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RESOURCE PREFERENCES: PAST COSTS AFFECT FUTURE CHOICES BY
LEAST CHIPMUNKS

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DEPARTMENT OF PSYCHOLOGY

BY

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Abstract

When given the choice between stimuli previously associated with equal quality resources, animals tend to choose the stimulus associated with greater deprivation and greater effort. However, past research has generally approached this issue using extensive, lab-based training on these associations. Such training regimens are unlikely to be seen in the natural foraging behavior of animals and it remains unclear whether or not such preferences emerge in more naturalistic-experimental paradigms. In the present series of studies, I corrected for this limitation by giving least chipmunks (*Tamias minimus*) minimal exposure to two patches of seeds, both presented under different cost circumstances. In all four experiments, one patch was easy to obtain while the other required more effort or more potential risk. Each patch was then associated with a different visual or olfactory stimulus in order to measure choice when the patches were later made equally available. Ultimately, the results were mixed. No effort-based preferences were observed in the visual cue studies, but emerged for both of the olfactory associated conditions. For chipmunks, it seems that costs can influence later preferences when the resources are obtained under semi-naturalistic foraging conditions and when those conditions involve the use of olfactory stimuli.

Resource Preferences: Past Costs Affect Future Choices By Least Chipmunks

Foragers face numerous resource-gathering decisions as they navigate their environment. In deciding where to seek food, foragers should consider the potential availability, the needed amount, and the possible risks of acquiring each item. These risks can be diverse. For example, the presence of other foragers may require direct competition for the likely limited resources, and predators also affect a forager's decisions (e.g., Winterrowd & Devenport, 2004). Increased vigilance due to these risks may reduce the rate of energetic gain (e.g., Lima & Dill, 1990). Moreover, the act of foraging itself can decrease potential gains as searching for food may require significant expenditure. According to the tenets of Optimal Foraging Theory, on the average, foragers should simultaneously try to minimize energy costs and maximize returns (MacArthur & Pianka, 1966). Adaptive foragers may need to consider both the costs and benefits of each directed foraging search. Foragers may gain the most by searching in areas that are easily accessible and in areas that lack competitors and predators. By selectively choosing these cost-reducing locations, foragers may develop a preference for the resources obtained there. Foragers may learn to favor items that have been acquired under conditions of low predator threat, low competition, and high ease of access. However, much of the previous literature suggests the opposite. Not only do animals prefer stimuli and resources previously associated with risk or cost, some animals have even been reported to prefer acquiring food that remains directly connected to that risk or cost.

Fifty years ago, a unique and curious finding emerged in the animal learning literature. Jensen (1963) reported that rats (*Rattus norvegicus*) will work for food despite the nearby presence of freely available food. During training, animals were given the

opportunity to bar press for a single pellet reward a minimum of 40 times. After reaching the criterion number of presses, rats were then presented with a choice. Jensen turned off the bar mechanism and placed a standard feeding dish in the box opposite the end on which the bar was located. The cup contained an abundance of freely available pellets and the rats were required to take two pellets before the bar press system was reactivated. Once the system was on, animals could freely choose between earning their reward and simply taking from the cup. One rat chose to exclusively “freeload” and took all of its food from the cup; the other 199 rats continued to work for their food. In fact, over 40% of the rats consumed more pellets obtained via the bar press response than they consumed from the free cup.

Since Jensen’s (1963) work, many researchers have found similar results. Neuringer (1969) tested for this effect in a different species and also examined the effect of deprivation on motivation in an operant conditioning paradigm. At the time, many researchers believed that deprivation was necessary in order to stimulate activity on lever or disc-pressing tasks. After seven training days, Neuringer presented two White Carneaux pigeons (*Columba livia*) with a choice. They could continue to disc peck in their operant training box to acquire food, or they could simply take it from a freely available dish located inside the box. Neuringer showed that the pigeons not only continued to peck at the disc, but also consumed more grain obtained via the disc than they consumed from the free food source. He then replicated this finding using two female rats. It became clear that deprivation was not necessary for motivation and that the work of Jensen (1963) was no fluke. Animals will continue to work for their food despite freely available resources.

This “contrafreeloading” effect has pervaded the literature for years and has been applied to numerous animal species. Most recently, grizzly bears (*Ursus arctos horribilis*) have been cited as engaging in such behavior (McGowan, Robbins, Alldredge, & Newberry, 2010). However, as early as the 1970s many inconsistencies began to emerge. While the basic effect was replicated by Carder and Berkowitz (1970), they argued that the earned-food preferences were constrained by the effort required to obtain the food. Their rats only showed earned-food preference if just one or two lever presses were required. At 10 lever presses per reward, the rats preferred the free food. Neuringer (1970) also reported conflicting results at these higher levels of effort. He showed that pigeons would maintain an earned food preference if the disc provided reward at a fixed ratio of 5:1 or on a 1-minute variable-interval schedule. However, the preference was absent if the fixed ratio was set at 10:1. This was true despite the fact that under the variable-interval preference conditions, pigeons averaged over 40 responses per reward. Additionally, while Singh (1970) argued that rats prefer response-based schedules, Morgan (1974) was only able to show that rats will continue to work when given a choice between response-dependent and response-independent schedules, but not that they prefer to do so. In fact, Morgan showed that rats generally prefer to take food from a compartment that delivers a pellet every 30 seconds rather than a compartment in which the rat must press a lever to receive a pellet reward. However, this does not mean that the rats stopped working for food, just that they spent more time in the free food compartment and took more food from there.

Failures to replicate the contrafreeloading effect have continued to appear. Using similar high-level pre-training procedures, Taylor (1972) was unable to find the effort-

related preference that Tarte and Synder (1973) did with lever-pressing rats. Others have also failed to find any effort-related preferences as seen in studies by Koffer and Coulson (1971) and Lambe and Guy (1973). Koffer and Coulson (1971) showed that cats (*Felis catus*) preferred freely available fish over those they would have to obtain via effort, while Lambe and Guy (1973) showed a similar free-food preference in both gerbils (*Meriones unguiculatus*) and rats (as cited in Osborne, 1977). A review by Osborne (1977) outlines many of these early inconsistencies in the contrafreeloading literature.

Both a later review by Inglis, Forkman, and Lazarus (1997) and the earlier review by Osborne (1977) have continued to shed additional light on the contrafreeloading phenomenon. Both reviews have argued that much of the contrafreeloading literature is attributable to more parsimonious explanations. For one, the authors claim that animals may show a neophobic response towards a food cup that was previously unseen. This alone may drive initial preference towards the lever response. It may also be that animals prefer to work not just for food, but rather they prefer to work for their food *and* for the secondary reinforcers that accompany food release. In many of the contrafreeloading studies, the lever pressing behavior was associated with a change in the light system or simply the addition of sounds via the dispenser itself. These stimuli changes may act as secondary reinforcers of the behavior and guide preference or at least allow maintained attendance at the food hopper. Even the act of lever pressing itself may be reinforcing. This can be especially true for animals reared in deprived environments. When given the opportunity to bar press for a reward, these animals are more likely to do so than animals raised in stimulus-rich environments; the latter group prefers to freeload (Tarte, Townsend, & Vernon, 1973). Such a preference towards activity and stimulus-

engagement may be no different than the preferences seen for other enrichment items (Bradshaw & Poling, 1991) or the tendency to run in a running wheel (Richter, Gass, & Fuss, 2014), and may more simply explain the tendency to lever press. These arguments against contrafreeloading interpretations are just a handful of those produced by both reviews.

Furthermore, Inglis et al. (1997) have argued that food is not the only thing obtained under a work-like condition. The food resource is often accompanied by information about the environment or the experimental context. Inglis et al. (1997) argued that information gathering is a vital process for animals that operate in naturally varied and changing environments. Working for their food can then be seen as providing information about the stability of the response-food relationship, especially when that response-food relationship is uncertain. This is exemplified in research by Havelka (1956). Here rats selected further-away food that varied in location, over food that was nearby and maintained in the same spot. The far-away food was randomly placed in one of four sites, requiring the animal to do increased search when approaching that end of the box. However, this preference was only seen when the location of the far-away food was uncertain. As soon as its placement was held constant, animals shifted their preferences to the nearby food. According to Inglis et al. (1997), this willingness to seek out the far-away food may help compensate for the uncertainties of the environment. Such behavior can provide information gains that will enable an animal to better prepare for and adjust to changes in a natural and varied environment.

While much of the contrafreeloading literature has been explained via mechanisms other than a simple preference for earning food, the information hypothesis

is particularly appealing. Learning about the resource and its associated costs may better enable an animal to exploit and predict the occurrence of that resource. The information hypothesis may also apply in situations where animals report a preference for a stimulus that has been previously associated with work, or effort. It is possible that animals are not just gaining a resource when they work, they may also be gaining information as well. If animals prefer to work as a means of gaining information, and the stimuli associated with such work are preferred, then it is possible the resources acquired under work conditions may rise in value.

Recently in the literature, numerous studies have demonstrated these work-related preference effects. It is suggested that by associating a resource or resource stimulus with a prior cost, preference for that resource or stimulus can increase. Kacelnik and Marsh (2002) clearly displayed this effect using starlings. In their study, they trained starlings to complete two separate flight distances. Starlings (*Sturnus vulgaris*) flew either 4 meters or 16 meters and then pecked a specifically colored key (Red or Green). One color was associated with each of the two flight distances, but both keys released the same peanut reward. After five training trials, birds were presented with a free choice between the red and green key. Either choice released the same reward given on the training trials. This continued for a total of 8 hours of sessions for each bird. Out of the twelve starlings tested, ten showed a preference for the key color that was previously associated with the 16 meter flight or more simply the flight requiring more effort. Marsh, Schuck-Paim, and Kacelnik (2004) have since argued that these results may be less specific to work, and more specific to the energetic state of the animal following work. These findings are further supplemented by the fact that starlings will stay in a patch longer and take more food

from a patch that required a longer travel time to reach (Cuthill, Kacelnik, Krebs, Haccou, & Iwasa, 1990).

Clement, Feltus, Kaiser, and Zentall (2000) showed a similar result by training pigeons on two simultaneous discriminations. Pigeons were trained to peck at a centrally located circle when illuminated. This circle required either 1 or 20 pecks per trial. When pecked once, two additional circles (one at each side of the central light) would illuminate in two different colors. Pecking one color would release a food reward (S1+), while pecks at the other color would end the trial (S1-). When the central circle required 20 pecks, a different color discrimination would appear; however, the contingencies would remain the same. A peck at one color would release a food reward (S20+), while a peck at the alternative color would end the trial (S20-). After a period of training on both discrimination tasks, pigeons were presented with choices between the two positively associated stimuli. These test pairings occurred at both the high effort and low effort levels. Results showed that over 69% of the choices between the S+ stimuli favored the S+ color initially associated with 20 pecks at the white central circle.

Furthering these results, Friedrich and Zentall (2004) have even shown that preferences for feeder location can be altered given changes in the amount of effort required to access those locations. After identifying an initial feeder preference for each pigeon, Friedrich and Zentall increased the number of pecks required to feed from the less preferred site. Following such training, test pigeons showed reduced choice for the initially preferred feeder simply due to the increased effort that had become associated with the previously non-preferred feeder location. As in both Kacelnik and Marsh (2002)

and Clement et al. (2000), choice tests always occurred at equal levels of workload and preferences were only attributable to the learned contingencies of previous exposures.

Collectively, these “work-ethic” preference results have been linked to the concept of contrast effects. Contrast effects occur when reinforcer value is inversely related to events that precede or follow the presentation of that reinforcer (Zentall & Singer, 2007). In cases of work-ethic preference, the amount of effort required to obtain a reward is related to the value of that reward on a free choice task. Zentall and Singer (2007) have coined this type of contrast as ‘within-trial contrast.’ As described, aversive effort reduces the initial value of the experimental context. When presented with a reinforcer of initially constant value, the value associated with the experimental context shifts to the level of the reinforcer. This shift then marks the associated stimulus or resource with that magnitude change in value. Shifts in value will be larger following initially aversive events than they will be when they follow events that were non-aversive. Thus, work-associated stimuli will be associated with a larger value shift and should result in a stronger value for that stimulus resource (as compared to non-work stimuli). Zentall and Singer (2007) have extended within-trial contrast beyond the realm of work conditions and have identified similar mechanisms in delay-reduction and deprivation contingencies. The relationship to deprivation is especially important given that others have argued that resulting preferences in a work-ethic paradigm may be due to the energetic state of the animal (Marsh et al. 2004; McNamara, Trimmer, & Houston, 2012).

Despite the evidence from Zentall and Singer (2007), other researchers have challenged the consistency of the within-trial contrast effect. In fact, some researchers have been unable to replicate the original findings of Clement et al. (2000). Vasconcelos,

Urcuioli, and Lionello-DeNolf (2007) were the first to attempt such a replication, and in six different experiments failed to do so. Both studies used pigeons in a simultaneous discrimination task associated with various workload levels. While Clement et al. (2000) showed an emergent preference for the work-associated stimuli, Vasconcelos et al. (2007) showed indifference. This replication failure occurred despite an increase in the effort associated with the work condition, and despite showing that pigeons found the effort condition to be aversive. Arantes and Grace (2008) also failed to replicate the effect.

When applied to deprivation levels, inconsistencies in the literature continue. Vasconcelos and Urcuioli (2008) reported two different experiments assessing the effects of deprivation on stimulus preferences. In one experiment, pigeons were separately trained on two discriminative stimuli, one following pre-feeding and one following a period of deprivation. As predicted by within-trial contrast, on free choice trials, pigeons preferred the stimulus previously associated with deprivation. However, when replicated using a simultaneous discrimination procedure, Vasconcelos and Urcuioli failed to reproduce the results seen in the successive procedure.

Zentall (2008) has challenged each of the inconsistent findings. He has claimed that the original replication failure of Vasconcelos et al. (2007) was due to a failure to provide sufficient over-training on each stimulus discrimination. Vasconcelos and Urcuioli (2008b) have denied the need for such over-training, as both their initial 2008 study and the work of Arantes and Grace (2008) report attempts at over-training levels much greater than those necessitated by Zentall (2008). Furthermore, a recent study by Vasconcelos and Urcuioli (2009) tested both the original findings of Clement et al. (2000) with significant over-training, as well as the basic findings of Kacelnik and Marsh (2002)

with significant over-training. Using pigeons in both experiments, Vasconcelos and Urcuioli (2009) again failed to find a reliable within-trial contrast effect.

As a second challenge, Zentall (2008) argued that Arantes and Grace (2008) used a sample of pigeons that had experience with aversive feeding schedules. He claimed that such experience would reduce the magnitude of the effect when training and testing in their deprivation paradigm. However, Arantes and Grace (2008b) counter that many of their pigeons required extra-training sessions on the 20 peck schedule due to unwillingness to participate consistently. Thus, it seems that if the pigeons found it aversive enough to not participate they should have then found it aversive enough to affect their preferences that would be established given within-trial contrast.

In sum, the literature regarding within-trial contrast and work ethic effects remains inconsistent. As recently as three years ago, Meindl (2012) reported that 22 studies found an increased preference for aversively-associated stimuli, while another 16 failed to replicate that same effect. Increased preferences have spanned a diverse number of species, including rats (e.g., Lydall, Gilmour, & Dwyer, 2010), mice (Johnson & Gallagher, 2011), pigeons (e.g., Zentall, 2010), starlings (e.g., Freidlin & Kacelnik, 2011), and even banded tetras (*Astyanax fasciatus*) (Aw, Holbrook, Burt de Perera, & Kacelnik, 2009). As much as these results have failed to be reliable, they have also failed to provide a clear explanation for why these preferences should emerge in the first place. All of the studies assessing within-trial contrast have occurred following long training procedures and have not been tested under more naturalistic conditions. These lab-based studies have also failed to consider any adaptive function associated with these emergent preferences. Additionally, the requirement of a significant number of over-training

sessions (as suggested by Zentall, 2008) is not a requirement easily met by an animal in the field. This is not to suggest that previous costs associated with specific resources should have no effect on future resource choice or preference, but rather to suggest that actual assessments of such behavior in a field-like paradigm are necessary. Foraging decisions in the field should occur quickly and in a way that provides each forager with an adaptive advantage. If, as Zentall (2008) suggested, a significant number of training trials are needed to establish any stimulus associated preference, then the value of conducting such experimentation in the first place is unclear. In the field, an animal that does not quickly learn which resources are associated with work or which resources are associated with predators or competitors is an animal that may be left behind.

Furthermore, from an adaptive standpoint, it is not clear that animals would benefit by showing a preference for work-associated resources. While it could be argued that when freely available, animals should capitalize on resources that are normally difficult or dangerous to obtain, it is hard to argue that this preference should emerge when paired with an identical resource occurring with nothing more than a differently associated stimulus (but see McNamara et al. 2012). Additionally, if past work histories can lead to a resource preference, then that preference may direct an animal to seek out that resource in the future. In other words, work may establish a resource preference, which then may feedback into the behaviors associated with acquiring that resource. Thus, foragers that have developed a work-associated preference might prefer to work for their food than not work. This claim would become especially problematic if resources acquired under predator threat activated the same suggested within-trial contrast. It may

then have to be argued that animals seek to find resources in areas of high predator density.

Alternatively, animals could show a preference for non-work associated stimuli, or simply show indifference; however, much like having a bias towards work-related stimuli, the benefits of showing either alternative preference are unclear. While it may be easy to argue that an animal that prefers non-work stimuli would seek out resources that could be obtained under non-work conditions, none of the previous studies have shown a bias towards non-work (but see, Shibasaki & Kawai, 2011). In fact, if a work-associated preference was not present, animals showed the third alternative: indifference. This lack of preference may be the most parsimonious expectation. When resources are identical in both quality and accessibility, it is rational to assume that no preference should emerge. However, Waite (2008) has suggested that any reason to choose one resource over another can facilitate quicker choice decisions. Thus, an animal with a reason, a preference, or a bias could save time that would otherwise be lost to evaluative decision making.

The current series of studies aimed to begin addressing these concerns and questions from a more naturalistic standpoint. First, a replication in the vein of Kacelnik and Marsh (2002) was conducted using a sample of least chipmunks (*Tamias minimus*). Animals were tasked with gathering seeds under high-work and low-work conditions, both of which were associated with climbing behavior and a unique color. After training, they were presented with a choice between the two previously presented colors but both were now placed at equal levels of work. Training schedules were drastically reduced given the reduction of exposure that would likely occur in a naturalistic environment. A second work-related study followed, but it was conducted using digging effort rather than

climbing to provide a comparative assessment of work with a behavior that appeals strongly to the natural foraging and pilfering tendencies of the least chipmunk (e.g., Penner & Devenport, 2011). Finally, a third study transitioned the supposed within-trial contrast effect into a new foraging task. Here, least chipmunks acquired resources under high or low levels of competition. Like work, high levels of competition should act as an “aversive” stimulus that can (according to Zentall and Singer, 2007) facilitate the onset of within-trial contrast.

General Methods

Subjects

Least chipmunks (*T. minimus*) are small, diurnal sciurids found throughout the north central United States and west through and beyond the Rocky Mountains. Subsisting on a variety of seeds, nuts, forbs, and berries, these chipmunks tend to prefer fairly open habitats that are often found at forest edges and clearings, or in mixed conifer-hardwood forests. However, the 32 subspecies have adapted to the arid deserts of Nevada to the damper climate of the upper great lakes area (Verts & Carraway, 2001). Previous work has identified these animals as adept foragers, hoarders, and pilferers. Least chipmunks have been shown to selectively choose cache locations that help guard against robbery (Penner & Devenport, 2011) and to construct their caches in ways that further this protection by suppressing olfactory signals (Jenkins & Devenport, 2014; Penner & Devenport, 2011). When choosing between caches that they have created and caches created by a competitor, these chipmunks selectively choose to pilfer from others. Such selection allows least chipmunks to gain new resources while maintaining their own stores for later use. These and many other adaptive behaviors likely enable the least

chipmunk to better compete with hoarders that would otherwise dominate at a resource patch based on size alone (Penner & Devenport, 2011).

In the present series of studies, least chipmunks were given basic foraging tasks. In each experiment, each animal underwent a series of six training trials, followed by two test trials. Prior to the training and testing sequence, animals were removed from their standard group-housed colonies (each containing approximately 10 animals) and placed in a smaller, solitary living environment. Each solitary environment contained a bed of hardwood chips, compressed cotton squares for nest-making, water access, and a glass or plastic nest bottle. Removal from the colony occurred no less than three days prior to the start of a training/testing sequence. During this time, animals were placed on a restricted diet of only small portions of rodent chow. This was done to reduce each animal's free feeding body weight by up to 10% and to increase foraging motivation in each of the experiments.

Primarily, the least chipmunks used in the current series of experiments were obtained from field sites near Grand Marais, MI; others resulted from breeding within the lab. Each chipmunk was given unique fur markings and a PIT chip allowing for easy identification. Both male and female chipmunks participated, and in each experiment, anywhere from 7 to 15 animals were used. Given our modest population of animals (~40 least chipmunks), many chipmunks were re-used across experiments. However, some subject variation was retained by using relatively small samples in each experimental design. Six animals participated in all four experiments, five took part in three, four took part in two, and the remaining three animals participated in just one design.

General Procedure

Each experiment used the same basic procedures. This allowed for an easy comparison across experiments and across the variables associated with patch choices. Each animal, in each experiment was run through a sequence of habituation, six training trials, and two test trials (see Figure 1). Each run of the entire sequence took five days to complete; however some animals required make-up training sessions when they failed to complete previous ones. On the first day, animals were placed individually in a foraging box or arena for 20 minutes to allow for exploration and habituation. All experiments were conducted in sand-filled foraging arenas, containing approximately 6 to 8 cm of medium grade industrial sand. Prior to habituation, the sand was mixed, sifted, and cleaned of any debris. Once the sand had been smoothed evenly throughout the environment, the animal was placed inside via a large, plastic transport bottle. Upon the exiting the bottle, a 20 minute habituation period began. After the time had passed, the animal was removed and returned to its solitary quarters.

On the following morning, a sequence of six training trials began. The training trials took place over a period of three days, one occurring each morning, and one each afternoon. As with habituation, sand was cleaned and smoothed prior to the beginning of each trial. Given the specifications of each protocol, trials were semi-randomly assigned to one of two conditions. For each condition, unhulled pumpkin seeds (obtained from a stock seed source) were paired with one of two given stimuli (color or scent). For example, in a work-associated experimental design, seeds obtained under the High-Work condition might be associated with red foraging platforms, while those seeds obtained in the Low-Work condition would be associated with green platforms.

For each training trial, animals were placed in the foraging area and given adequate time to completely deplete the available seeds. If the animal did not deplete the seeds after 45 minutes on its first trial, the session was terminated and the animal was removed from the experiment. Some of these animals were allowed to try again at a later date, or were dropped from the experiment and used later in a different experiment. If an animal was successful on the first trial, but failed to collect seeds in a later trial, the later trial was re-attempted either next morning or afternoon depending on when that failed trial took place. For some of those animals, this pushed their entire sequence to six days rather than the standard five day protocol. Three minutes after each animal depleted the available seeds, the trial was ended, and the animal was captured and returned to its individual living quarters. While the vast majority of animals depleted all seeds in a given trial; there were a few exceptions throughout the training (and testing) sequences.

After the six training trials were completed, a test trial took place on the morning of day five. Generally known as the cost preference testing trial, each animal was presented with both training patches simultaneously. This allowed the animals the opportunity to directly compare the costs associated with each patch. It also allowed for a display of preference. Animals had free choice to select from either patch first and also the opportunity to sample prior to depleting either patch. The first choice of each animal, the first set of seeds depleted, and the order of seed choice were recorded for analysis. Animals were removed from the arena 3 minutes after depleting both patches.

Following the first test trial, animals were given a second test trial in the afternoon of Day 5. This trial was used to assess stimulus (color or odor) preference, following an associated cost-history, by equalizing the current costs of each patch. This test trial came

in one of two forms: high-cost or low-cost. In the high-cost test, animals were presented with both patches, but the previously low-cost patch was adjusted to the high-cost level. In the low-cost test, the reverse was true—the high-cost patch was adjusted to the low-cost level. While the current costs for each patch were now equal in a given test trial, the color or odor associated with each patch's cost history was maintained. Having both trial types was necessary to ensure that an animal's preference was not affected simply by the change in cost in one direction. For example, if I only tested color or odor preference by equalizing at the high-cost level, then it would be difficult to tease apart the influence of previous cost-history and patch variability. If the animals showed a preference for the resources obtained at the high-cost patch, then I would not know if animals preferred resources that had been previously acquired under high-cost conditions or if they simply avoided going to patches that had recently changed. To correct for this, animals were randomly assigned to one of the two test trial types. Each animal was allowed to deplete both sets of seeds and was removed following the complete depletion of the patches or 20 minutes after they took their first seed. As in the previous test trial, each animal's first choice, first depletion, and order of choice were recorded for analysis.

Centered above each of the foraging environments hung a black and white video camera system. Each trial was monitored from a nearby video monitoring room and all trials were tape-recorded. Each researcher sat quietly, observed each session, and manually recorded the timing of each seed choice. Tapes were reviewed as needed to resolve any uncertainties. To help control for auditory distraction, each trial was accompanied by static white noise produced from a nearby audio system. This helped to

block out sounds from the neighboring hallway, as well as any sounds made by the researcher.

Data Analysis

For the two preference tests, binomial analyses were conducted on the first choice of each animal and for the cost preference test, the first patch depleted by each animal was also assessed using a binomial test. Any significant deviations from indifference (0.5 probability) would indicate a patch preference. To further establish any animal preference, the order of choice-sequences across the two test patches was also assessed. This was done using a statistical analysis program called RSWHAC. This program was originally developed to handle the maximum likelihood estimations of the Arthur, Manly, McDonald, and Garner (1996) dataset, specific to habitat selection. In the present studies as each animal chose a seed, the proportional availability of each of the two seed types remaining changed. At each choice point, each animal faced its own unique decision, in light of what they have previously done. RSWHAC handles this type of heterogeneity in animal choice by using a maximum likelihood technique to estimate the probability that one resource will be selected relative to all other available options. These “selection indices” are calculated through an iterative process involving the proportional availability of each resource type, specific to successive choices. Availabilities are obtained by looking at each animal’s choice set on each selection. Once calculated, the selection indices are used in estimating the probability of obtaining each observation in the data set. The product of these probabilities is the likelihood estimate of the dataset occurring under the given selection-based model. This likelihood is then compared to a non-selection model in which the selection values or probabilities of choice for all options are

assumed equal. Models are compared by testing the difference between each model's deviance value ($\text{Deviance} = -2\text{Log}_e(\text{Likelihood})$) against a χ^2 distribution. The RSWHAC program was obtained from Western Ecosystems Inc. (Cheyenne, WY).

Experiment 1: Climbing Behavior

In order to model the procedure of Kacelnik and Marsh (2002), least chipmunks were trained on two patches. One patch was a high-work patch that required animals to climb the length of a pole to access seeds. The second patch, the low-work patch, did not require any such climbing behavior. For both patches, a textured pole stood vertically in a patio umbrella base with an attached, closed-off platform containing a bowl of seeds. The platform could be placed at the very top of the pole, leaving it 1.22 m in the air (high-work), or left resting at the bottom of the pole, just atop the umbrella base (low-work). Bases, poles, platforms, and bowls were all painted either highly saturated red or highly saturated green in order to associate a given amount of effort with a unique color stimulus.

The goal of this experiment was to compare preferences developed between previously high-work and low-work associated resources. To do this, each patch was associated with a given color and a given degree of work. Four animals were trained with a green, high-work association and a red, low-work association, while the remaining six animals had the opposite set of pairings: red, high-work and green, low-work. While no research has shown red-green color discrimination in the least chipmunk, the grey squirrel, a family member has been shown to make this discrimination (MacDonald, 1992).

After the standard habituation trial, animals proceeded through six training trials: three for high-work and three for low-work (see Figure 1). Trials were presented in

random order; however, no animal was presented with three of the same trial type in three consecutive training sessions. In each trial, chipmunks were placed into a square arena (1.83 m sides with 0.91 m high walls) and were presented with only one condition. Every presentation of each condition occurred in a consistent location that was on the opposite side of the room from where the alternate condition was presented (see Figure 2). This spatial cue was counterbalanced across animals and conditions.

After completing the six training trials, animals were presented with their first test trial on the morning of day 5. This work preference trial presented animals with both the high-work patch and the low-work patch. Patch locations and colors were maintained and each animal was given a free choice between working hard for their seeds and not working so hard for their seeds. Animals were placed in the arena and were allowed to deplete the seeds found at both patches. The researcher in the video observation room live-recorded each animal's first patch choice, first depleted patch, and the order in which seeds were taken from each patch. While allowing for an assessment of work preference, this trial also served as a final training of the association between the work required at a given patch and color associated with that work-level.

The final trial was the color preference trial. Here, animals were asked to choose between the two colored patches when they were equated at work-levels. Some animals ($n = 6$) were given the high-work color preference test, in which the platform for the low-work condition was raised to the standard high-work height and paired for choice with the high-work patch. Other animals ($n = 4$) were given the low-work color preference test in which the previously high-work associated platform was lowered to match the non-work standard. To control for any side preferences and to help ensure that color was the

cue used for choice, six of animals had the placement of their patches switched from their initial training positions. If they were trained with a red, high-work patch on the right, they were tested with the red patch on the left. During both the high-work and low-work tests, each patch was provisioned with nine pumpkin seeds and animals were allowed to deplete the seeds up until 20 minutes had elapsed following their first seed removal. This test allowed for the comparing of color preferences that may have emerged following training trials on which each color was associated with different degrees of work. This design also allowed for an assessment of whether or not animals capitalize on resources that have become easily available and if that preference extends to conditions in which both resources have become difficult to obtain. That is, do animals prefer resources and stimuli associated with work when both resources are equally difficult to acquire?

Experiment 1: Climbing Behavior Results

A total of 10 successfully trained animals were used in the present experiment. A number of other animals had to be dropped from the study during their training trials. In this experiment, it was required that each animal take all three seeds during each of the six training trials. A total of eight animals failed to do this on their first trial, while another seven animals failed during trials 2 through 6. The likelihood of failure appears to be unrelated to the training trial type on which the animal failed; seven animals ended on trials tied to the low-work condition, while the remaining eight animals failed on high-work training trials. In many of these cases, the animals simply stayed in their transport bottle and did not even approach the patch. An additional two animals were dropped due to experimenter error.

Animals were monitored for first choice and first depletion on the cost preference choice test. Given that the animals had to dig in order to obtain seeds at the high-work patch, as compared to the low-work patch, it was expected that chipmunks would initially chose (based on the first seed taken) the low-work patch in this simultaneous preference test. Nine of the ten animals did just that ($p = .01$). The initial depletion of each animal generally followed its first choice. In fact, only three animals even sampled the alternative patch prior to depleting their initial choice. A total of seven animals first depleted the low-work patch, while only two emptied the high-work patch first. The remaining animal failed to deplete either, only taking 2 seeds from each. According to the binomial analysis, the bias towards low-work patch depletion was only marginally significant ($p = .09$).

Regardless of their behavior in the work preference test, all 10 animals continued on to the simultaneous color preference test. Patches were now equated at work levels and the goal was to assess whether or not animals would prefer taking resources from patches that have a high-work history or if they would prefer taking seeds from patches with a low-work history. The first choice of each animal revealed no consistent pattern of behavior. Six of the animals first selected a seed from the patch that had a history of high-work, while the remaining four first chose from the patch that had a history of low-work ($p = .38$). This indifference was not related the type of test (high-work or low-work) the animals experienced. Of the animals that chose from the high-work history patch, three were tested with two high-work patches and three were tested with two low-work patches ($\chi^2 = 0.63$, $df = 1$, $p = 0.43$). Similar to the work preference test, sampling behavior between patches was limited. Only three animals chose seeds from the alternative patch by their third seed selection (see Figure 3), and some ($n = 4$) never

switched. The number of seeds taken varied for each animal, ranging anywhere from 1 to 17 seeds. In total, almost half of the seeds available ($M = 8.20$, $SD = 4.89$) were taken.

All choice data were subjected to the RSWHAC maximum likelihood analysis which produced different selection indices for the high-work-associated patch (0.55) and the low-work-associated patch (0.45). These values represent an estimated proportional likelihood of choice given an equal availability of seeds at both patch types. Specifically on any given choice in which the patches were equally provisioned, each chipmunk would have a 55% likelihood of selecting the patch with the high-work history and a 45% chance of selecting the patch with the low-work history. However, this estimation model was not a significantly better fit to the data than was a random chance model of equal likelihoods ($\Delta\chi^2 = 0.86$, $df = 1$, $p = .35$).

The goal of the RSWHAC analysis was to examine choice when the patches were equalized with regard to the effort required to obtain seeds. In other words, if the patches now only differed in color, would chipmunks choose the patch that required more work during training? Included within the initial analysis of this question was one animal that preferred, based on first choice in the work preference test, the high-work patch. Given that this animal may have assessed the patches differently from the rest of the sample, the RSWHAC analysis was re-run with the outlier removed from the dataset. While this dropped total sample size to 9, the results did begin to shift. The reanalysis yielded markedly different selection indices for the high-work associated patch (0.61) and low-work associated patch (0.39). However, this resulting model was only a marginally better fit to the data than was the non-selection, equal preference model ($\Delta\chi^2 = 3.12$, $df = 1$, $p = .08$). Significance was also not affected by the type of test the animals were exposed to.

For those tested with the low-work setup, the results remained marginally significant ($\Delta\chi^2 = 3.51$, $df = 1$, $p = .06$), and for those tested with the high work setup, the model showed no improvement over a non-selection model ($\Delta\chi^2 = 0.80$, $df = 1$, $p = .37$).

Experiment 1: Climbing Behavior Discussion

In the present experiment, least chipmunks displayed a slight preference (albeit of marginal significance) towards patches with a prior high-work history. In the work preference test, chipmunks generally avoided doing work, as only one animal chose the high-work patch prior to taking from the low-work patch. However, some animals switched between patches in the work preference test. The one animal that did choose to work in the work preference test was dropped from the RSWHAC analysis which then revealed the trend towards a work-associated bias. Animals that preferred low-work in the work preference test, now preferred to take from the patch that had a high-work history. Similarly, the animal that was dropped for preferring high-work preferred the low-work patch later in the color preference test. Eight of its first nine seed selections were pulled from the low-work history patch. This suggests that animals may prefer stimuli associated with resources that were initially avoided when the patches were unequal in the amount of work required.

It remains unclear how effortful climbing was for least chipmunks. While 10 animals successfully participated in the full series of trials, 15 others failed, but that failure seems unrelated to the effort required in a given trial. Almost as many animals failed on a low-work trial ($n = 7$) as did on a non-work trial ($n = 8$). Furthermore, many of those that did participate showed no signs of trouble as they scurried up the pole and some even chose to climb to the top of the low-work pole despite the seeds being located

in the box below. It is possible that the height afforded by the tall pole facilitated additional interest in the climbing behavior. When higher in the air, chipmunks had better visual access to the room containing the foraging arena and some showed interest in trying to escape the arena from this higher access point. While I tried to limit such behaviors by placing the seeds in an enclosed box, many would peek out of the box entry point throughout their trial. Despite these potential attractions to the tall pole, most animals initially avoided it when given a choice between the high-work and low-work patches. While the actual costs associated with the high-work patch are unknown, the majority of animals preferred to first take from the low-work patch, suggesting at least some avoidance of paying costs associated with climbing. And in nature, this would be expected. According to Optimal Foraging Theory, animals should seek to maximize energetic gains while minimizing the costs (MacArthur & Pianka, 1966). Taking resources from a patch that requires work likely uses more stored energy than taking from a patch that does not require an access cost. This is especially true when the amount of resource available at either patch is equal.

Across both test trials, but particularly in the work preference test, once an animal had made its first choice it usually fully exploited that patch prior to even sampling from the other. This may be akin to a more naturalistic context, especially if discrete types are separated by large travel distances. There was also limited switching behavior in the color preference test, even when both patches were placed at the low-work height. However, this may not be surprising when framed from a notion of energetic gain. The resources were identical and once a patch choice had been made there was no benefit to switching.

If anything, there was a cost, especially when both patches were placed in the high-work position.

Individual side and color preferences were not tested, although chipmunks were counterbalanced across the conditions. To my knowledge, chipmunks have shown no specific side preferences and the present study found no noticeable pattern of such choice. Empirically, least chipmunks have not been shown to discriminate between green and red, but a close relative has (MacDonald, 1992). If they were unable to tell the difference between the two colors, their choice ability would be significantly affected on the color preference test, but only that test. In all other trials, positioning also served to indicate required effort. If these animals could not discriminate red and green, then those animals that experienced the color preference test without a shift in their patch placements should show the anticipated work bias more strongly than the animals that did lose their positioning cue. However, this was not the case. Two of the animals that did not have their patches switched first took from the colored patch that had been associated with the low-work condition. Still, the most parsimonious explanation for the muted findings is simply that these animals could not differentiate between red and green. Other *Sciuridae* species are dichromatic (Jacobs, 1993; Jacobs, Neitz, & Crognale, 1985), and it is very likely that these least chipmunks fit that description.

Experiment 2: Climbing Behavior Follow-Up

One of the concerns with the previous work-assessment design was the limited sampling behavior seen across the two patches during the color preference test. This forced the results to be heavily dependent on initial choice, rather than the potential complexities of choice that may be seen if the animal sampled from patch to patch. The

overall lack of sampling behavior seen in the previous test trials may be more attributable to the conditions at test than to the animal's choice preferences. During each color preference test, animals were required to enter the enclosed pole box and obtain their seeds. For some animals, this also required them to experience a high level of work to get those seeds. If the animal chose to sample, it would have to exit the box, travel across the arena, and potentially climb up another 1.22 m pole to access another high-work patch.

Therefore, in this follow-up study, a third color preference test was designed that reduced both the travel distance between patches, as well as the similarity between the tested patches and the initial training patches. In this third condition, only the two colored bowls (Red and Green) that had been previously contained within the pole boxes were used during the color preference test. Each bowl was located in the corner opposite the animal entry point (see Figure 2), and sat within 20 cm of the other bowl on the surface of the sand. Aside from this final test session, all other trials proceeded just as they did in the previous pole assessment.

Experiment 2: Climbing Behavior Follow-Up Results

Nine animals participated in this test; however, two of these animals were dropped due to a procedural error during the test trials. Of the remaining seven, all but one had fully participated in the initial pole study at least 10 weeks prior to the start of the current assessment. The requirements for completion were relaxed in this study design, as two animals did not completely deplete a patch during their training trials, leaving one seed apiece. Both animals missed a work-associated seed; one miss was on Trial 4 and the other on Trial 6. All other animals completely depleted the training patches.

As in the previous work design, animals were monitored for initial patch choice and first depletion during their work preference test. I again expected animals to initially target the patch with the easy-to-obtain seeds and deplete them before turning to the high-work patch. The initial choice data supported this; all seven animals first took from the low-work patch ($p = .01$). However, two animals sampled away from the low-work patch after their first visit and ended up depleting the high-work patch first, leaving the depletion trend non-significant ($p = .23$).

All animals continued on to the color preference test. In this test, only the colored bowls remained and each was provisioned with nine seeds. Animals were monitored for their first choice and for all successive choices made within a 20 minute time window following that first selection. The initial choice data revealed no significant preference between the two patch types ($p = .50$). Four animals chose the high-work associated bowl while the remaining three first chose the low-work associated bowl (see Figure 4). Almost 70% of the seeds available were taken ($M = 12.14$, $SD = 5.37$). All choice data were then subjected to a RSWHAC analysis, which confirmed the lack of any obvious preference. The selection indices (High-Work: 0.44, Low-Work: 0.56) provided no better fit to the data than did a non-selection model of equal likelihood ($\Delta\chi^2 = 0.86$, $df = 1$, $p = .35$).

Experiment 2: Climbing Behavior Follow-Up Discussion

As in Experiment 1, the majority of animals in the follow-up experiment first took from and first depleted the low-patch in the work preference test. Even the two additional animals that were dropped for a later procedural error took from the low-work patch first. This cements the notion that least chipmunks prefer not to perform extra work for their food. While the depletion data were not significant, the general direction matched initial

choice. Least chipmunks generally preferred to take seeds from easy patches when both high-work and low-work patches were available. However, this work-avoidance bias did not appear to influence choice during the color preference test. All seeds were now placed at ground level in two neighboring bowls located at the opposite end of the box. Initial choice showed no preference, nor did the successive choices of each chipmunk indicate a work bias. While there was noticeably more sampling behavior, this behavior did not match the expected preference toward the work-associated seeds. In this design and the previous one, least chipmunks showed indifference to the associated history of a colored patch. Patches previously associated with high-work were not preferred over patches that had been previously easy to obtain.

One obvious concern is that many of the animals in this design had previously participated in the initial climbing tests. This would be a concern regardless of the findings, but in their current form, it is possible that already-learned associations interfered with learning in this follow-up condition. There was no effort made to match up color and side associations with the same condition type that the animal had received in the previous experiment. After participating twice, each animal may have fully evaluated the costs and benefits of each choice. While this may have led them to be less attentive to the color conditions, it is arguable that they should have actually been more attentive. These animals had increased exposure to paying the costs associated with work, and that increased training should have encouraged them to be more discriminatory in order to avoid continuing to pay those costs. Of course this would have to assume that the animals were able to discriminate the colors of bowls, which is a very tenuous assumption.

At the color preference test, there was little cost for switching between the two patches and that may have also influenced the successive choice behavior of the chipmunks. By placing the bowls on the surface and side by side, the animals may have more easily assessed the change in costs and the sudden similarity in costs and may have simply chosen at random. However this should not matter if animals are truly experiencing contrast and looking for any opportunity to secure a high value resource without paying the costs associated with acquiring it. The novelty of the patch conditions may have also affected their behavior. By moving the bowls out of the patch setup and placing them on the sand, the animals may have viewed the patches as new patches operating under new contingencies; contingencies that must be sampled for new learning to take place.

Both this experiment and Experiment 1 employed climbing a pole as the work condition in order to mimic previous research. Much like Kacelnik and Marsh (2002), each distance was paired with a color association. However given the results, least chipmunks may not have been able to easily differentiate the red patch from the green patch, but color is certainly not the only important associative characteristic used by foraging rodents. While it would be disingenuous to suggest that color or visual cues play no role in foraging, other cues may also be important to a forager in a patchy environment.

Experiment 3: Digging Behavior

One of the goals of this research project was to provide a more naturalistic perspective on the work ethic phenomenon. Because the climbing results were inconclusive, a new design was implemented that avoided color discrimination while incorporating natural behaviors and foraging mechanisms used by least chipmunks,

animals are adept foragers, cachers, and pilferers (e.g., Jenkins & Devenport, 2014; Penner & Devenport, 2011; Devenport, Humphries, & Devenport, 1998). According to Vander Wall (1991), one of the main foraging strategies used by naïve pilferers is olfaction. In order to find patches buried beneath the substrate, there is a heavy reliance on odor cues (e.g., Jenkins & Devenport, 2014; Geluso, 2006, Winterrowd & Weigl, 2006).

In this second work-assessment experiment, least chipmunks were required to forage at ground level for each of the two resource patches: low-work and high-work. In order to magnify the difference in needed effort, the high-work patch was buried 3 cm below the surface of the sand with a bait seed on top, while the low-work patch consisted of four seeds that were simply clumped together and placed atop the sand surface. Three centimeters, the depth of the high-work patch, is nearly double the depth observed for the average cache placement by least chipmunks in our lab (Penner & Devenport, 2011).

I paired each seed type with a specific scent, raspberry or banana. The two seed scents were chosen because of their noticeably different odors and because few, if any, of the animals had any experience consuming raspberries and definitely none of them had ever consumed bananas. While all animals had consumed other fruits in the lab, these particular food types were not provided during captivity. Additionally, two scent preference tests were conducted to ensure that there was no standard preference for either scent type; neither of which suggested any noticeable difference (See Appendix A). Each scent was obtained using the McCormick & Company® flavored extract product line. Specifically, I used McCormick's Raspberry Extract and McCormick's Imitation Banana

Extract. While only the banana flavor was listed as an imitation, the raspberry extract contained other products suggesting that neither extract was natural.

For scent application, small plastic bottles (~2.5 cm in diameter) were cleaned with a 10% ethanol solution and dried. Then, just prior to the start of each trial, a researcher would place four unhulled pumpkin seeds into a clean bottle, followed by 0.3 ml of the assigned scent. The researcher then sealed and shook the bottle for a 5-minute period to ensure that each seed was fully coated with the extract. After which, the seeds were placed in (or on) the sand and the trial would begin within another 5 to 10 minute period. Given the short time frame between scent application and patch placement, the seeds remained damp. This likely increased the strength of the olfactory cue furthering the salience of the conditions (Geluso, 2006; Vander Wall, 2000).

The basic procedure paralleled that of the previous work assessments. Animals had a 20-minute habituation period, followed by three successive days of two training trials each, and concluded with two test sessions on Day 5 (see Figure 1). During every training trial, each animal was presented with a patch containing four seeds. On half of the trials, the animals received low-work patches which consisted of four seeds placed in a small clump on the sand surface. While on the other half, each animal was given a high-work patch which consisted of three seeds placed 3 cm below the surface of the sand, and fourth seed atop the patch to attract the animal to dig. To create the high-work patch, a small piece of PVC pipe (3.8 cm in diameter) was forced into the sand until the top of sand lined up with the top of the pipe. Using a small metal spatula, sand was then flipped out of the pipe until the researcher could see just beyond the 3 cm marking located on the inside of the PVC pipe. Seeds were then placed through the pipe, into the patch, and then

the pipe was refilled to the surface with sand. The researcher would then slowly twist and pull up on the pipe to carefully remove it, while maintaining the appropriate patch depth. The location of the patch was then smoothed over to remove any noticeable substrate cues, but a bait seed was placed atop the patch to mark its location. This was done in order to increase the reliability of finding the hidden patch. This seed remained visually conspicuous, but was partially pushed down into the sand so that it still had to be pulled from the sand by the animal. One bait seed should not have affected the animal's perception of work as it still needed to dig for the three remaining buried seeds. Standard patch locations were held consistent across animals and because of this, the sand was very thoroughly mixed between trials.

For this experiment, animals were trained and tested in a small foraging box which measured 1.21 m long by 0.61 m wide. The box had 0.30 m high walls, with 6-8 cm of medium grade industrial sand on the box floor. The box was completely enclosed with a one-half inch hardware cloth top allowing for good camera access. To enter the box, a large plastic bottle containing the animal was affixed to an access hole which allowed the animal to enter the foraging area on its own volition (see Figure 5). During the six training trials, each patch was presented successively and placed slightly to the left or right of center in the foraging box (see Figure 5). The order of these training trials was randomized, with the rule that three successive trials could not consist of the same patch type; and the scent-associations and patch locations were counterbalanced across subjects.

After an animal completed training trials 1 through 6, it was presented with a work preference test on the morning of day 5. Here, the animal was given access to both

previously trained patches. For each animal, the researcher recorded its first patch choice, the order of successive seed removals, and the first patch depleted. Once the animal had depleted both patches, it was removed five minutes following removal of the last seed. This test was done in order to see if least chipmunks prefer to work and dig for their food, or if they prefer to experience less work and simply take items off of the sand surface.

During the afternoon of Day 5, animals were presented with a simultaneous odor preference test. This test was done to assess whether or not least chipmunks prefer a scent associated with a high-work history, or if they prefer the scent associated with a low-work history. Some of the animals ($n = 5$) were presented a choice between a set of two differently scented (banana and raspberry) patches requiring a high amount of work, while others ($n = 7$) chose between a set of two differently scented patches requiring a low amount of work. Having both test types ensured that any preferences associated with high- or low-work histories could be teased apart from preferences associated with a change in patch condition (e.g., a banana-scented patch moving from a high-work history to a low-work patch).

For the odor preference test, the patches were relocated to the end of the box furthest away from the entry point, placed centrally, and located within 10 cm of each other (see Figure 5). This was done to avoid the animals simply running to their previously patch locations and choosing based on the amount of work involved rather than the scent cue. The patches were placed near each other to make sure they were approached simultaneously by each foraging chipmunk. Each patch was stocked with 12 seeds. Much like in the previous studies, this was done to extend choice behavior and to help ensure that reduce reliance on the animal's first choice. In the low-work test setup,

all 12 seeds for each patch were placed in a small clump atop the sand surface, while in the high-work test setup, 11 seeds at each patch were buried 3 cm below the sand surface with one seed remaining atop each patch to serve as bait. As before, animals were monitored for their first patch choice, as well as for each of their successive choices for 20 minutes following their first seed take.

Experiment 3: Digging Behavior Results

Twelve animals successfully participated in this study; however, a number of other animals ($n = 10$) were dropped after failing to completely deplete their training seeds on trials 1 or 2. There was no clear pattern to these failures. Six of the animals failed on a high-work trial (4 Raspberry, 2 Banana), while the remaining four failed on an low-work trial (2 Raspberry, 2 Banana). Of the 10 successful animals, four had been previously tested in a similar scent-based study (competitor assessment) and two of those four had also been tested in the initial work designs. For each of the re-tested animals, at least four weeks had passed since participating in a previous experiment. The current study was also conducted in a different room and in a different testing box which further alleviated any confounded-training concerns.

During the work preference test, animals were asked to choose between digging for seeds and taking seeds from the surface. Both patches remained associated with their initial training scent which was counterbalanced across animals. Each animal was monitored for first choice and first depletion. Binomial tests conducted on each assessment revealed no overall preference for work or non-work associated seeds. Eight of the 12 animals selected the low-work patch first ($p = 0.19$), and 7 of 10 depleted the low-work patch first ($p = 0.17$). The remaining two animals failed to deplete either.

Interestingly, sampling behavior between patches was minimal as only four animals showed any sampling beyond the selection of the bait work seed; all of which still ended up depleting the high-work patch prior to the low-work seeds. Of the remaining six non-sampling chipmunks, five chose to deplete the low-work seeds first. In sum, least chipmunks showed no preference to take easily available seeds over those that were more difficult to obtain and required digging.

All twelve animals were then presented with the odor preference test on the afternoon of Day 5. Here, animals were asked to choose between two patches that were equally difficult to obtain and that had scents that were associated with different work histories. Animals were monitored for first choice and for each successive choice occurring within a 20 minute period following that first selection. Unlike the results for the work preference test, a clear bias quickly emerged. Ten of the 12 animals first took from the patch with the high-work associated scent ($p = .02$). Collectively, a total of 119 seeds were selected by the 12 animals ($M = 9.92$, $SD = 4.90$) and only 51 of those seeds were pulled from the previously low-work condition. The order of these selections is also of theoretical importance so the data were subjected to a RSWHAC analysis. This revealed noticeably divergent selection indices. Specifically, the choice model suggested a 65% likelihood of taking a seed from the high-work scented patch and only a 35% likelihood of taking a seed from the low-work scented patch. This model provided a significantly better fit to the data than did a non-selection model of random choice ($\Delta\chi^2 = 9.42$, $df = 1$, $p = .002$) suggesting that least chipmunks strongly preferred taking seeds from the patch that was associated with a high-work history (see Figure 6).

In the odor preference test, five of the animals were tested with two patches that required a high degree of work to access, while the remaining five animals were tested with patches of differently scented seeds that were discretely clumped on the sand surface. Given these different testing procedures, additional RSWHAC analyses were conducted on each of these independent groups. For those tested with patches on the surface, the results held. In fact, the results strengthened. All seven animals that were tested with two surface patches initially took from the patch containing the high-work scent. In total, 86 seeds were selected and 52 came from the patch containing the odor associated with a high-work history. Only one of the seven animals took any seeds patch containing the odor associated with a low-work history within their first three seed selections. The RSWHAC analysis provided a significant model with a strong preference, yielding a 74% likelihood of choosing from the patch with the odor associated with a high-work history and only a 26% likelihood of choosing from the patch associated with a low-work history odor ($\Delta\chi^2 = 19.19$, $df = 1$, $p < .001$). However, the results changed drastically for the animals tested using two differently scented, high-work patches. This RSWHAC analysis provided selection indices in the opposite direction of the previous two analyses, but the resulting model was not a significantly better fit to the data than was a random selection model ($\Delta\chi^2 = 1.14$, $df = 1$, $p = .29$). Collectively, these animals showed indifference.

The indifference seen in the previous analysis may have been influenced by the work-related preferences of the animals. While they showed no preference for stimuli that had been previously associated with a high work history, three of five animals tested with high-work patches had shown a preference to work for their food rather than take it from the sand surface in the earlier work preference test. Two of those three animals even

depleted the high-work patch prior to depleting the low-work patch during that earlier test trial. It is possible that these animals may have viewed the costs associated with the high-work patch differently from those animals that preferred not to work for their food. To examine this further, two additional RSWHAC analyses were run using the odor preference data. The first analysis was conducted using only those animals that initially chose the low-work patch ($n = 8$) in the work preference test. Here, the results suggested a strong preference towards a patch with a work-associated scent. The model proposed a 65% likelihood of choosing from the high-work associated patch and only a 35% likelihood of choosing from the low-work associated patch. This model was a significantly better fit to the data than the random choice model ($\Delta\chi^2 = 6.26$, $df = 1$, $p = .012$). This basic finding was also seen when using those animals that preferred to work for their food ($n = 4$). While only marginally significant ($\Delta\chi^2 = 3.16$, $df = 1$, $p = .075$), this last RSWHAC analysis suggested a 64% preference for a patch containing seeds scented with the high-work history scent.

Experiment 3: Digging Behavior Discussion

Given a choice between digging for food and taking food freely from the surface, the majority of chipmunks first select and exploit the easier option. While the results of the work preference tests were not significant, the pattern of choice matched the exploitation patterns seen in the previous two experiments. A much stronger preference was seen in the odor preference test. Least chipmunks clearly showed a bias towards patch scent cues that were associated with high levels of previous effort. This finding matches that of Kacelnik and Marsh (2002) and the many other studies showing a bias towards high-work associated stimuli or resources. Importantly, this experiment was able to show

these effects with only a limited amount of patch experience. Unlike in the previous literature, least chipmunks were only given three training trials on each patch and each associated scent cue. The fact that this preference emerged after such limited experience also serves to counter the claim by Zentall (2008) who argued that significant over-training was necessary for work-related preferences.

Surprisingly, this preference towards a high-work associated scent cue emerged despite the fact that animals did not show a significant bias away from the high-work patch during the work preference test. In fact, some animals targeted and depleted it first when both the high-work and low-work patches were present. Two of the animals that first took from the high-work patch in the present study also showed a similar work bias in the work preference test of experiment 2. These consistent preferences may be stable patterns of behavior that apply across situations. Carrying such preferences across the varied contexts of each design could easily affect the interpretation of the results and would also generate new insight into the mechanisms driving choice behavior. However, attempting to draw such trait-related insight from the current study would be tenuous given the many factors that may have influenced the current patch preferences. Furthermore, when examining only those animals that showed an initial preference for digging in the work preference test, the basic pattern of results held in the odor preference test albeit not significantly so. Assuming that the trend is indicative of the overall pattern, it appears that even when high-work is not perceived as costly, animals may still form a preference toward resources obtained under such conditions.

The results only held to the overall pattern when both of the testing patches were held at low-work levels. In this setup, the scent that was previously associated with a

high-work patch was now applied to a patch placed on the surface. Here, animals showed a very strong preference for that particular scent which had been associated with a high-work history. This suggests that when a seed scent that had been previously difficult to access becomes easily available, least chipmunks preferred to target it. However, the opposite trend was seen when the patch conditions were equated at the high-work level. When the odor preference test consisted of two patches of buried seeds, least chipmunks showed a reduced preference towards the scent that had been previously associated with high-work and an increased preference towards the scent associated with seeds that had never been hard to get. While this shift was not a significant one, the fluctuation may suggest that an important factor in any patch choice is the potential for information updating. If the costs associated with a given scent cue have changed, animals may prefer to update their knowledge rather than follow any previously established preferences. Further work is needed to tease apart these components of choice.

As a scatter hoarding species, least chipmunks regularly dig in the foraging substrate to bury and recover their own resources, as well as to steal from other caching animals (Penner & Devenport, 2011). When presented with the opportunity to take buried seeds, least chipmunks may have processed such behavior as an indirect gain over other competitor animals. In fact, additional work in our lab has indicated that least chipmunks actually prefer to pilfer rather than first recovering their own resources and thus taking from a buried patch may have not been seen as a cost-inducing experience. However, most chipmunks in the present experiment did take what was easy first in that work preference test and while it may behoove future studies to ramp up the cost associated with the high-work condition, the current study balanced those costs against the potential

trade-off of non-participation, or potential trial failure. Regardless, during the odor preference test, least chipmunks showed a strong preference towards a patch that was ultimately no different from a neighboring patch other than the scent associated with each and prior costs paid for access to seeds marked with that scent. This experiment provided further evidence for a work-ethic bias, and did so with a limited training procedure.

Experiment 4: Competitor Assessment

Previous research has suggested that work ethic effects may not be due to the specific nature of work, but to more general valuation mechanisms. For example, if resources are acquired after a period of deprivation, those resources come to be preferred by the animal over resources not acquired during a deprivation state (Zentall & Singer, 2007). This finding is similar to that reported for work preferences. It is possible that other effects might also be revealed. Any circumstance that increases the cost, or difficulty, of acquiring a resource, may alter the value associated with that resource. This might lead to preferences for the stimuli associated with that resource and the circumstances, or costs under which the resource was acquired.

To assess whether this general mechanism exists, I devised a study that compared the preferences of chipmunks under two conditions of competitor exposure: Presence and Absence. In the natural environment, least chipmunks compete with a wide variety of other foragers and hoarders including a larger and more physically dominant congener, the eastern chipmunk (*Tamias striatus*). Despite their size disadvantage, least chipmunks are thought to even the competition, in part by using strategic hoarding and pilfering (Penner & Devenport, 2011). However, it remains to be seen how their food preferences might be influenced by the presence of a competitor eastern chipmunk.

For this experiment, least chipmunks were habituated, placed in a large foraging arena (1.83 m X 1.83 m), and presented with six individual training trials. Three of the trials were associated with competitor presence, while the other three trials were conducted without a competitor in the arena. At the start of each training trial, a least chipmunk was transported to the arena by means of a large plastic nest bottle and placed along the center of one of the four arena walls (see Figure 7). A large live trap (50.8 cm X 17.8 cm X 17.8 cm) was placed in one of the opposing corners of the arena. If the current trial was a non-competitor trial, the cage was left closed and empty. If the trial was a competitor trial, the cage was moved to the other opposite corner and contained an eastern chipmunk. For both the safety of the least chipmunk and to allow it to complete the trial, the cage always remained closed providing no direct access to the competitor. The two animals could see, hear, and smell each other and have some interaction through the gratings of the wire trap, but the least chipmunk remained out of danger and the eastern chipmunk had no actual access to the seeds for which it was supposed to be competing.

For each training trial, the seeds were placed towards the inside of the arena along one side of the cage containing a competitor or along one side of the empty cage (see Figure 7). Each patch was within 10 cm of the competitor or empty cage, which required the least chipmunk to get relatively close to any presented eastern chipmunk. Every training trial patch contained three scent-associated seeds using the raspberry or banana extracts seen in the previous work assessment. These seeds were simply placed atop the sand surface. The order of the training trials varied for each chipmunk and the scents and competitor locations were counterbalanced across animals.

After the six training trials, animals were given a competitor preference test during which both the empty cage and seeds were in one corner of the arena and the competitor and seeds were in the other. This presented each animal with two patches of three seeds each, both patches retaining their original scent cue and competitor condition. This was done to assess whether or not least chipmunks prefer to take resources from areas associated with a competitor or not. Animals were monitored for their first choice and for their first depletion. This test trial was followed by an afternoon test trial in which both patches of seeds were presented either near the competitor or near an empty cage. This served as the odor preference test, which allowed animals the opportunity to display a preference for a scent that was either associated with competitor presence or competitor absence in the previous training trials. For the test of preference that occurred near a competitor ($n = 8$), the competitor was present and the cage containing the competitor was moved approximately 30 cm from the side wall on which it was originally trained. This left a small alleyway in which the two patches of scented seeds could be placed together (see Figure 8). A total 18 seeds were given (9 per scented patch) placed on the surface of the sand and each patch was placed within 10 cm of the other. The increase in seed number was again done to examine the overall pattern of choice and reduce reliance on first choice. The competitor absence test ($n = 7$) was done identically, except that no eastern chipmunk was present during the trial. As always, animals were monitored for their first choice and for each successive choice occurring within a 20 minute window following the first seed take.

Experiment 4: Competitor Assessment Results

Fifteen animals successfully participated in this study; however a number of animals were dropped ($n = 7$) after failing to take at least two seeds on training trials 1 through 4. Some of the successful animals had similar early failures and were re-run at a later date. In fact, many animals were attempted, yet there was a high failure and non-participation rate. A total of 34 training sessions (some animals repeating more than once) started and ended in failure. The majority ($n = 28$) of these failures occurred on competitor present training trials. This pattern was consistent regardless of how many trials had been completed by the animal. Of the ten animals that failed on trials 2, 3, or 4, only one of those animals failed on an empty cage trial.

The fifteen successful animals were presented with the competitor preference test on the morning of day 5. Researchers recorded the successive choices of each animal and binomial tests were conducted on both the first choice and first patch depletion of each animal. Eight of the 15 animals initially chose the patch closest to the empty cage ($p = 0.50$). The results better matched the expected direction when looking at which patch the animals first depleted. While not all animals depleted both patches, nine of the fourteen that did, emptied the patch nearest the empty cage first. However, this was not significantly different from chance expectations ($p = 0.21$).

Each of the fifteen animals then participated in the odor preference test. Seven of the animals were tested using the empty cage, while the remaining eight were tested with the competitor present. As in the competitor preference test, the first choice of each animal revealed no significant preference. Ten animals first chose the patch that was scented with the non-competitor associated scent, while the remaining seven chose the

patch with the competitor-associated scent ($p = .15$). In total, 180 seeds ($M = 12.20$, $SD = 5.36$) were taken out of the available 270. Of those 180 seeds, 92 seeds were scented with the olfactory stimulus that had been previously associated with the competitor condition. This suggested no preference. However when the data were subjected to a RSWHAC analysis, a general pattern emerged (see Figure 9). Specifically, the RSWHAC generated selection indices revealed a preference for the patch with competitor-associated scent (0.62) over the patch with the non-competitor scent (0.38). This model was a significantly better fit to the data than was a non-selection, random choice model ($\Delta\chi^2 = 7.10$, $df = 1$, $p = .007$).

Additional RSWHAC analyses were conducted to determine if the type of odor preference test had any influence on the pattern of choice. Using just those animals tested with the competitor present, the results held ($\Delta\chi^2 = 24.01$, $df = 1$, $p < .001$). On any given equal choice, animals had an estimated 78% likelihood of choosing the patch with the competitor-associated scent and only a 22% chance of selecting seeds from the patch with the non-competitor scent. While staying in the same direction, this pattern faded when using only those animals tested without the competitor. The selection model (Competitor Seeds: 0.58; Non-Competitor: 0.42) failed to provide a significantly better fit to the data than the non-selection model for those choosing in the presence of an empty cage ($\Delta\chi^2 = 1.54$, $df = 1$, $p = .215$).

An animal's initial preference during the competitor preference test may have also influenced their long-term selections in the odor preference test. A fourth RSWHAC analysis was conducted using just those animals that preferred to take from the empty cage patch in the earlier competitor preference test. The results matched the overall

picture. Animals showed a 65% likelihood of taking seeds from the competitor-associated patch and only a 35% likelihood of selecting a seed from the patch that was scented with the non-competitor scent ($\Delta\chi^2 = 5.75, df = 1, p = .016$). The same pattern was seen for those animals that first chose the competitor patch in the competitor preference tests (Competitor: 0.58; Non-Competitor: 0.42); however, this model was not significant ($\Delta\chi^2 = 2.00, df = 1, p = .157$).

Experiment 4: Competitor Assessment Discussion

In the competitor-preference tests, animals showed no overall preference for the competitor absent patches. During this test, many animals chose to initially take from, and even deplete the patch closest to the competitor. This is true despite the fact that the attrition trends seen during training indicated that the competitor was often avoided. Unexpected behavior was also seen in the first choice data associated with the odor preference test. Only 7 of the 15 animals first took from the patch containing the competitor associated scent. Based on this, one might expect the full set of choices to reveal a preference for the scent associated with the absence of a competitor or no preference at all. However, RSWHAC analyses conducted on the full set of odor preference data revealed a very different pattern of behavior. Least chipmunks were shown to have a pronounced preference for the scent that was associated with a competitor-history. Using all 15 animals, the analysis revealed a preference for the competitor-associated scent that was only slightly smaller than that seen in the digging patch design for the high-work associated cue. While the first choice data fail to match this result, it is clearly the exception to the rule. It's possible that the change in the structure of the test setup affected that first choice finding. The cage was moved away

from the wall to create an alleyway so that each animal was presented with the two scent patches at the same point of approach. This shift may have altered the animals' perception of risk and they may have grabbed randomly while they reassessed the current conditions. Despite this very minor anomaly, the overall results advance the literature by adding a new condition in which later preference can be inflated by increasing the costs experienced during training. Competition joins the cost of work (e.g., Kacelnik & Marsh (2002) and the cost of deprivation (Zentall & Singer, 2007) as a factor that can increase preference for stimuli and/or resources simply by experiencing them simultaneously.

While the overall pattern seems to be clear, the results must be qualified by some limitations of the design. For one, a high number of animals failed on training trials involving a competitor as they were unwilling to approach a patch near the competitor cage. In fact, many animals stayed in or near their nest bottle for the duration of each failed trial. Unfortunately, this also led to biased participation as only animals that would approach the competitor could be used. This may have even affected the trial on which animals began their training. Animals that were willing to approach the competitor likely succeeded regardless of the trial on which they started, while animals that hesitated when the competitor was present were probably more likely to participate if their first training trial was one conducted under competitor absence. Had I been able to include all of the animals that had previously failed, it is possible that the results would have been even stronger. Most of the animals that failed, failed on a competitor trial, which suggests that they individually found the competitor to be risky and/or competitive foraging to be costly. If these animals had made it to the competitor-preference test, it is likely that they would have preferred to first target the competitor-absent patch. When looking at data

from the 15 animals that made it to this test, it is clear that those that initially avoided the competitor patch, later went on to show a very strong preference for the competitor scent in the odor preference test. Animals that failed on competitor training trials may have increased this preference simply due to the fact that they found the competitor so aversive that they refused to even participate in training.

Of the animals that were successfully trained, many behaved in ways that were very different from their failed counterparts. While there was often some initial hesitation towards the competitor, by the end of a training sequence, many of the trained animals were not only cavalier in their approach to the competitor cage, but were impressively bold enough to sit atop it and consume their seeds. This was done all while the eastern chipmunk sat just underneath. This may suggest a general fading of the perceived costs of competitive foraging in this experimental design. It also may have further reduced the potential strength of preference towards competitor-associated scent. Once these animals realized there was no real risk, the costs that would otherwise be associated with competitive foraging, may have become negligible.

Given that only eight of the successfully trained and tested animals chose from the competitor-absent patch in the competitor preference test, it is possible that the remaining seven used different assessment mechanisms to drive their preference. In the field, tracking the foraging behavior of others can provide some benefits (e.g., Makenbach, Waterman, & Roth, 2013; Valone, 2007). While these effects are probably less likely in a laboratory setting, the effects of local enhancement may not be. Least chipmunks that seem not to be scared of the competitor may have also just been drawn to the patch location because of the presence of the competitor. However, local enhancement

would only draw attention to a patch's location on the first trial and would be redundant afterwards. While the present study made no effort to differentiate between which mechanisms were used by these animals, the high failure rate on competitor-present trials should indicate the general strategy of foraging chipmunks. Most prefer to avoid foraging near a competitor eastern chipmunk. It is possible that animals that preferred the competitor patch in the competitor-test may have also learned that the caged eastern chipmunk posed no threat to themselves or their resources as the cage remained closed. Had the competitor risk been real, the results favoring a competitor-associated cue may have been even stronger.

I also looked to see if there were any differences between animals tested with the competitor present or without the competitor during the odor preference test. This was done to ensure that animals were showing consistent preference for the competitor scent and not just a preference for the patch that changed. Both tests reported the same result. There was a strong preference towards the competitor-associated patch when the competitor was present and that preference was maintained, although reduced, during odor tests that occurred without the presence of a competitor.

In sum, the pattern of selection here was strongly in favor of the competitor-associated seeds. This may indicate that the mechanism used to describe the choice of work-associated resources may easily apply to other instances of costly foraging. If the conditions of training are sufficiently costly, the animal may experience a bigger contrast shift when the resource is actually gained than it would under less negative conditions (e.g., Zentall & Singer, 2007). This should lead to foraging preferences related to the resources acquired while in a negative state, or just when foraging is a costly experience.

While the present experiment shows no strong evidence that animals will initially target a resource that has become more accessible, or avoid paying the high costs associated with a given resource, it does show that preferences can emerge. Least chipmunks clearly prefer scents associated with a past competitive history and this preference could continue to drive future choice behavior.

General Discussion

Previous research conducted on work-ethic and within-trial contrast has been notoriously mixed (Meindl, 2012). Some authors have found evidence for such biases (e.g., Clement et al. 2000), while others struggle to find any semblance of evidence even after extensive over-training on associations (e.g., Vasconcelos et al. 2007). The present set of studies matches that history. In both of the climbing contexts, animals preferred low-work when the conditions differed in work amount. Generally, they first selected and first depleted the patch that was lower to the ground, indicating an avoidance of work. Yet when the patches were adjusted to be equal in terms the difficulty of obtaining seeds, no significant preference was seen. The data revealed just a marginally significant trend of animals preferring to the exploit the colored patch that had been previously associated with the high-work condition. This suggests only that animals *might* have been attending to the costs associated with each patch and each color during training. Confidence in this finding certainly fades when combined with the data from the follow-up study in which the animals showed indifference to work history.

In experiment 3, least chipmunks appeared equally willing to dig or not dig for their food, contrasting with the avoidance of work seen in experiments 1 and 2. However, they then showed a very clear preference to take scented seeds that had been previously

associated with high-work once the patches were made equally available. This finding replicated and extended the work ethic findings identified in the literature. A final extension was made in experiment 4, the competitor assessment experiment. Instead of using work to exact a foraging cost, animals were presented with the opportunity to take resources under the presence of competitor threat (or not). Much like experiment 3, animals were indifferent with regards to selecting seeds from either a competitor-present patch or a competitor-absence patch. But when they were presented with both scented patches under equal conditions of competitor threat, strong preferences did emerge. Least chipmunks selectively preferred to exploit the patch that was scented with the olfactory cue that had been previously associated with a competitive foraging environment.

Despite replicating and extending the effects seen in the literature, these effects remain theoretically difficult. When resources are equal in quality and accessibility, the economically rational approach is to assign equal value. However, least chipmunks (and other animals) do something very different. They selectively choose the resources that had been previously associated with effort or competitor threat. The adaptive function of this preference is unclear. It may be that the resources that were previously acquired under high-cost conditions increase in value by eliminating the costs associated with foraging for them. This shift in value may steer an animal towards that resource over others. This would not be unlike the contrast effects reported by Crespi (1942). Crespi trained rats to run down an alleyway for a low-value reward and then increased the magnitude of that reward on a later trial. He found that the rats would then begin to run faster to obtain the high value reward than they would have if he had simply began their training with the high-value reward and maintained it. It appears that rats and chipmunks may capitalize

on resources that suddenly become higher in value, because based on their experience, this was not expected and may not happen again. In other words, they preferentially exploit such resources when it is suddenly easy to do so, which in a natural foraging environment could serve an adaptive function.

When the resources became equally costly to obtain, a similar assessment behavior may have been seen. For the color and odor preference tests, some animals were presented with two patches both associated with the high cost conditions. This effectively changed the low-cost patch to a high-cost patch, while maintaining the high-cost patch at its normal cost levels. Here, the animals still preferred to exploit the patches that were associated with high-cost history. The Crespi (1942) study may also shed light on this finding. In a second test, rats were trained with a high value resource that was downshifted to a low value. Rats that experienced this then began to run more slowly to the resource than they would have, had they only ever experienced the low value reward. This is not unlike the downshift in reward quality that would be associated with the scented patch with a low-cost history. Resources that had been previously easy to obtain suddenly become difficult, decreasing beyond expectation, the effort the animals were willing to put in to obtaining them, and subsequently driving preference up for the patch with the high-cost history. Based on experience, animals might view the downshift as being temporary and they may see no benefit in taking from that patch when those resources might be more easily found later. This may serve to avoid putting energy into securing resources that typically do not require significant expenditure to obtain.

While temporary shifts in subjective value may explain the results and may do so from a naturalistic perspective, other researchers have suggested that the value of a

resource is more dependent on past experience than it is on the current costs of acquiring it. According to Marsh et al. (2004), after paying a large cost to acquire a resource, the state of the animal will be sufficiently negative, allowing for a higher perceived value of that resource. An animal in a sated, or positive state, has less need for the resource and values that resource less than an animal in a high-need state. Thus when an animal has experienced different resources (or cues) acquired under different costs, they will have established a preference for one of those resources (or cues) because of the costs of acquiring them previously. The higher the cost associated with gaining a resource, the bigger the contrast seen when the resource is gained. This could also explain why a preference for cost-associated resources is maintained even when both resources become equally difficult to acquire. However, that does not explain the adaptive function of these preferences.

In the present study and in the literature generally, these preferences for work-associated resources are not considered economically rational. The preferred item is of no greater objective value than the non-preferred item. In this case, both patches were stocked with pumpkin seeds. However, if the difficult-to-obtain rewards were of objectively higher values because they suddenly become easier to exploit, then it would be economically rational to take those resources in that moment of easy availability. This tendency to over-value difficult-to-obtain items or more costly items may be a generalized expression of this otherwise adaptive response. Animals can suddenly gain access to a resource that they otherwise wouldn't be willing to pay the costs to get. In the field, it is unlikely that animals would expend extra energy or run the risks unless a resource was objectively more valuable. The current study and others forced animals to

work harder for items of equal quality by eliminating access to them during the individual training trials. In other words, animals were tasked with doing a behavior they would not be likely to normally do. In natural settings, animals have plenty of choices and do not spontaneously select patches that are costly to access, they simply go elsewhere (e.g., Winterrowd & Devenport, 2004; Lima & Dill, 1990; Grubb & Greenwald, 1982).

By focusing on the shift in costs that are associated with the presented resources it may be possible to better unify the field of studies showing these ‘irrational’ biases. Such biases have been reported exist for such a wide variety of conditions. These include work (e.g., Kacelnik & Marsh, 2002), deprivation (Zentall & Singer, 2007), non-preferred feeding locations (Friedrich & Zentall, 2004), and now, competition. The costs associated with each of these would be costs unpaid by the animals in the field. However, the downshift in costs for these resources (or the upshift in the cost of others) may lead animals to capitalize on what has suddenly become equal in cost to the other available resources, but was previously too costly to obtain. It may benefit an animal that capitalizes on these resources now, when it is unclear, based on past experience, that they will remain this way.

Study Limitations

Given the differences seen across experimental designs, a number of factors may be invoked to explain such an apparent lack of consistency. In each design, patches were associated with various stimuli (color and odors) and standardized locations. While those locations were counterbalanced across animals, it remains possible that underlying, individual side preferences contributed to the variability. This is especially true when looking at smaller samples. To help correct for this, patch locations were moved from

their training spots to new locations during the final test setup in three of the four experimental designs (follow-up, digging behavior, and competitor presence). Additionally, some animals had their patches reversed (in all four designs) in such a way that if the patch was given a right side placement during training, the patch was then placed towards the left side of the animal's approach during the final test.

While reducing the concerns about side preferences, the movement of these patches during the color and odor test sessions may have affected foraging behavior in other ways. It is possible that such movement led to a greater display of sampling behavior than would have otherwise been seen. This may have reduced the strength of the results. Animals may have perceived the moved patches as new patches operating under different expectations. A new patch may suggest new foraging rules and animals might be expected to sample the new conditions (Inglis, Langton, Forkman, & Lazarus, 2001). Despite this possibility, in both the digging experiment and competitor experiment, least chipmunks strongly preferred the patches that had an associated high cost history. This suggests that in spite of the location shift, animals are using the past history of the cue to guide foraging decisions rather than assuming completely new contingencies.

Changing the location of a patch was not the only change that may have affected some of the preference results. Between the cost preference test and final preference test (color or odor), one of the patches either increased or decreased in terms of the costs associated with acquiring seeds from it. This was done to make the two patches equally costly. While the overall preference leaned strongly towards the scented patch that was associated with a high-cost history, some animals may have simply preferred to take from the patch that shifted the most in terms of the associated costs. When both patches were

presented on the surface in the digging experiment, animals preferred to take from the patch with the scent that had been previously associated with high-work. Framed differently, they preferred to take from the patch that had become unexpectedly easy to access. However when the patches were buried, such a preference faded and least chipmunks leaned towards preferring the scented patch associated with a low-work history. It is possible that these animals were not choosing based on past work but rather were updating their information on patches that changed in terms of work amount. However, this pattern of choice was not observed in the competitor assessment design. It's unclear what this inconsistency means, but it is clear that more work needs to be done to assess the importance of patch change in relation to contrast effects.

Patches were also associated with different sensory cues. In the climbing-based designs, each patch was tied to a color, while both the digging and competitor tests involved olfactory-cued associations. Inspired by Kacelnik and Marsh's (2002) work with trichromatic birds, red and green colors were chosen for the climbing-based work ethic experiment. While chipmunks and other squirrel species are dichromatic with only short and medium wavelength (i.e., blue and green) absorptive opsins (e.g., van Arsdell & Loop, 2004; Jacobs, 1993; Jacobs, Neitz, & Crognale, 1985), at least one squirrel species (*Sciurus carolinensis*) has been shown to discriminate between red and green stimuli (MacDonald, 1992). These abilities were not tested in least chipmunks, nor were any color preferences assessed. It remains possible that these animals struggled with distinguishing between the two patch colors.

If least chipmunks were unable to distinguish between the patches then that may explain why the results were so categorically different when the tests involved odor

discrimination rather than color cues. This alone may explain some of the inconsistencies across experiments. In both of the climbing-based experiments, least chipmunks may have selected randomly, or based on location, rather than selecting based on the color associations. In contrast, these animals should have had no problem distinguishing between the odor cues in both the digging and competitor setups. In both, animals showed a clear olfactory-driven preference for the patch scent that was associated with buried patches and with competitor threat. Had the correct color choices been made for the climbing tests, the consistency of the four experimental results would have likely increased.

While the olfactory-based preferences eventually emerged in the both of the associated odor preference tests, olfactory cues did not seem to drive the first choice behavior of least chipmunks. This is interesting because if animals are not using training information to drive initial preference or first choice, it is unclear why they would start using that information later. An animal foraging in a natural environment may not have opportunities to display long-emergent preferences and thus if a true preference exists, one should expect to see that preference on trial one. Surprisingly, less than half of the animals in the competitor design initially took from the previously competitor associated seeds, yet most clearly preferred those seeds over the course of the odor preference test.

One of the other concerns with the present series of studies is the population of animals used and often repeatedly used in each design. All four studies were plagued by a relatively high attrition rate. Many animals successfully started a series of trials, only to later fail during training, and even more animals were unsuccessful from the very start. Anywhere from 7 to 15 animals were unsuccessful participants in a given experiment and

some that did participate failed in a previous attempt. Ultimately, this led to a biased sample of animals that would actively participate *and* a reduced sample size. While this is likely no different from other studies that use wild animal populations, the biased participation may be affecting the results. This influence was most strongly seen during the competitor experiment. Some animals were exceptionally hesitant when presented with a competitor trial, while others boldly approached the competitor and even sat atop that cage hulling their seeds. Such bold attributes were very likely to influence the foraging decisions of these animals and recent research on albatross (*Thalassarche melanophrys*) (Patrick & Weimerskirch, 2014), barnacle geese (*Branta leucopsis*) (Kurvers, Nolet, Prins, Ydenberg, & van Oers, 2012), and rats (Weiss & Neuringer, 2012) has confirmed such expectations. Weiss and Neuringer (2012) reported that bold rats showed increased variability in foraging efforts and increased overall success. If only the bold animals were participating in the current design, the overall conclusions made about chipmunk foraging behavior may not be generalizable ones. In fact, it is possible that the results would be stronger had I been able to use the less bold animals. The shyer an animal was, the more threatening they may have found the competitor to be. This reticence may have also carried over in each of the other study designs and might explain some of the variability seen.

Knowing what is actually assessed as costly by a given animal is crucial to any design aimed at assessing work ethic effects. Animals may show preferences for effortful behaviors that increase information gain (e.g., Bean, Mason, & Bateson, 1999) or reduce individual risk (Makenbach et al. 2013), rather than what naturally seems costly in a foraging paradigm. These preferences may vary across individual animals and it is

unlikely that one stimulus preference test is sufficient enough to know what an animal truly prefers to do. Some studies (Friedrich & Zentall, 2004) have adjusted for these variable preferences and have still found clear evidence of an effect. Future work should continue to attend to these concerns.

Conclusion

Animals do appear to develop preferences based on the costs paid for resources during previous foraging bouts. The present design has provided support for the ‘work ethic effect,’ but also a more general mechanism that influences preferences not just when work occurs, but also when an animal experiences competitor threat. Least chipmunks in both the digging-based experiment and in the competitor experiment showed clear preferences for patch scents associated with seeds acquired under the conditions of high work and high competitor threat. While other mechanisms may have played a role in preference establishment, or even the strength of the effect, the overall finding remains. The foraging choices of least chipmunks are affected by the prior costs paid for resources. This study has helped to fill a gap in the literature by significantly reducing the exposure to the different patches and their associated costs, and by adding the cost of competitor threat. These new twists on a classic design argue for continued research related to work ethic behavior and other foraging costs, and particularly new research in more naturalistic designs. In the wild, animals would not be expected to experience hundreds of training trials before learning the costs associated with a given resource. This is why it was so important to find these effects without complicated and overdone training paradigms. With just three training exposures to each patch cost, least chipmunks began to alter their foraging preferences and the work ethic bias emerged. While it is important to remember

this bias is still economically irrational when the resources are of equal quality, such preferences should emerge in natural conditions in which difficult-to-obtain rewards are suddenly easy to access.

References

- Arantes, J. & Grace, R. C. (2008). Failure to obtain value enhancement by within-trial contrast in simultaneous and successive discriminations. *Learning & Behavior*, *36* (1), 1-11.
- Arantes, J. & Grace, R. C. (2008b). Contrast and value : Beyond the work ethic effect. A reply to Zentall (2008). *Learning & Behavior*, *36* (1), 26-28.
- Arthur, S. M., Manly, B. F. J., McDonald, L. L., & Garner G. W. (1996). Assessing habitat selection when availability changes. *Ecology*, *77*, 215-227.
- Aw, J. M., Holbrook, R. I., Burt de Perera, T., & Kacelnik, A. (2009). State-dependent valuation learning in fish: Banded tetras prefer stimuli associated with greater past deprivation. *Behavioural Processes*, *81*, 333-336.
- Bean, D., Mason, G. J., & Bateson, M. (1999). Contrafreeloading in starlings: testing the information hypothesis. *Behaviour*, *136*, 1267-1282.
- Bradshaw, A. L. & Poling, A. (1991). Choice by rats for enriched versus standard home cages: plastic pipes, wood platforms, wood chips, and paper towels as enrichment items. *Journal of the Experimental Analysis of Behavior*, *55*, 245-250.
- Carder, B. & Berkowitz, K. (1970). Rats' preference for earned in comparison with free food. *Science*, *167*, 1273-1274.
- Clement, T. S., Feltus, J. R., Kaiser, D. H., & Zentall, T. R. (2000). "Work ethic" in pigeons: Reward value is directly related to the effort or time required to obtain the reward. *Psychonomic Bulletin & Review*, *7* (1), 100-106.
- Crespi, L. P. (1942). Quantitative variation of incentive and performance in the white rat. *The American Journal of Psychology*, *55* (4), 467-517.
- Cuthill, I. C., Kacelnik, A., Krebs, J. R., Haccou, P., & Iwasa, Y. (1990). Starlings exploiting patches: The effect of recent experience on foraging decisions. *Animal Behaviour*, *40*, 625-640.
- Devenport, L., Humphries, T., & Devenport, J. (1998). Future value and patch choice in least chipmunks. *Animal Behaviour*, *55* (6), 1571-1581.
- Friedin, E. & Kacelnik, A. (2011). Rational choice, context dependence, and the value of information in european starlings (*Sturnus vulgaris*). *Science*, *334*, 1000-1002.

- Friedrich, A. M. & Zentall, T. R. (2004). Pigeons shift their preference toward locations of food that take more effort to obtain. *Behavioural Processes*, 67, 405-415.
- Geluso, K. (2006). Benefits of small-sized caches for scatter-hoarding rodents: influence of cache size, depth, and soil moisture. *Journal of Mammalogy*, 86 (6), 1186-1192.
- Grubb Jr., T. C. & Greenwald, L. (1986). Sparrows and a brushpile: Foraging responses to different combinations of predation risk and energy cost. *Animal Behaviour*, 30 (3), 637-640.
- Havelka, J. (1956). Problem-seeking behavior in rats. *Canadian Journal of Psychology*, 10 (2), 91-97.
- Inglis, I. R., Forkman, B., & Lazarus, J. (1997). Free food or earned food? A review and fuzzy model of contrafreeloading. *Animal Behaviour*, 53 (6), 1171-1191.
- Inglis, I. R., Langton, S., Forkman, B., & Lazarus, J. (2001). An information primacy model of exploratory and foraging behavior. *Animal Behaviour*, 62, 543-557.
- Jacobs, G. H. (1993). The distribution and nature of colour vision among the mammals. *Biological Reviews*, 68, 413-471.
- Jacobs, G. H., Neitz, J., & Crognale, M. (1985). Spectral sensitivity of ground squirrel cones measured with ERG flicker photometry. *Journal of Comparative Physiology A*, 156, 503-509.
- Jenkins, J. R. & Devenport, L. D. (2014). Seed preparation diminishes cache loss in least chipmunks. *Journal of Mammalogy*, 95 (2), 276-283.
- Jensen, G. D. (1963). Preference for bar pressing over “freeloading” as a function of number of reward presses. *Journal of Experimental Psychology*, 65 (5), 451-454.
- Johnson, A. W. & Gallagher, M. (2011). Greater effort boosts the affective taste properties of food. *Proceedings of the Royal Society B*, 278, 1450-1456.
- Kacelnik, A. & Marsh, B. (2002). Cost can increase preference in starlings. *Animal Behaviour*, 63, 245-250.
- Koffer, K. & Coulson, G. (1971). Feline indolence: Cats prefer free to response-produced food. *Psychonomic Science*, 24, 41-42.
- Kurvers, R. H. J. M., Nolet, B. A., Prins, H. H. T., Ydenberg, R. C., & van Oers, K. (2012). Boldness affects foraging decisions in barnacle geese: an experimental approach. *Behavioral Ecology*, 23, 1155-1161.

- Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619-640.
- Lydall, E. S., Gilmour, G., & Dwyer, D. M. (2010). Rats place greater value on rewards produced by high effort: An animal analogue of the “effort justification” effect. *Journal of Experimental Social Psychology*, 46, 1134-1137.
- MacArthur, R. H. & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100, 603-609.
- MacDonald, I. M. (1992). Grey squirrels discriminate red from green in a foraging situation. *Animal Behavior*, 43 (4), 694-695.
- Makenbach, S. A., Waterman, J. M., & Roth, J. D. (2013). Predator detection and dilution as benefits of associations between yellow mongooses and Cape ground squirrels. *Behavioral Ecology and Sociobiology*, 67, 1187-1194.
- Marsh, B., Schuck-Paim, C., & Kacelnik, A. (2004). Energetic state during learning affects foraging choices in starlings. *Behavioral Ecology*, 15 (3), 396-399.
- Meindl, J. N. (2012) Understanding preference shifts: A review and alternate explanation of within-trial contrast and state-dependent valuation. *The Behavior Analyst*, 35 (2), 179-195.
- McGowan, R. T. S., Robbins, C. T., Alldredge, J. R., & Newberry, R. (2010). Contrafreeloading in grizzly bears: Implications for captive foraging enrichment. *Zoo Biology*, 29, 484-502.
- McNamara, J. M., Trimmer, P. C., & Houston, A. I. (2012). The ecological rationality of state-dependent valuation. *Psychological Review*, 119 (1), 114-119.
- Morgan, M. J. (1974). Do rats like to work for their food? *Learning and Motivation*, 5, 352-368.
- Neuringer, A. J. (1969). Animals respond for food in the presence of free food. *Science*, 166, 399-401.
- Neuringer, A. J. (1970). Many responses per food reward with free food present. *Science*, 169, 503-504.
- Osborne, S. R. (1977). The free food (contrafreeloading) phenomenon: A review and analysis. *Animal Learning & Behavior*, 5 (3), 221-235.
- Patrick, S. C. & Weimerskirch, H. (2014). Personality, foraging and fitness consequences in a long lived seabird. *PLoS ONE*, 9 (2), e87269.

- Penner, J. L. & Devenport, L. D. (2011). A comparative study of caching and pilfering behavior in two sympatric species, least chipmunks (*Tamias minimus*) and eastern chipmunks (*Tamias striatus*). *Journal of Comparative Psychology*, 125 (4), 375-384.
- Richter, S. H., Gass, P., & Fuss, J. (2014). Resting is rusting: a critical view on rodent wheel-running behavior. *The Neuroscientist*, 20 (4), 313-325.
- Singer, R. A. & Zentall, T. R. (2011). Preference for the outcome that follows a relatively aversive event: Contrast or delay reduction? *Learning and Motivation*, 42, 255-271.
- Singh, D. (1970). Preference for bar pressing to obtain reward over freeloading in rats and children. *Journal of Comparative and Physiological Psychology*, 73 (2), 320-237.
- Shibasaki, M. & Kawai, N. (2011). The reversed work-ethic effect: Monkeys avoid stimuli associated with high-effort. *Japanese Psychological Research*, 53 (1), 77-85.
- Tarte, R. D. & Synder, R. L. (1973). Some sources of variation in the bar pressing versus freeloading phenomenon in rats. *Journal of Comparative and Physiological Psychology*, 84, 128-133.
- Tarte, R. D., Townsend, S. G., & Vernon, C. R. (1973). Housing environments and the barpressing vs freeloading phenomenon in rats. *Bulletin of the Psychonomic Society*, 2 (2), 69-71.
- Taylor, G. T. (1972). A limitation of the contrafreeloading phenomenon. *Psychonomic Science*, 29, 173-174.
- Valone, T. J. (2007). From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behavioral Ecology and Sociobiology*, 62, 1-14.
- Van Arsdel, R. E. & Loop, M. S. (2004). Color vision sensitivity in normally dichromatic species and humans. *Visual Neuroscience*, 21, 685-692.
- Vander Wall, S. B. (1991). Mechanisms of cache recovery by yellow pine chipmunks. *Animal Behaviour*, 41, 851-863.
- Vander Wall, S. B. (2000). The influence of environmental conditions on cache recovery and cache pilferage by yellow pin chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology*, 11 (5), 544-549.

- Vasconcelos, M. & Urcuioli, P. J. (2008). Deprivation level and choice in pigeons: A test of within-trial contrast. *Learning & Behavior*, 36 (1), 12-18.
- Vasconcelos, M. & Urcuioli, P. J. (2008b). Certainties and mysteries in the within-trial contrast literature : A reply to Zentall (2008). *Learning & Behavior*, 36 (1), 23-25.
- Vasconcelos, M. & Urcuioli, P. J. (2009). Extensive training is insufficient to produce the work-ethic effect in pigeons. *Journal of the Experimental Analysis of Behavior*, 91, 143-152.
- Vasconcelos, M., Urcuioli, P. J., & Lionello-DeNolf, K. M. (2007). Failure to replicate the “work ethic” effect in pigeons. *Journal of the Experimental Analysis of Behavior*, 87, 383-399.
- Verts, B. J. and L. N. Carraway. (2001). *Tamias minimus*. *Mammalian Species*, 653, 1-10.
- Waite, T. A. (2008). Preference for oddity: Uniqueness heuristic or hierarchical choice process? *Animal Cognition*, 11 (4), 707-713.
- Weiss, A. & Neuringer, A. (2012). Reinforced variability enhances object exploration in shy and bold rats. *Physiology & Behavior*, 107, 451-457.
- Winterrowd, M. F. & Devenport, L. D. (2004). Balancing variable patch quality with predation risk. *Behavioural Processes*, 67 (1), 39-46.
- Winterrowd, M. F., & Weigl, P. D. (2006). Mechanisms of cache retrieval in the group nesting southern flying squirrel (*Glaucomys Volans*). *Ethology*, 112 (11), 1136-1144.
- Zentall, T. R. (2008). Within-trial contrast: When you see it and when you don't. *Learning & Behavior*, 36 (1), 19-22.
- Zentall, T. R. (2010). Justification of effort by humans and pigeons: Cognitive dissonance or contrast? *Current Directions in Psychological Science*, 19 (5), 296-300.
- Zentall, T. R. & Singer, R. A. (2007). Within-trial contrast: Pigeons prefer conditioned reinforcers that follow a relatively more rather than a less aversive event. *Journal of the Experimental Analysis of Behavior*, 88, 131-149.

Appendix A

Simultaneous Choice Preference: Banana and Raspberry Scent

Eight animals were subjected to a preference test involving the simultaneous choice between the two scent stimuli. Four of the tested animals were also used as subjects in the digging test, the competitor test, or both. For this basic assessment, animals were removed from their living quarters, and placed in a solitary cage for a period of 3-5 days prior to the start of testing. Each animal was kept on a restricted diet of rodent chow and weighed daily. On the first day of the testing protocol, each animal was placed inside a foraging box similar to the one used in the digging test design. The box sand had been previously sifted, cleaned, and smoothed over and the animal was then given a 20 minute habituation period to explore the box environment. The animal was then returned to its cage and fed. On the next day, the animal was again placed in the box, but the box now contained the two relevant scent cues (banana and raspberry). Opposite the entry port, two cleaned aluminum food dishes were placed on the surface of the sand and approximately 15 cm from each other. Each dish contained a cotton square coated with 0.3 ml of the appropriate extract. Side of extract placement was counterbalanced between animals in order to control for any side-based preferences. Each aluminum dish was covered with an aluminum lid which had a hole in its center. The hole was approximately 2.5 cm in diameter and it prevented the animal from removing the cotton square, but still allowed the animal to smell the scent cue. Each animal was monitored for their first choice and a binomial test was conducted to assess any general scent-based preferences. Animals were removed approximately 20 minutes after their initial choice was made.

Simultaneous Choice Preference Results and Discussion

The majority of the tested animals approached one of the two aluminum dishes within a matter of minutes upon exiting the transport bottle. Exactly half of the animals ($n = 4$) first approached the aluminum dish containing the raspberry odor cue, while the remaining animals all first approached the dish containing the banana cue ($p = .27$). To ensure that this lack of preference was reliable, another set of animals was subjected to an alternative preference test involving the sequential, singular presentation of odors rather than the simultaneous presentation seen here in this current design.

Sequential Test Preference: Banana and Raspberry Scent

Eight animals were given two trials, separated by a day, involving the individual presentation of one of the two scent cues (Banana, Raspberry). Seven of the eight animals were also participants in the digging test, the competitor test, or both; however, only four of those seven had already participated in those studies prior to participating in the current preference design. Each animal was given a 20 minute habituation period on Day 1, and all of the standard preparation procedures seen in the previous preference test were maintained. Following the habituation day, each animal was then presented with one of the two scents in an aluminum dish located at the opposite end of the foraging box. Upon exiting the transport bottle, the animal was time-monitored for its approach to the aluminum dish and the presented scent. Ten minutes after the initial encounter the animal was removed from the box and returned to its solitary environment. On the next day, the animal was run through the same procedure, but with the alternative scent. The order of scent presentation was counterbalanced across animals.

Sequential Choice Preference Results and Discussion

The number of seconds between entry and interaction with the dish was recorded for each trial of each animal; and a dependent samples t-test was used to compare latency times for each of the two scent cues. While animals do seem to be taking longer to approach the banana scented patch ($M = 74.25$, $SD = 126.61$) as compared to the raspberry scented patch ($M = 42.13$, $SD = 66.80$), this difference was not significant, $t(7) = .869$, $p = .414$. Given the noticeably high variability in animal approach times, animals that had approach times over 100 seconds were dropped and the analysis was re-run with no significant change in result ($p = .752$). On this second run, the means for each of the scent patch arrival times were within one second of each other, suggestive of no strong preference for either the banana scent cue or the raspberry scent cue.

Figure 1.

<i>Sample Sequence</i>					
	<i>Day 1</i>	<i>Day 2</i>	<i>Day 3</i>	<i>Day 4</i>	<i>Day 5</i>
Morning (9AM to 12PM)	Habituation (20 Minutes)	High-Cost Training Trial	High-Cost Training Trial	Low-Cost Training Trial	Cost Preference Test
		Animals were placed in the foraging arena with the High-Cost Patch.	Animals were placed in the foraging arena with the High-Cost Patch.	Animals were placed in the foraging arena with the Low-Cost Patch.	
Afternoon (1PM to 4PM)		Low-Cost Training Trial	High-Cost Training Trial	Low-Cost Training Trial	Stimulus (Color or Odor) Preference Test
		Animals were placed in the foraging arena with the Low-Cost Patch.	Animals were placed in the foraging arena with the High-Cost Patch.	Animals were placed in the foraging arena with the Low-Cost Patch.	Some animals were presented with both the High-Cost Patch and the Low-Cost Patch, but the High-Cost Patch was altered to match the demand of the Low-Cost Patch.
					----- Other animals were presented with both the High-Cost Patch and the Low-Cost Patch, but the Low-Cost Patch was altered to match the demand of the High-Cost Patch.

Figure 2.

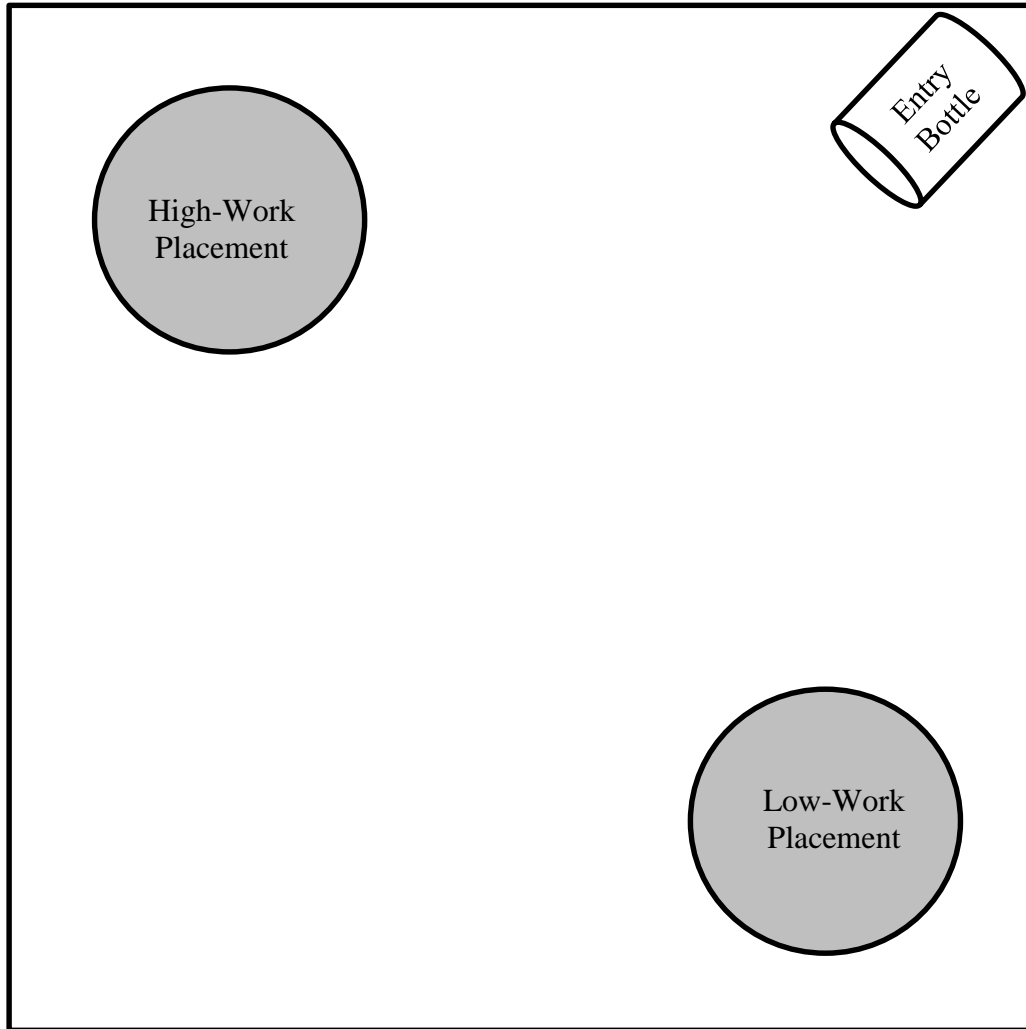


Figure 3.

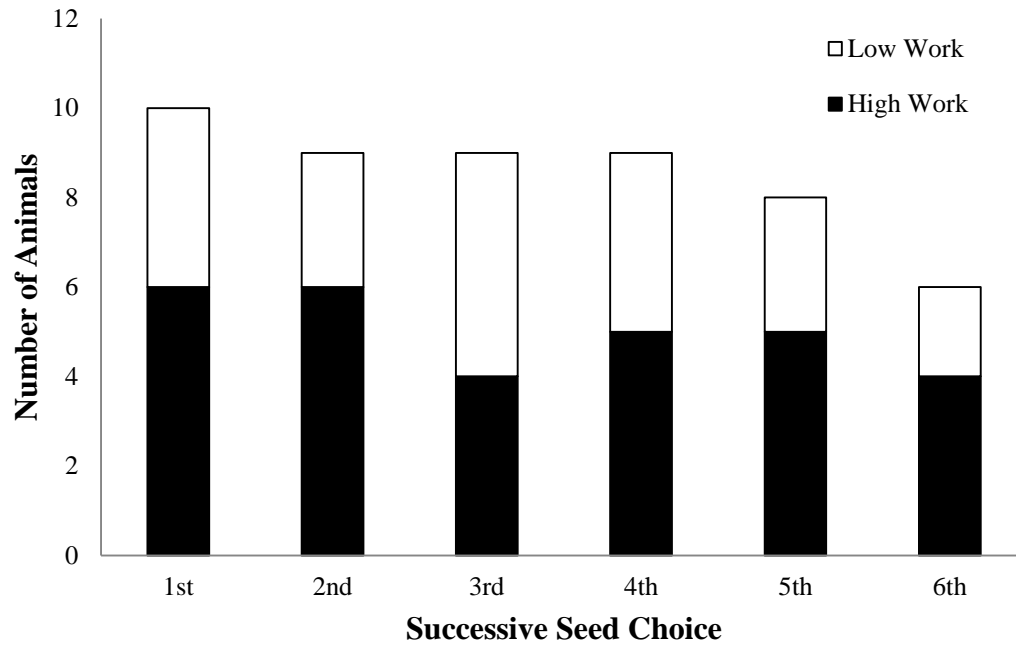


Figure 4.

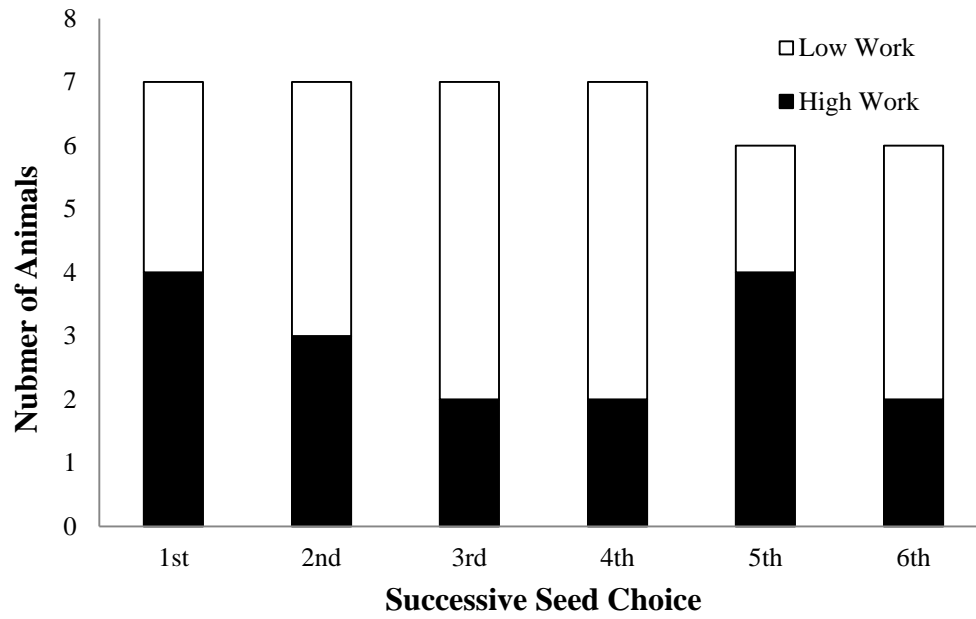


Figure 5.

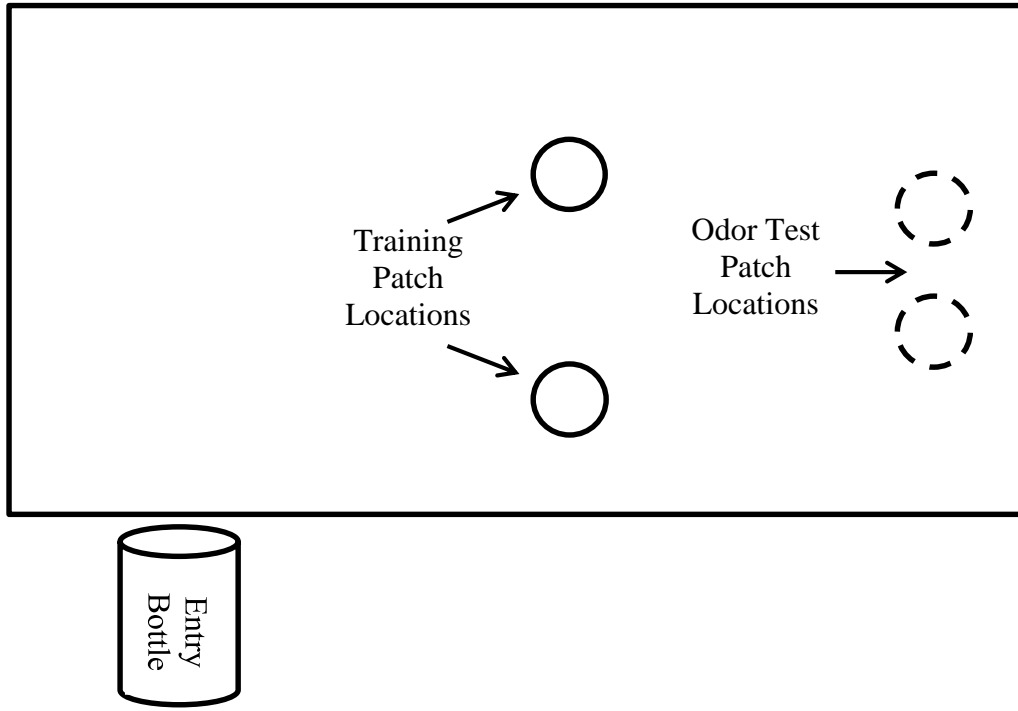


Figure 6.

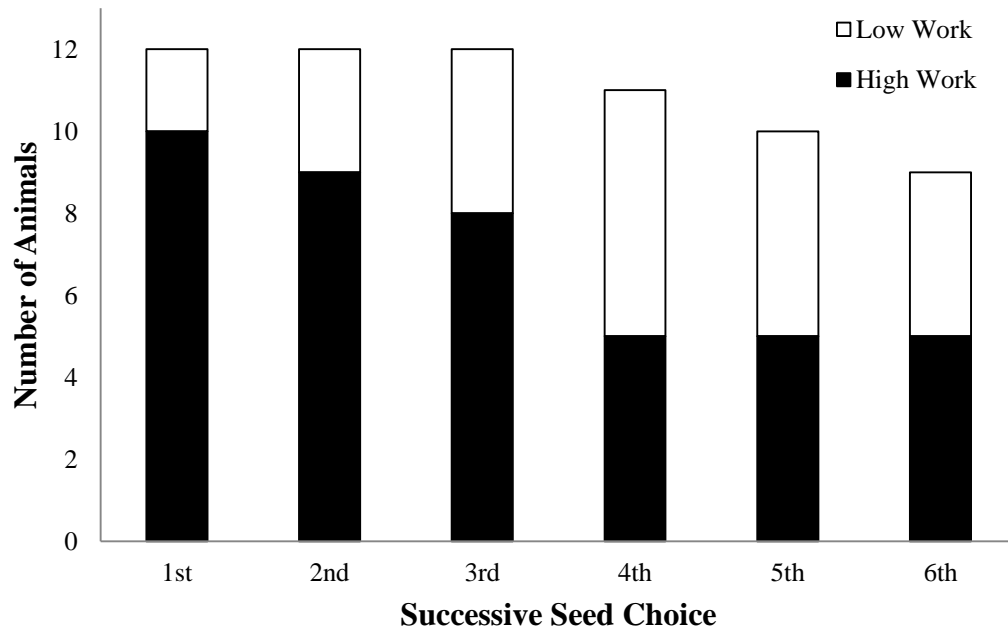


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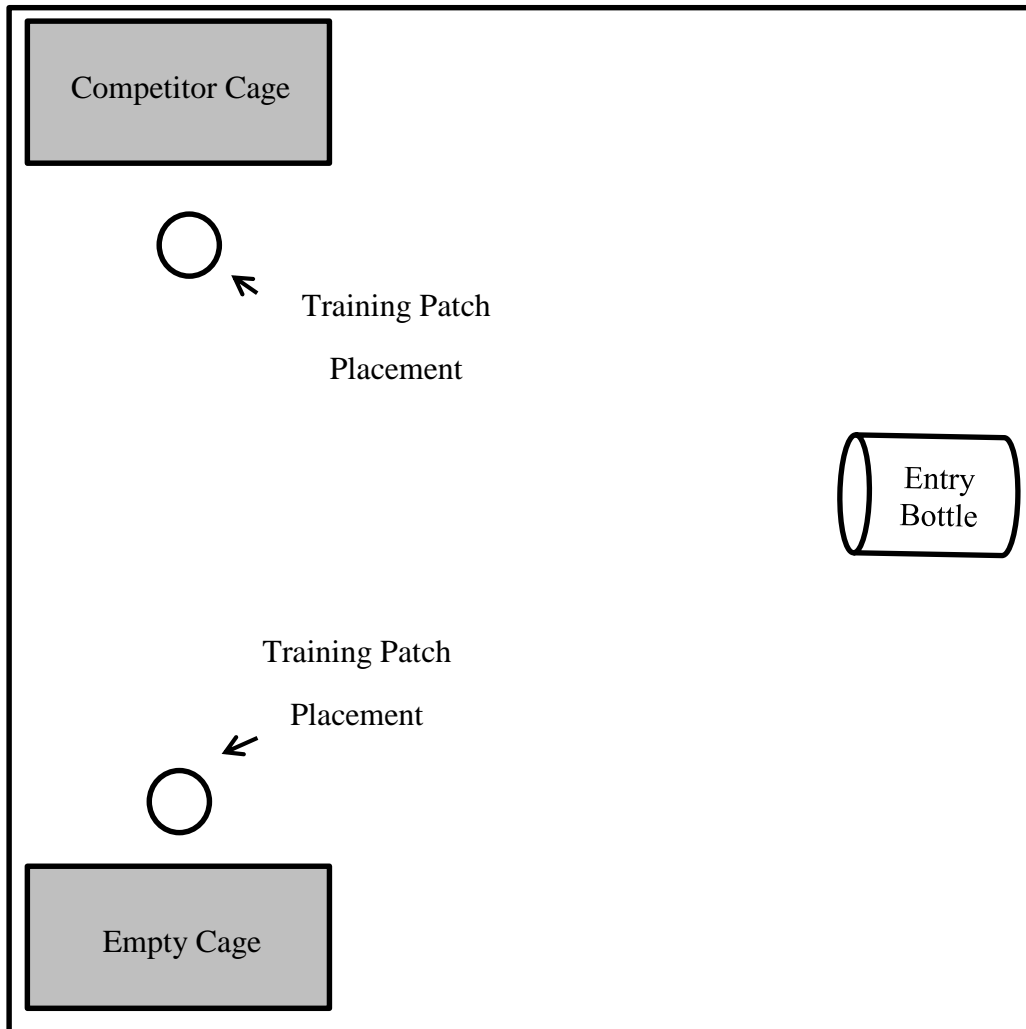


Figure 8.

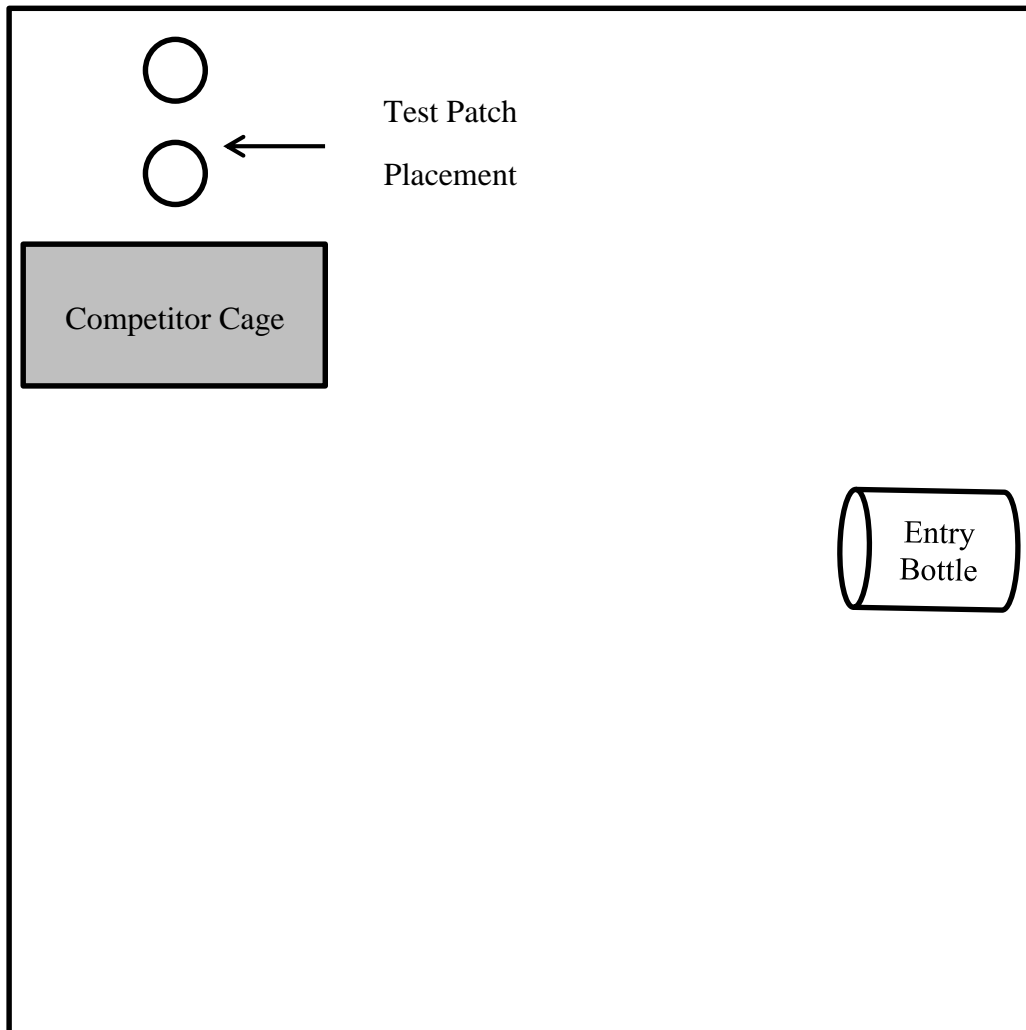


Figure 9.

