior invasive species (Schlaepfer et al. 2005; Wilcox and Fletcher 2016; Goetz et al. 2018), and 2) contributing to the spread of the invasive species (Nuñez et al. 2012). The vast majority of California's ecosystems are impacted by highly invasive plant species, many of which are considered to be largest threat to native populations in the region

(Bossard et al. 2000). Because invasive plants like *Erodium spp.* not only threaten to replace native food options of PPM, but also grow in such a manner that they eliminate potential burrowing habitat for PPM, being able to consume invasive seed types like *Erodium* might enable the expansion of foraging options and even habitat. PPM are unlikely to develop a preference for non-native invasive seed types because other wild heteromyids do not seem to preferentially forage for invasive seeds (Keane and Crawley 2002; Lucero 2018). The native and non-native invasive seed species analyzed in this study have similar levels of moisture, but differ in degree of other nutritional characteristics. PPM are also unlikely to contribute to the spread of invasive plant species as a result of their caching behavior. When native and invasive seeds are cached together, invasive seeds usually die before producing viable seeds in the clumped conditions (Longland et al. 1996; McMurray et al. 1997; Longland 2007), therefore the caching behavior of heteromyids is associated with native plant species recovery (Longland et al. 1996; Longland and Ostoja 2013). Additionally, because the population size and range of released PPM is so small, it is unlikely that PPM will affect the current distribution of invasive species in their habitat. Given the generally positive impacts of incorporating non-native invasive seeds into their captive diet, the recovery program for PPM is likely to benefit greatly from the results of this study.

While conservation-breeding programs are crucial to adaptive management efforts, many are limited in scope as a result of rigorous protocol associated with recovering an endangered species. First, we could not significantly alter the diet of trial subjects for a long duration of time, and therefore could not implement a more rigorous assessment of dietary preferences using the Rodgers Index (Rodgers 1990). Second, because the facility requires all non-commercial seeds to be autoclave-sterilized, our experiments had an additional condition of not autoclave-sterilized

(non-native commercial seeds) and autoclave-sterilized (native and non-native invasive seeds). An exploratory Wilcoxon paired analysis of 10 mice showed a preference for autoclave-sterilized *Panicum miliaceum* over not autoclave-sterilized *Panicum miliaceum* (foraged: z = 2.412, t = 0.026, *n* = 10, p = 0.02; time investigated: z = 0.380, t = 0.708, *n* = 10, p = 0.70). Although significant, the foraging preference for autoclave-sterilized seeds was driven by 2 of the 10 mice, and therefore additional research is needed to fully understand the effects of autoclaving on PPM seed preferences. The autoclaving process has been shown in other seed species to increase total fat, but reduce moisture, protein, sugars, and ash (Negedu et al. 2013). The process was also shown to remove anti-nutrients, which are plant compounds that reduce the consumer's ability to absorb some of the nutrients (Alagbaoso et al. 2015). Future tests should investigate the importance of autoclave-sterilization on PPM foraging choices as well as to determine how the process alters the nutritional composition of native and non-native invasive seeds. And finally, due to the difficulty of observing specific foraging behaviors with the mounted video camera, other factors that could influence foraging choices, such as seed husking time or actual seed consumption as opposed to caching amount, could not be investigated. Despite these limitations, our food choice experiments allowed us to isolate when foraging preferences are likely to develop, what nutritional characteristics likely influence foraging preferences, and if PPM can be induced to willingly consume non-native invasive species.

Here, we show that conservation-breeding and reintroduction programs have the potential to prepare endangered captive-bred animals for a rapidly changing environment. By providing a series of food choice experiments, we determined that PPM foraging preferences form during Pre-Weaned development and that they will consume non-native invasive food types. Future studies should focus on determining how foraging preferences change by season and if they

change when trained captive-bred animals are released, as the relative abundance of native and invasive species present at the release site may alter foraging behaviors. Additionally, when released, long-term assessments of native and invasive plant species distribution should be assessed to determine if PPM can act as a natural biological control. Other conservation-breeding programs facing obstacles imposed by invasive species can look to this study as a starting point in creating novel adaptive management strategies to ensure the long-term persistence of reintroduced endangered populations.

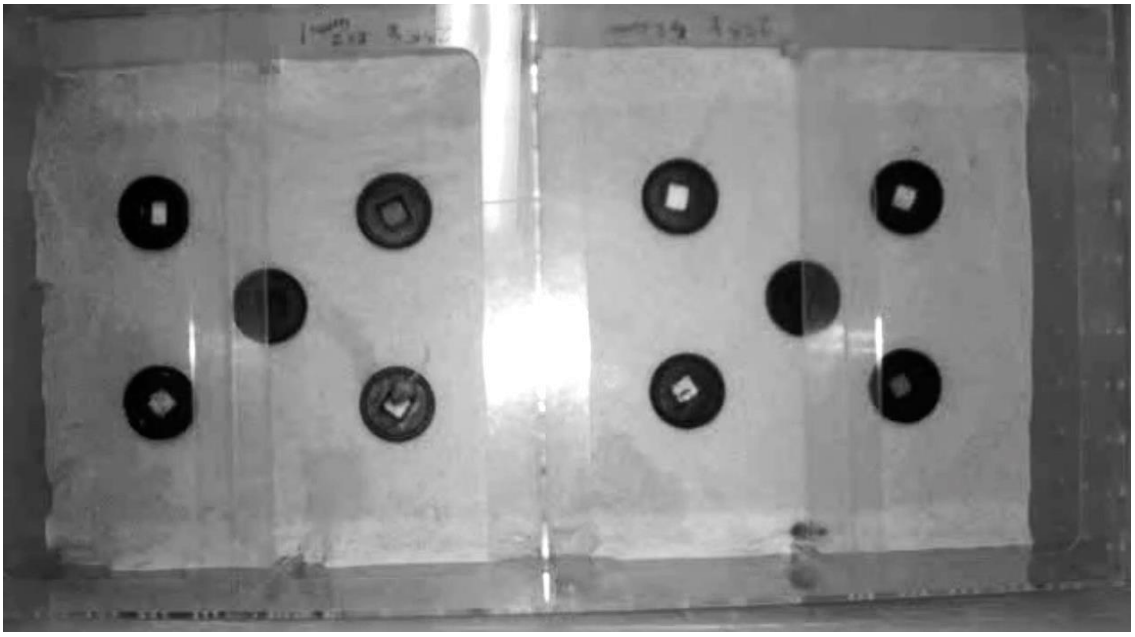

Figure 1-1. Top-down view from the wall-mounted video camera displaying the preference trials of mouse 233 and mouse 235. Mouse 233, on the left, is investigating the bottom right seed cup and mouse 235, on the right, is exploring the arena.

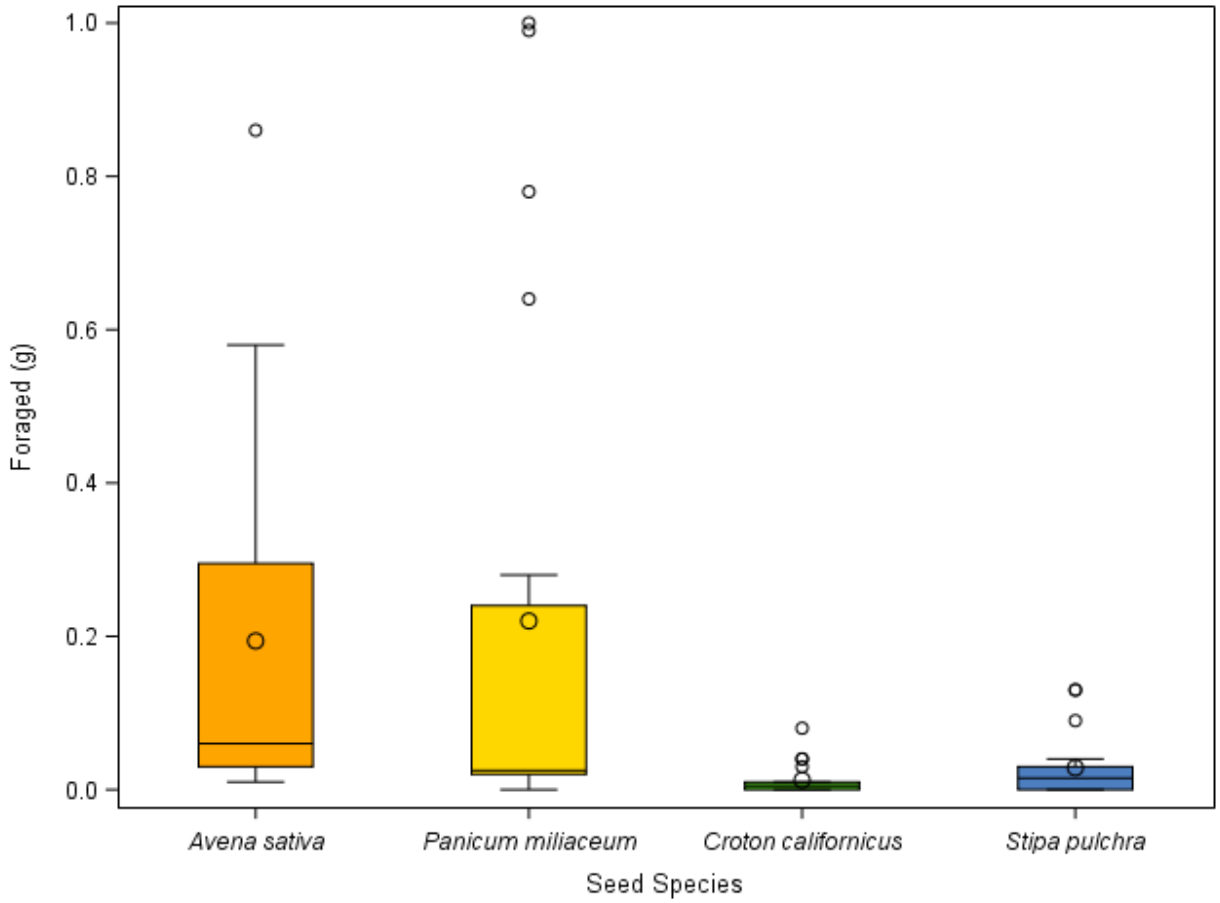

Figure 1-2. Influence of seed origin on the quantity of seeds foraged by PPM in Experiment 1. Boxplot depicts the median (horizontal line within the box), the interquartile range (box), lower and upper adjacent values (whiskers), and outside values (open circles). *N* = 20 foraging events on all 4 seed species.

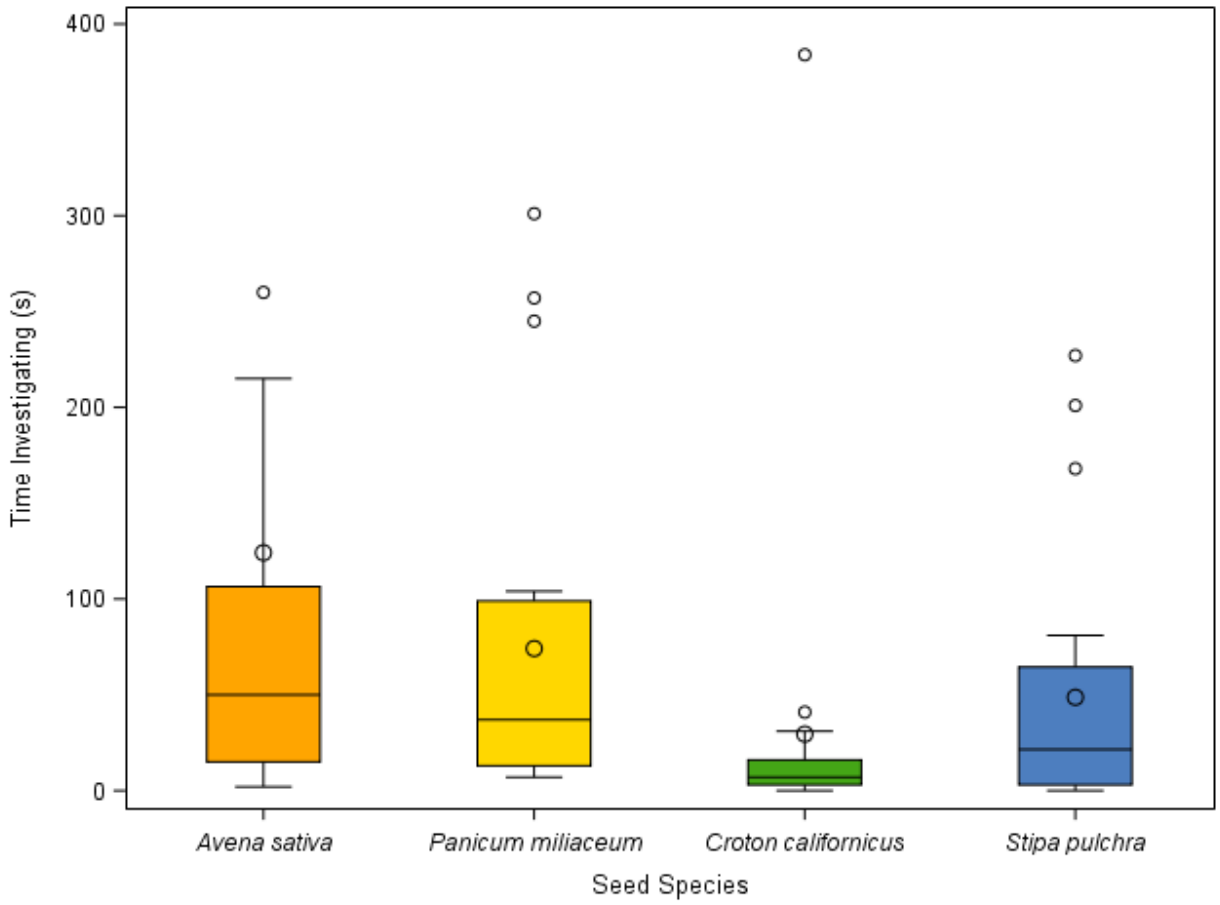

Figure 1-3. Influence of seed origin on the time PPM spent exploring seeds in Experiment 1. Boxplot depicts the median (horizontal line within the box), the interquartile range (box), lower and upper adjacent values (whiskers), and outside values (open circles). *N* = 20 foraging events on all 4 seed species. For clarity, I removed an outlier from *Avena sativa* (1180 s) from the figure.

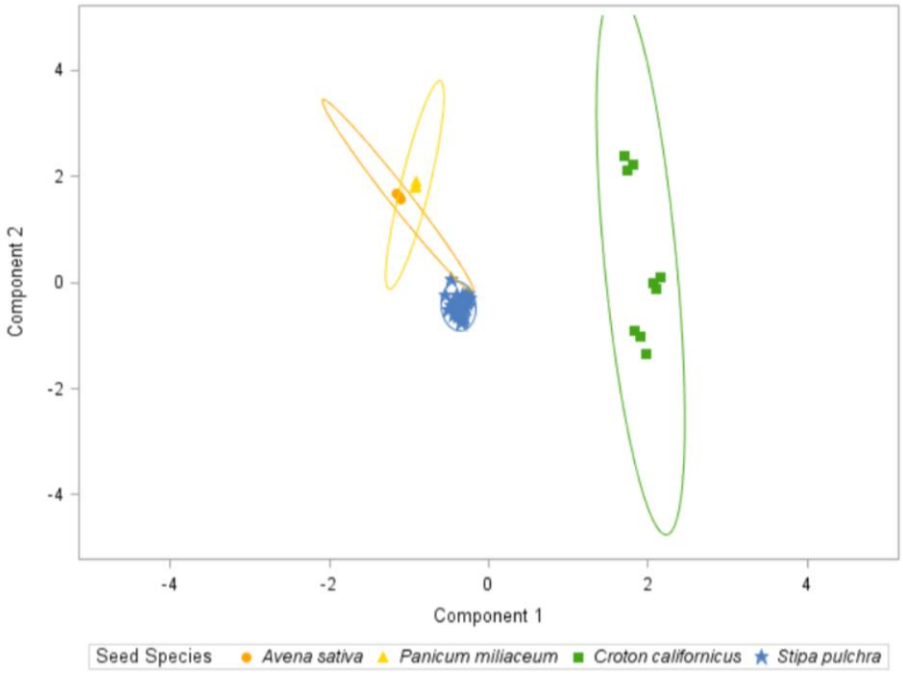

Figure 1-4a

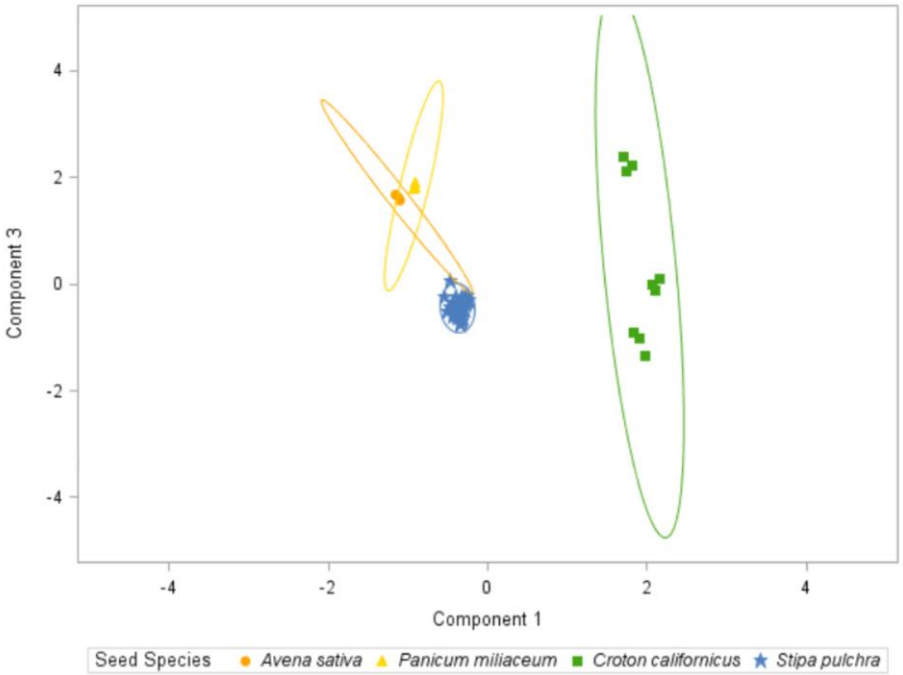

Figure 1-4b

Figures 1-4a and 1-4b. Scatterplot of principal component scores from nutritional analysis on nonnative (commercial) seed species and native seed species. Ellipses indicate scoring coefficient variation range within a 95% confidence interval. Symbols indicate the number of observations by each seed species. Component 1 separates seeds that are high in fat, protein, nitrogen, ash and fiber (positive values) from those that are high in starch (negative values). Component 2 mainly separates seeds by moisture content. Component 3 mainly separates seeds by protein and nitrogen content.

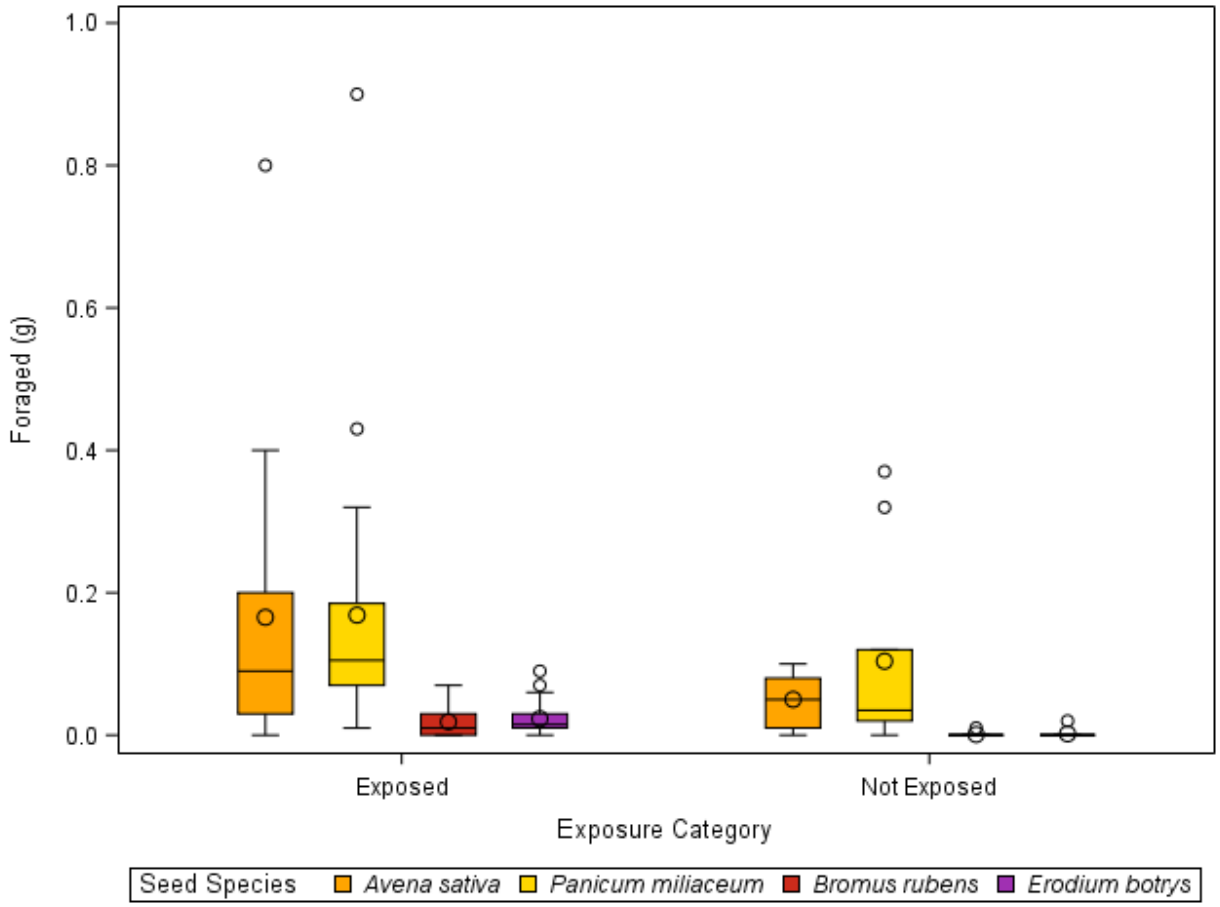

Figure 2-1. Influence of early exposure on the quantity of seeds foraged in Experiment 2. Boxplot depicts the median (horizontal line within the box), interquartile range (box), lower and upper adjacent values (whiskers), and outside values (open circles). *N* = 10 mice in each exposure category.

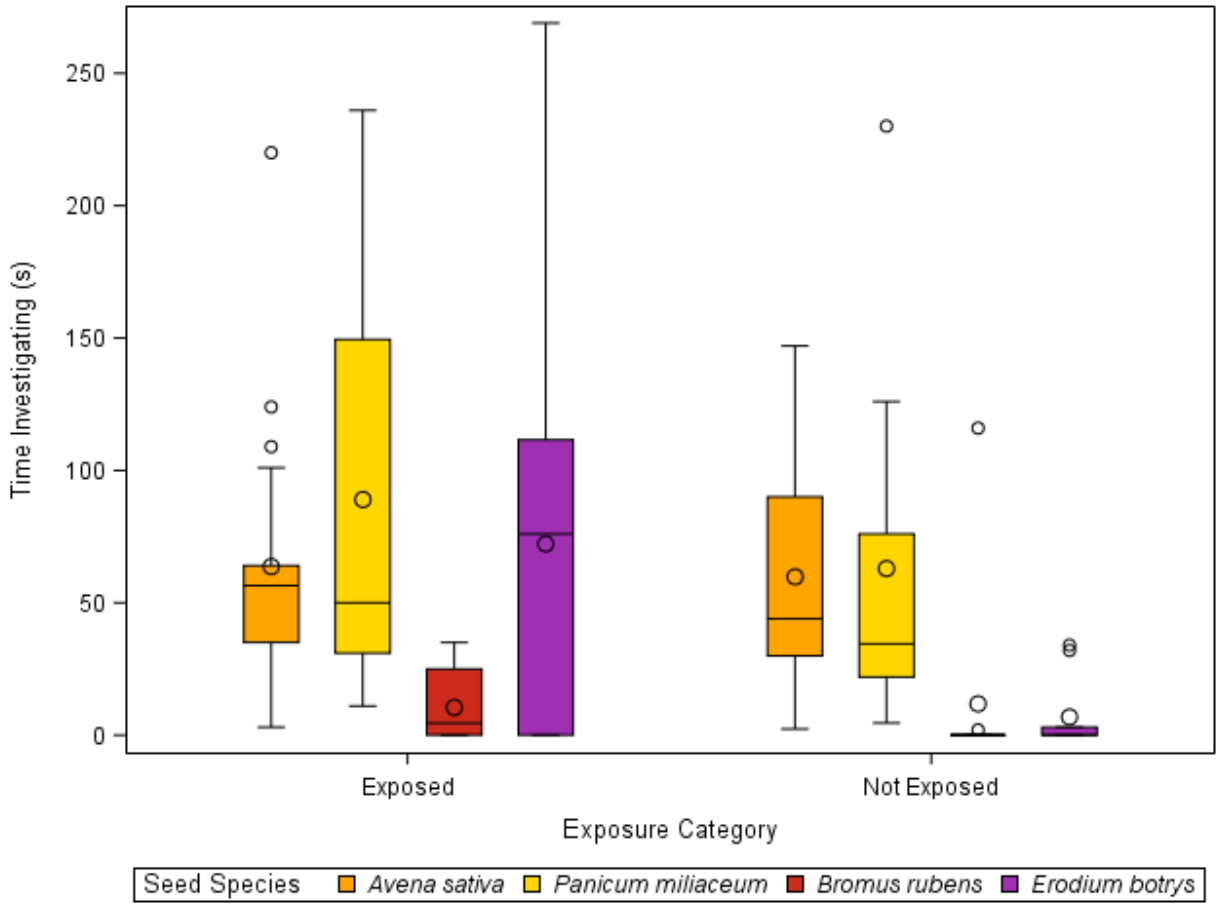

Figure 2-2. Influence of early exposure on the time spent investigating seeds in Experiment 2. Boxplot depicts the median (horizontal line within the box), interquartile range (box), lower and upper adjacent values (whiskers), and outside values (open circles). *N* = 10 mice in the Exposed Category and *N* = 20 mice in the Exposed Category.

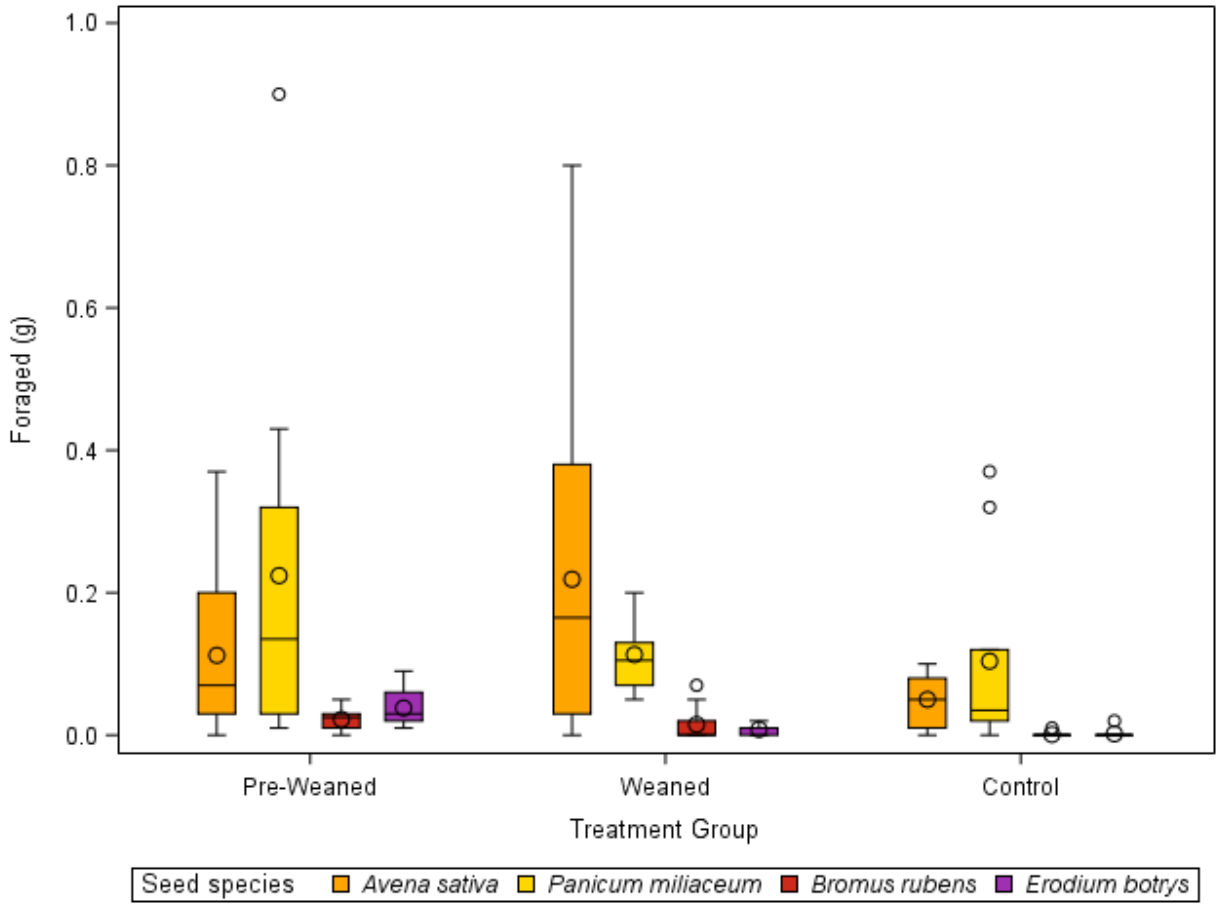

Figure 2-3. Influence of developmental stage on the quantity of seeds foraged in Experiment 2. Boxplot depicts the median (horizontal line within the box), interquartile range (box), lower and upper adjacent values (whiskers), and outside values (open circles). *N* = 10 mice in the Pre-Weaned treatment, *N* = 10 mice in the Weaned treatment, and *N* = 10 mice in the Control treatment.

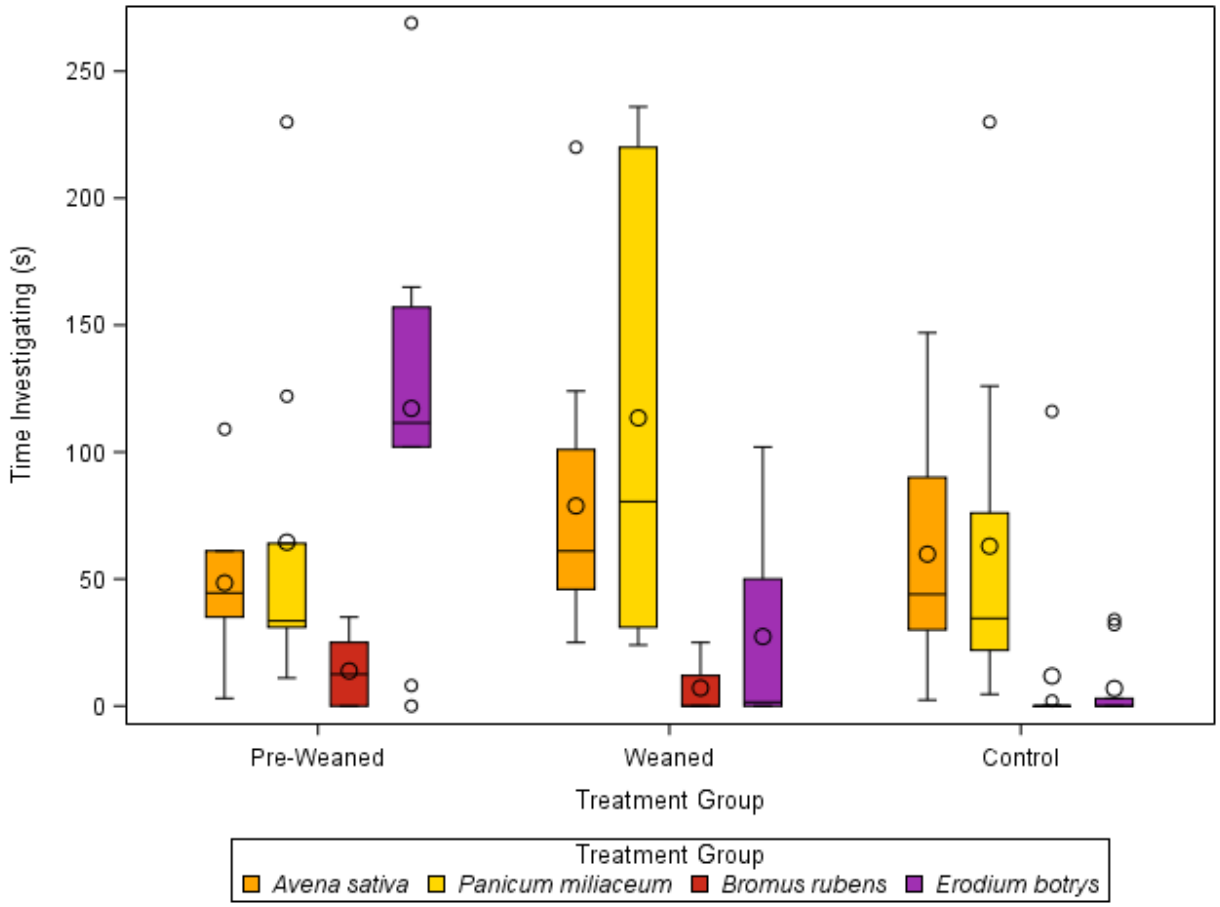

Figure 2-4. Influence of developmental stage on the time spent investigating seeds in Experiment 2. Boxplot depicts the median (horizontal line within the box), interquartile range (box), lower and upper adjacent values (whiskers), and outside values (open circles). *N* = 10 mice in the Pre-Weaned treatment, *N* = 10 mice in the Weaned treatment, and *N* = 10 mice in the Control treatment.

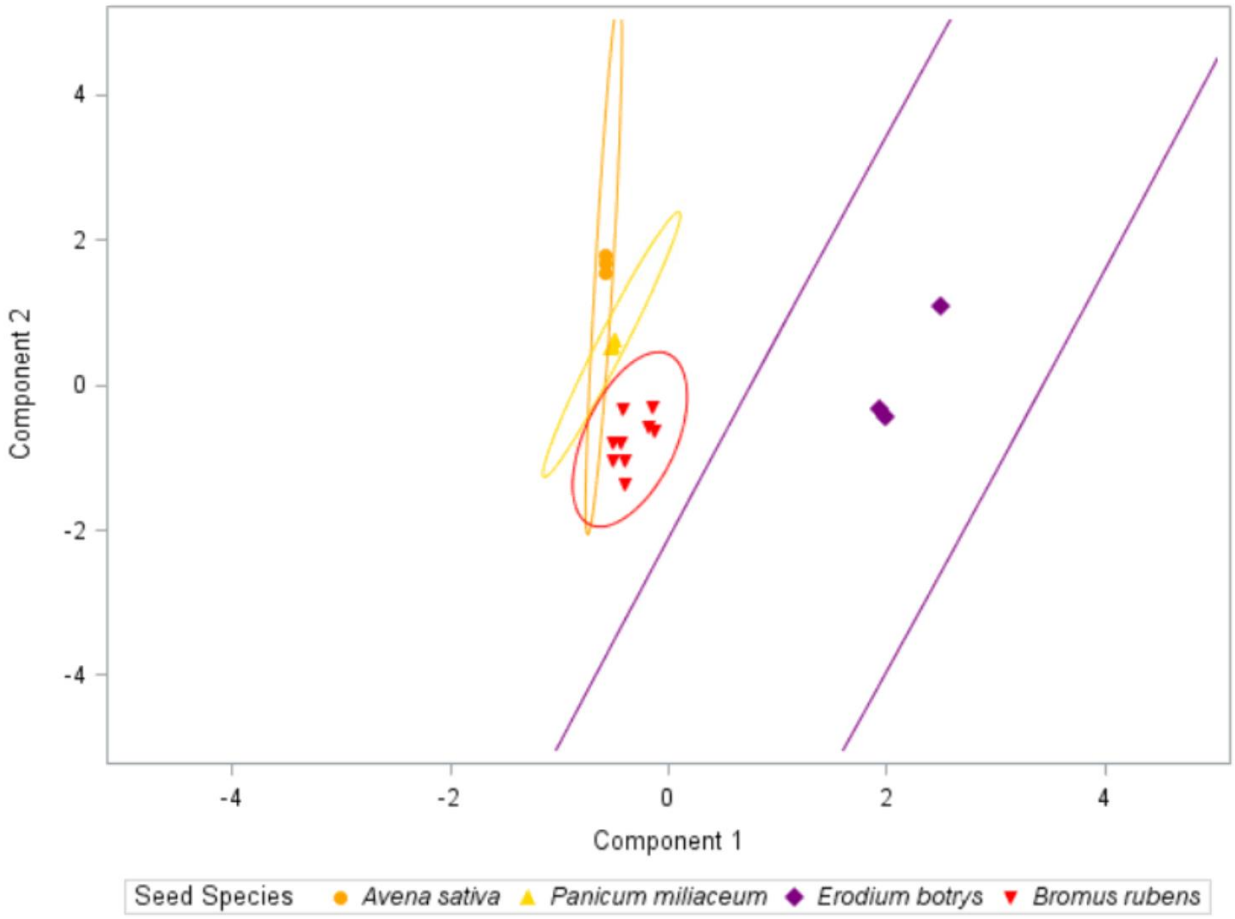

Figure 2-5. Scatterplot of principal component scores from nutritional analysis on nonnative (commercial) seed species and nonnative (invasive) seed species. Ellipses indicate scoring coefficient variation range within a 95% confidence interval. Symbols indicate the number of observations by each seed species. Component 1 separates seeds that are high in protein, nitrogen, fat, and ash (positive values). Component 2 mainly separates seeds that are high in moisture content (positive values) and low in fiber content (negative values).

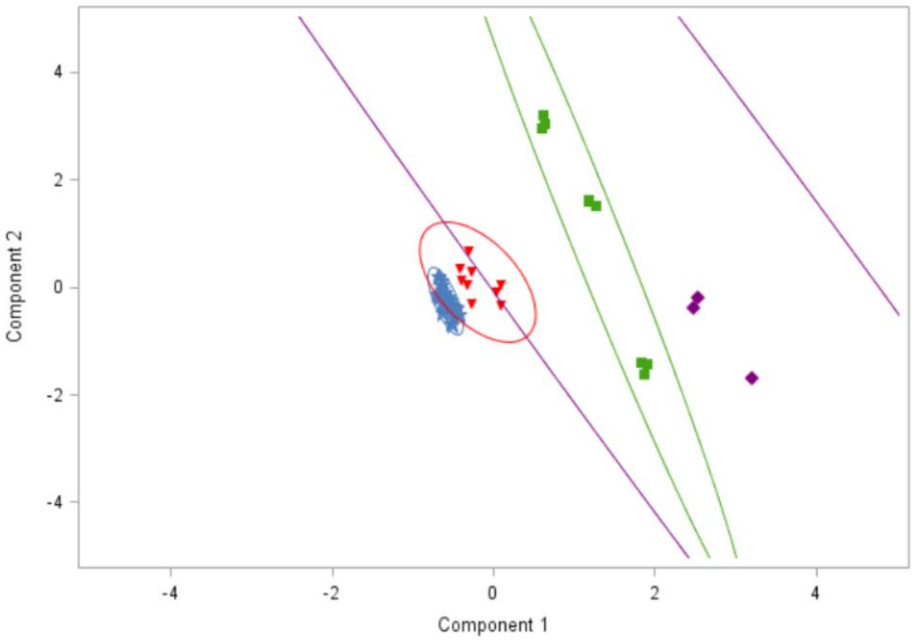

Figure 2-6a

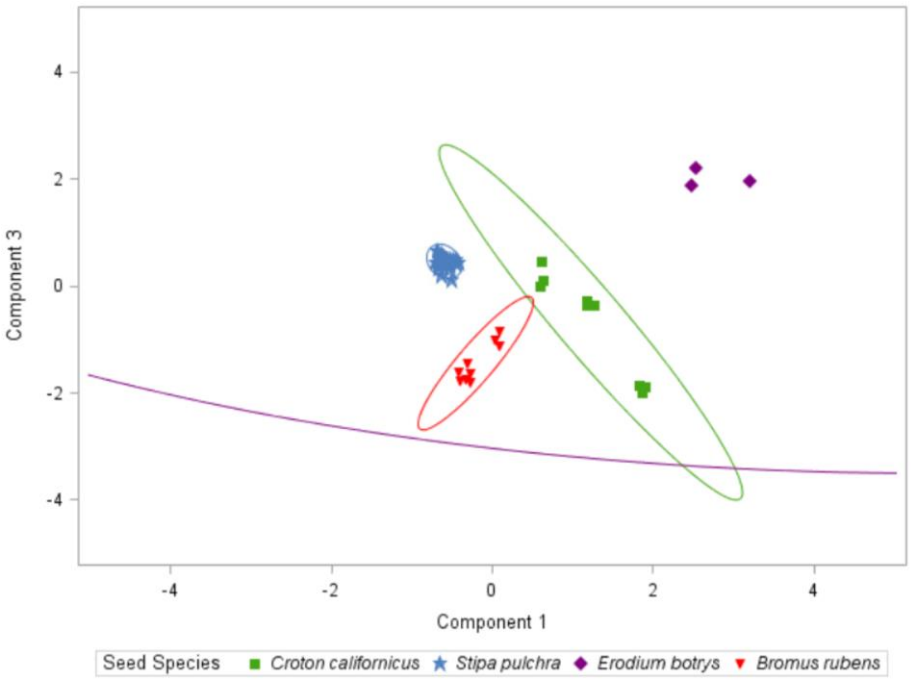

Figure 2-6b

Figures 2-6a and 2-6b. Scatterplot of principal component scores from nutritional analysis on nonnative (invasive) seed species and native seed species from Experiments 1 and 2. Ellipses indicate scoring coefficient variation range within a 95% confidence interval. Symbols indicate the number of observations by each seed species. Component 1 separates seeds that are high in protein, nitrogen, fat, and ash (positive values), but low in starch content (negative values). Component 2 mainly separates seeds that are high in moisture content. Component 3 separates seeds by protein and nitrogen content.

Behavioral Element	Description
Exploring the Arena	Moving around the arena without interacting with the seed cups or sand
Near Seed Cup	On top of the platform surrounding the seed cup but not reaching into the cup
Investigating Seed Cup	Reaching into the seed cup, entire body in seed cup
Caching	Digging and clearly inserting seeds from cheek pouches into the sand
Jumping	Stereotypic jumping against arena walls
Sand bathing	Cleaning fur and rolling in sand
Digging	Digging in place or while moving without caching seeds

Table 1-1. Ethogram of 7 behavioral elements used for behavioral observations. Observations were recorded using BORIS software.

Experiment 1 Average Foraged				
Identification	**Average (g)**	**STD**	**SE**	**% of Seeds Foraged**
Nonnative (Commercial) Seeds	**0.414**	**0.472**	**0.105**	**90.99**
Panicum miliaceum	0.220	0.340	0.076	48.35
Avena sativa	0.194	0.239	0.053	42.64
Native Seeds	**0.041**	**0.046**	**0.010**	**9.01**
Stipa pulchra	0.029	0.040	0.009	6.26
Croton californicus	0.013	0.021	0.005	2.74

Table 1-2a. Average quantity of seeds foraged in Experiment 1.

Experiment 1 Average Investigation				
Identification	**Average (s)**	**STD**	**SE**	**% Time Investigated**
Nonnative (Commercial) Seeds	**198.300**	**257.944**	**57.678**	**71.73**
Panicum miliaceum	74.150	89.845	20.090	25.73
Avena sativa	124.150	258.131	57.720	44.91
Native Seeds	**78.150**	**102.305**	**22.876**	**28.27**
Stipa pulchra	48.650	69.591	15.561	17.59
Croton californicus	29.500	84.212	18.830	10.67

Figure 1-2b. Average time spent investigating seeds in Experiment 1.

	Component 1	Component 2	Component 3
Moisture	-0.18292	0.87714	0.44389
Dry Matter	0.1812	-0.87908	-0.44071
Protein	0.70044	-0.48298	0.52078
Fiber	0.93776	0.28562	-0.17365
Starch	-0.98913	-0.10456	0.02374
Fat	0.93706	0.28562	-0.13778
Ash	0.71823	0.51882	-0.35321
Nitrogen	0.69789	-0.48314	0.52358
Variance (%)	53.70	30.53	13.89

Table 1-3. Loading matrix for PCA of nutrient composition of seeds used in Experiment 1.

Experiment 1 Average Seed Nutritional Composition									
Species	**Category**	**Crude Protein**	**Crude Fat**	**Moisture**	**Crude Fiber**	**Starch**	**Dry Matter**	**Ash**	**Nitrogen**
Avena sativa	Nonnative (Commercial)	13.77 (0.08)	6.27 (0.07)	11.93 (0.09)	1.8 (0.25)	63.47 (0.19)	88.07 (0.08)	1.91 (0.06)	2.2 (0.00)
Croton californicus	Native	26.46 (0.36)	26.74 (0.35)	9.99 (0.88)	35.4 (0.44)	0.59 (0.06)	90.01 (0.88)	3.55 (0.12)	4.22 (0.06)
Panicum miliaceum	Nonnative (Commercial)	11.17 (0.03)	4.13 (0.03)	11.13 (0.03)	8.2 (0.12)	62.33 (0.33)	88.87 (0.03)	3.43 (0.06)	1.8 (0.00)
Stipa pulchra	Native	22.65 (0.14)	2.10 (0.07)	9.87 (0.05)	0.24 (0.03)	55.08 (0.20)	90.14 (0.05)	1.72 (0.05)	3.62 (0.02)

Table 1-4. Seed nutritional characteristic composition of nonnative (commercial) finch seed mix diet and native seed diet used in Experiment 1. *N* = 3 *Avena sativa*, *N* = 9 *Croton californicus*, *N* = 3 *Panicum miliaceum*, and *N* = 30 *Stipa pulchra*. Values are average percentages with SE in parentheses.

Identification	Average (g)	STD	SE	% of Seeds Foraged
Nonnative (Commercial) Seeds	**0.273**	**0.287**	**0.052**	**89.90**
Nonnative (Invasive) Seeds	**0.031**	**0.035**	**0.006**	**10.10**
Previously Exposed	**0.094**	**0.157**	**0.018**	**82.77**
Nonnative (Commercial) Seeds	**0.333**	**0.322**	**0.072**	**88.20**
Panicum miliaceum	0.169	0.200	0.045	44.56
Avena sativa	0.166	0.197	0.044	43.63
Nonnative (Invasive) Seeds	**0.045**	**0.035**	**0.008**	**11.80**
Erodium botrys	0.023	0.025	0.006	6.63
Bromus rubens	0.019	0.021	0.005	5.17
Not Previously Exposed	**0.039**	**0.079**	**0.013**	**17.23**
Nonnative (Commercial) Seeds	**0.154**	**0.150**	**0.047**	**98.09**
Panicum miliaceum	0.104	0.133	0.042	66.24
Avena sativa	0.050	0.037	0.012	31.85
Nonnative (Invasive) Seeds	**0.003**	**0.007**	**0.002**	**1.91**
Erodium botrys	0.002	0.006	0.002	1.27
Bromus rubens	0.001	0.003	0.001	0.64

Table 2-1a. Average quantity of seeds foraged by exposure in Experiment 2.

Identification	Average (s)	STD	SE	% of Seeds Foraged
Control Treatment	**0.039**	**0.079**	**0.013**	**17.23**
Nonnative (Commercial) Seeds	**0.154**	**0.150**	**0.047**	**98.09**
Panicum miliaceum	0.104	0.133	0.042	66.24
Avena sativa	0.050	0.037	0.012	31.85
Nonnative (Invasive) Seeds	**0.003**	**0.007**	**0.002**	**1.91**
Erodium botrys	0.002	0.006	0.002	1.27
Bromus rubens	0.001	0.003	0.001	0.64
Pre-Weaned Treatment	**0.099**	**0.165**	**0.026**	**43.80**
Nonnative (Commercial) Seeds	**0.333**	**0.366**	**0.116**	**83.46**
Panicum miliaceum	0.224	0.274	0.087	55.89
Avena sativa	0.112	0.114	0.036	27.57
Nonnative (Invasive) Seeds	**0.066**	**0.032**	**0.010**	**16.54**
Erodium botrys	0.038	0.027	0.008	10.53
Bromus rubens	0.022	0.017	0.005	6.02
Weaned Treatment	**0.089**	**0.150**	**0.024**	**38.97**
Nonnative (Commercial) Seeds	**0.332**	**0.291**	**0.092**	**93.52**
Panicum miliaceum	0.113	0.048	0.015	31.83
Avena sativa	0.219	0.2498	0.079	61.69
Nonnative (Invasive) Seeds	**0.023**	**0.024**	**0.008**	**6.93**
Erodium botrys	0.008	0.008	0.003	2.25
Bromus rubens	0.015	0.025	0.008	4.23

Table 2-1b. Average quantity of seeds foraged by treatment in Experiment 2.

Identification	Average (g)	STD	SE	% Time Investigated
Nonnative (Commercial) Seeds	**141.164**	**106.045**	**19.361**	**67.73**
Nonnative (Invasive) Seeds	**67.266**	**89.058**	**16.260**	**32.27**
Previously Exposed	**58.838**	**66.478**	**7.433**	**77.37**
Nonnative (Commercial) Seeds	**150.350**	**110.855**	**24.788**	**62.15**
Panicum miliaceum	89.000	81.085	18.131	36.38
Avena sativa	63.650	46.842	10.474	25.78
Nonnative (Invasive) Seeds	**91.550**	**97.779**	**21.864**	**37.85**
Erodium botrys	72.250	76.310	17.063	33.32
Bromus rubens	10.450	12.133	2.713	4.53
Not Previously Exposed	**35.373**	**51.723**	**8.178**	**22.63**
Nonnative (Commercial) Seeds	**122.793**	**98.639**	**31.192**	**86.78**
Panicum miliaceum	62.960	69.449	21.962	44.50
Avena sativa	59.834	47.009	14.866	42.29
Nonnative (Invasive) Seeds	**18.699**	**37.978**	**12.007**	**13.22**
Erodium botrys	6.899	13.794	4.362	4.88
Bromus rubens	11.800	36.618	11.580	8.34

Table 2-2a. Average time spent exploring by exposure in Experiment 1.

Identification	Average (s)	STD	SE	% Time Investigated
Control Treatment	**35.373**	**51.723**	**8.178**	**22.63**
Nonnative (Commercial) Seeds	**122.793**	**98.639**	**31.192**	**86.78**
Panicum miliaceum	62.960	69.449	21.962	44.50
Avena sativa	59.834	47.009	14.866	42.29
Nonnative (Invasive) Seeds	**18.700**	**37.971**	**12.007**	**13.22**
Erodium botrys	6.899	13.794	4.362	4.88
Bromus rubens	11.800	36.618	11.579	8.34
Pre-Weaned Treatment	61.000	63.563	10.050	**41.12**
Nonnative (Commercial) Seeds	**108.400**	**68.093**	**21.533**	**42.16**
Panicum miliaceum	64.500	66.080	20.896	24.31
Avena sativa	48.500	27.918	8.828	17.85
Nonnative (Invasive) Seeds	**148.700**	**100.903**	**31.908**	**57.84**
Erodium botrys	117.200	77.538	24.520	52.08
Bromus rubens	13.800	13.340	4.218	5.76
Weaned Treatment	56.675	70.016	11.070	**36.26**
Nonnative (Commercial) Seeds	**192.300**	**131.893**	**41.708**	**84.43**
Panicum miliaceum	113.500	90.442	28.600	50.07
Avena sativa	78.800	57.815	18.283	34.76
Nonnative (Invasive) Seeds	**34.400**	**52.386**	**16.566**	**17.89**
Erodium botrys	27.300	42.322	13.383	12.04
Bromus rubens	7.100	10.386	3.285	3.13

Table 2-2b. Average time spent exploring by treatment in Experiment 2.

	Component 1	Component 2
Moisture	0.201	0.956
Dry Matter	-0.201	-0.956
Protein	0.994	0.003
Fiber	0.231	-0.906
Starch	-0.415	0.804
Fat	0.928	0.314
Ash	0.954	-0.146
Nitrogen	0.994	0.005
Variance (%)	50.68	42.67

Table 2-3. Loading matrix for PCA of nutrient composition of seeds used in Experiment 2.

Experiment 2 Average Seed Nutritional Composition

Species	Category	Crude Protein	Crude Fat	Moisture	Crude Fiber	Starch	Dry Matter	Ash	Nitrogen
Avena sativa	Nonnative (Commercial)	13.77 (0.08)	6.27 (0.07)	11.93 (0.09)	1.80 (0.25)	63.47 (0.19)	88.07 (0.08)	1.91 (0.06)	2.20 (0.00)
Bromus rubens	Nonnative (Invasive)	15.73 (0.98)	0.30 (0.14)	10.28 (0.12)	10.89 (0.57)	2.06 (0.11)	89.72 (0.12)	3.14 (0.16)	2.51 (0.16)
Erodium botrys	Nonnative (Invasive)	48.33 (1.52)	23.8 (1.01)	11.23 (0.59)	10.43 (1.01)	0.47 (0.03)	88.77 (0.59)	6.88 (0.27)	7.73 (0.24)
Panicum miliaceum	Nonnative (Commercial)	11.17 (0.03)	4.13 (0.03)	11.13 (0.03)	8.20 (0.12)	62.33 (0.33)	88.87 (0.03)	3.43 (0.06)	1.80 (0.00)
*Artemisia californica**	Native	9.45 (1.24)	90.57 (1.26)	17.92 (0.42)	18.42 (0.83)	0.70 (0.06)	7.03 (1.20)	8.00 (0.32)	2.85 (0.08)
*Croton californicus**	Native	9.99 (2.50)	90.01 (2.50)	25.30 (0.83)	35.40 (1.25)	0.59 (0.16)	26.74 (1.00)	3.55 (0.33)	4.22 (0.16)
*Eriogonum fasciculatum**	Native	7.34 (1.19)	92.66 (1.19)	5.68 (0.43)	12.71 (1.11)	3.00 (1.13)	1.50 (0.27)	4.99 (0.28)	0.91 (0.07)
*Salvia apiana**	Native	8.00 (0.80)	92.00 (0.80)	12.80 (1.70)	30.50 (2.50)	0.30 (0.10)	12.10 (2.70)	4.40 (0.30)	2.00 (0.30)
*Salvia mellifera**	Native	8.20 (1.00)	91.80 (1.00)	12.40 (1.80)	27.10 (3.40)	0.30 (0.10)	17.60 (2.70)	5.10 (0.20)	2.00 (0.30)
*Stipa pulchra**	Native	9.90 (0.30)	90.1 (0.30)	22.60 (0.70)	0.20 (0.20)	55.10 (1.10)	2.10 (0.40)	1.70 (0.30)	3.60 (0.10)

Table 2-4. Seed nutritional characteristic composition of nonnative (commercial) finch seed mix diet and native seed diet used in Experiment 1. *N* = 3 *Avena sativa*, *N* = 9 *Croton californicus*, *N* = 3 *Panicum miliaceum*, and *N* = 30 *Stipa pulchra*. Values are average percentages with SE in parentheses.

	Component 1	Component 2	Component 3
Moisture	0.42459	-0.84148	-0.32471
Dry Matter	-0.42711	0.83937	0.32711
Protein	0.76584	-0.12087	0.63006
Fiber	0.68771	0.48152	-0.46418
Starch	-0.7154	-0.32176	0.52818
Fat	0.87107	0.3428	-0.000015
Ash	0.90715	0.04814	0.01086
Nitrogen	0.76426	-0.12462	0.63121
Variance (%)	51.25	23.72	18.78

Table 2-5. Loading matrix for PCA of nutrient composition of native seeds used in Experiment 1 and non-native invasive seeds used in Experiment 2.

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