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REDUCTION OF ASYMMETRICAL COMPETITION THROUGH COGNITIVE ADAPTATIONS IN TWO SYMPATRIC CHIPMUNKS

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KATHERINE M. DANIELS
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REDUCTION OF ASYMMETRICAL COMPETITION THROUGH COGNITIVE ADAPTATIONS IN TWO SYMPATRIC CHIPMUNKS

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF PSYCHOLOGY

BY

Dr. Scott Gronlund, Chair

Dr. Lynn Devenport

Dr. Ingo Schlupp

Dr. Robert Terry

Dr. Jorge Mendoza

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Abstract

Asymmetrical competition occurs frequently and can potentially lead to a small species facing resource exclusion. When this competition occurs for food resources, smaller species often have to compensate for this pressure by becoming more efficient foragers. This can include harvesting food more efficiently (Brown, Kotler & Mitchell, 1994), knowing when one should revisit a patch site (Devenport, Humphries, & Devenport (1998), and expertly hiding one's stores to prevent theft (Devenport, Luna, & Devenport, 2000; Penner & Devenport, 2011). There has been indirect evidence that suggests that some of these behavioral differences are the result of cognitive adaptations (Devenport et al., 2000; Penner & Devenport, 2011, Vander Wall, 1991). This study assessed whether a pair of asymmetrical competitors (small *Tamias minimus* and large *T. striatus*) would display different foraging strategies and if these differences were the result of underlying cognitive differences between them. These expectations were partially supported by this study. Using a well-validated measure of cognitive mapping, *T.minimus* was found to create more complex maps suggesting that *T.minimus* can rely more on their memory of cache location, thereby hide them more effectively, and perhaps allow more time for robbing the larger and more easily found caches of *T. striatus*. While *T.minimus* is disadvantaged at harvest sites because of its size, it may narrow the competitive gap owing to improved caching and pilfering behavior.

The influence of interspecific competition on behavior is determined, in part, by the degree of overlap in resource use. The more similar, the more intense the competition will be. In fact, other things being equal, two species cannot completely overlap in their resource use as the poorer competitor will be excluded (MacArthur, 1984). The direction of this competitive pressure is often determined by body size with the larger species excluding the smaller (Basset, 1995; Bowers & Brown, 1982; Vander Wall, Enders, & Waitman, 2009). In sympatric populations affected by asymmetrical competition, the smaller poorer competitor must find ways to survive by adjusting its behavior or it will be outcompeted.

One way small animals may limit the amount of resource overlap and lessen the influence of competition, is by creating specialized niches. For example, sympatric desert rodents may preferentially forage for seeds of different sizes (Dayan & Simberloff, 1994) or in differing microhabitats (Price & Waser, 1985). Some strategies may be facultative, with a species shifting its behavior only in the presence of a competitor. Ziv et al. (1993) reported shifts in habitat preference and foraging patterns of smaller competitors only when larger competitors were present in the environment. Once the larger species was removed, the smaller switched back to its preferred foraging pattern. This suggests that animals may have multiple behavioral strategies that can be conditionally employed based on the environment and degree of competition.

Competition may also be lessened if a species can become more efficient at obtaining resources. Foraging, for example, represents a complex series of behaviors: an animal must determine how to handle food, how long to stay at a particular patch, whether to return to a patch, whether to hoard its food, and how to avoid theft. At each of these stages, a species may reduce competitive pressure by increasing its efficiency.

When an animal encounters a patch during foraging, it must first decide how to handle each item. Some food items require more work to extract nutrients costing both time and energy. Animals that do not need to immediately eat food must decide whether the energy should be spent processing each item. This decision is particularly important for species with cheek pouches. These species frequently eat grains and nuts which have a hard outer shell, by removing the shell before pouching the item, an animal can double its transport capacity (Jenkins & Devenport, 2014). However, as noted, this takes time which may give a competitor the opportunity to exploit more of the patch.

Setting aside the influence of direct competition at harvest sites (where large competitors should have an advantage), once an animal has decided to exploit a patch, it must decide how long to stay at that patch. The longer it spends foraging in one location, the lower the rate of return. An optimizing forager should have a rule for deciding when it is worth the travel time to find another patch (Charnov, 1976; Stephens, Brown, & Ydenberg, 2007). Should it decide to leave a site, it must also determine whether to return to that patch later on. An individual would only benefit from returning if a patch is renewable and can estimate its rate of renewal (McNamara & Houston, 1985).

The final major foraging questions that must be addressed are whether to store items and where to do so. For many non-migratory species, food sources are both seasonal and ephemeral. One solution to this problem is for animals to cache food for use during these periods of scarcity (Vander Wall, 1990). When caching, animals can make large defended larder hoards located either in or near their nesting sites; or, they may make smaller, undefended scatter-caches that are spread throughout the environment. Placing each food item in a larder hoard reduces foraging efficiency as it requires multiple trips from a patch to the nest. While an animal is making these trips, competitors may be steadily reducing the amount of food available at that patch. Additionally, an animal must be physically dominant enough to protect their larders. Scatter-caching, on the other hand, allows for fast sequestering of food, maximizing the rate an animal can remove items from a patch (Vander Wall, 1990). This strategy may be particularly beneficial for small species that cannot rely on physical aggression to protect their stores. Leaving scatter-caches undefended could allow for their theft by competitors; but, spreading them through the environment can make it more difficult for others to locate them (Vander Wall, 1990).

Foragers are constantly competing with others for access to patches and as such must address most if not all of these issues in order to outcompete others and survive. For direct foraging competitors, the key to winning these battles if often increasing one’s efficiency. One way this might be accomplished is if one has a cognitive advantage over others. Cognitive adaptations (e.g., mental rules or capabilities) can drive increases in efficiency in many of the foraging dimensions reducing the effects of competition.

Mental rules are frequently used by foragers when determining when to leave a patch and whether or not to return to it. The best time to leave a patch while maximizing gains can be predicted using the marginal value theorem. This theorem takes into account the amount of time it would take to find a new food patch compared to the rate of return at its current patch (Charnov, 1976; Stephens et al., 2007). Once the rate of return on the current patch has hit a certain point, the best way to maximize energy gain would be to find a new patch to exploit. Some species are able to do this more efficiently than others. In overlapping habitats, *Gerbillus allenbyi* leaves at the time when its energy rate maximization is highest making it a more efficient forager than its larger competitor *G.pyramidum* (Brown, Kotler & Mitchell, 1994). By maximizing rate of return, a species may maximize its energy intake by foraging more efficiently rather than by controlling a patch or collecting food quickly.

A species could further increase its efficiency by making optimal decisions about when it is best to revisit a patch. Unless a site never replenishes, animals should return to that location to acquire food. There are several cognitive rules used to make these decisions. Devenport, Humphries, and Devenport (1998) reported that least chipmunks (*Tamias minimus*) discount the value of previously visited patches by the amount remaining in them. If a chipmunk visited two patches and depleted one halfway and the other by one-third, it would preferentially return to the patch with more food remaining, indicating that they remember something quite precise about the quantity removed or remaining in a patch. This discounting can be overridden if they learn (in one trial) that the patches are renewable to full capacity (Devenport et al., 1998).

If an animal is unable to deterministically predict the quality of a patch, they may be able to use averaging to infer its quality. Bateson and Kacelnik (1996) allowed starlings to choose between receiving a reward at a fixed interval or variable interval. The variable interval was preferred initially, but the researchers were able to adjust the fixed interval until that preference difference disappeared. When the preference was gone, the fixed interval ended up being the approximate mean of the variable interval. This suggests that the amount of reward received across time is noted by animals and used to make decisions on patch quality.

If they are able to recall the variations in patch quality, however, they can use the temporal discounting to determine its current condition (Devenport & Devenport, 1993; Devenport & Devenport, 1994b; Devenport, Hill, Wilson & Ogden, 1997; Devenport, Patterson, & Devenport, 2005). This rule posits that newer information should preferentially weight decisions compared with old information. When a good patch turns bad, and at the same time another turns good, animals given a choice a few minutes later, chose the most recently yielding patch. However, after a day, they returned to using averaging, preferring the patch that had provided them with the most food. This suggests that animals can be aware that information changes over time and, if foraging efficiently, should act only on the best information available. An animal that can use any of these rules should be able to forage more efficiently than a competitor who cannot, potentially decreasing the competitive pressure between them.

While some cognitive rules can increase the efficiency of a forager at a patch, other cognitive adaptations aid in protecting one’s own cached stores. Caching is only effective if the cacher retrieves more of its stores than competitors (Andersson & Krebs, 1978). Larder hoarders ensure this by physically protecting their stores. Scatter-caching species can achieve their advantage by better concealing caches from pilferers. This can be accomplished by suppressing olfactory signals emanating from a patch, by placing caches away from areas that robbers are known to search, or through awareness of social cues that indicate a competitor is in the area.

Olfactory cues can serve as a strong indicator of where hidden stores are located and are heavily affected by environmental context. These cues emanate most strongly from stores made of unhulled seeds (Jenkins & Devenport, 2014; Vander Wall et al., 2003) that are placed in damp substrates (Devenport et al, in prep; Vander Wall, 1991; Vander Wall, 1993; Vander Wall, 1995; Vander Wall, 2000). Caches that do not suppress olfaction give no competitive advantage to cachers as sympatric competitors would be just as likely to locate stores. In fact, pilferers rely primarily on olfaction to steal. By suppressing these cues, caches are concealed not only from robbers but also from the cacher. Cachers who optimize concealment must rely on exceptionally accurate spatial memory because this private information is the only way to pinpoint cache locations (Barkley & Jacobs, 2007; Devenport & Devenport, 1994a; Devenport, Luna & Devenport, 2000; Jacobs & Liman, 1991; Penner & Devenport, 2011; Vander Wall, 1991; Vander Wall et al., 2006); however, the degree sophistication of a hoarder's spatial memory differs between competing scatter-hoarding species and is highly associated with their preferred type of cache protection strategy.

Spatial memory provides hoarders with an internal representation of cache locations with respect to either local landmarks or more distal relational cues (Goulde-Beierle & Kamil, 1996; Kamil & Jones, 1997). Where these hoarders place their caches is strongly related to which type of cues they remember. Some hoarders place their caches near landmarks, and subsequently, these landmarks serve as beacons guiding cachers to where their stores have been placed. Once near the beacon, hoarders can relocate stores by engaging in a local area search. Eastern chipmunks (*T.striatus*) tend to place their caches near objects suggesting that they need only simple object memory to relocate them (Penner & Devenport, 2011). However, competitors frequently target beacons when conducting local area searches for others' hidden stores (Clarke & Kramer, 1994; Daly, Clayton, & Emery, 2006; Jenkins & Breck, 1998; Penner & Devenport; Vander Wall, 1982; Vander Wall, 1991; Vander Wall, 1996). To avoid the most pilferage, cachers should not rely on beacons as location markers but should use multiple distal cues.

Memory for distal relational cues, otherwise known as cognitive mapping, involves hoarders learning the geometrical relationships between multiple landmarks and cache sites. This, subsequently, allows cachers to use more of the environment and to take novel routes (e.g., shortcuts) to caches based on knowledge of relative landmark position (Gallistel, 1990; Poucet, 1993). Both field and laboratory studies (Devenport et al., 2000; Penner & Devenport, 2011) have shown that cachers capable of spatial mapping actively avoid placing caches too closely to landmarks but experience no difficulties relocating stores even after olfactory cues have been removed suggesting that cognitive mapping alone guided cache relocation. Detailed spatial memory can give hoarders additional advantages over competitors as it can allow for recovery of stores placed in dry substrates which typically have few olfactory cues indicating cache location (Devenport et al., in prep; Geluso, 2005; Vander Wall, 1991; Winterrowd & Weigl, 2006) and hyperdispersed caches which are more difficult for potential thieves to locate via local area searches (Male & Smulders, 2007). Scatter-cachers with the ability to make spatial maps have the greatest advantage over competitors because they can engage in these cache protection behaviors.

Although sensitivity to landmark position has been interpreted as evidence for cognitive mapping (Vander Wall, 1991), it could also be argued that this suggests hoarders remember rules about where caches are placed rather than memory for their location. However, cachers have been shown to remember not only the location of multiple cache sites, but specific information regarding the amount of food left in sampled patches suggesting that they have detailed memories for each of their hidden stores (Devenport et al., 1998).

Hoarders do not have to rely solely on memory advantages to find their caches before a competitor. Some have been shown to be very sensitive to potential competitors when storing food. This may be particularly true of those that would be at a disadvantage when forced to compete for resources. Pilferage-sensitive cachers have been shown to orient away from observers when making caches, move caches, and even create false caches in order to hide the true location of their stores (Daly et al., 2006; Leaver, Hopewell, Caldwell, & Mallarky, 2007). In some species, cachers are not necessarily wary of all observers unless their stores have been robbed. Preston and Jacobs (2001, 2005) reported no change in the behavior of the smallest kangaroo rat species (Merriam's kangaroo rat, *Dipodomys merriami*) when a competitor was present, but when that was paired with pilferage, animals changed the location of their caches and also shifted to primarily larder hoarding. Both of these tactics allow this small cacher to protect more of their caches from thieves.

Research has suggested that some smaller species may use pilfering as a strategy to compete with larger heterospecifics (Leaver & Daly, 2001; Penner & Devenport, 2011; Vander Wall et al. 2009). Large competitors can physically exclude smaller hetero- or conspecifics. In response, some smaller competitors shift their habitat or foraging preferences when larger individuals are present (Ziv et al., 1993). Small pocket mice (*Chaetodipus* spp.) may take this shift one step further relying more on pilfering while their larger competitor, *D. merriami*, physically controls food sources (Leaver & Daly, 2001). These studies suggest that small species that are excluded from harvest sites by larger competitors can compensate by covertly obtaining food through pilfering. This does not mean that only small species engage exclusively in pilfering; only that they may use it as competition demands. Further, these small species may engage in more cache protection behaviors such as hulling seeds and avoiding prominent objects. Large harvesters may be less strict with anti-theft tactics because they are able to acquire more food directly and can sustain losses in their scatter-caches (Jenkins & Vander Wall, 2003). Their smaller pilfering competitors may have to be more wary of other robbers because it is more difficult for them to control food harvest sites which subsequently places greater value on each of their caches, many of which may contain stolen food.

Scatter-caching and pilfering rely primarily on an animal's cognitive capabilities. Ideally, to avoid theft, cachers should make deep, widely spaced caches that are far from prominent objects and in dry substrates. Using these methods, cachers reduce pilferage, but they must have the ability to make complex spatial maps to accurately retrieve stores. In addition to protecting their own caches, animals should also steal from others whenever possible. This allows them to reduce a competitor's more easily found stores while protecting their own (Vander Wall, 1990; Penner & Devenport, 2011; Jenkins & Devenport, 2014). By employing these strategies, animals can indirectly compete for resources. However, these strategies can only be employed if an animal has the appropriate cognitive adaptations.

T.minimus

Least chipmunks are small sciurids that appear to benefit from a number of foraging-related cognitive adaptations. This species removes food from foraging sites by transporting it via their cheek pouches to consume in at a safer site or to deposit it in storage. They are the smallest *Tamias* species and thus are always found with larger competitors that exploit the same resources (e.g., golden mantled ground squirrels *S. lateralis,* Carey, 1978, Devenport & Devenport, 1994; yellow pine chipmunks *T.amoenus,* Sheppard, 1971; Hopi chipmunks *T. rufus,* Root et al., 2001; *T.striatus,* Verts & Carraway, 2001) which are likely to dominate the resources. Previous studies (Devenport, 2012; Devenport, et al., 1999; Devenport et al., in prep; Jenkins & Devenport, 2014; Penner & Devenport, 2011) suggest that *T.minimus* may compensate for its size disadvantage by better protecting their own stores and stealing more from the larger competitor's more poorly placed caches, while successfully securing their own caches against robbery. These studies have also indicated that the reason for this advantage is due to cognitive adaptations that least chipmunks have but their competitors do not. Specifically, it has been suggested that *T.minimus* is capable of creating complex spatial maps; however, these suggestions have thus far been inferential. No study has compared the cognitive mapping capabilities of least chipmunks and their competitors using a rigorously controlled laboratory study.

Current study

In the Great Lakes region, least chipmunks are found in sympatric populations with *T.striatus*. Due to their much larger size (80-100g v. 30-50g) (Criddle, 1943; Elliot, 1978; Verts & Carraway, 2001), eastern chipmunks physically dominate *T.minimus* if any skirmishes occur and frequently drive *T.minimus* away from any shared feeding sites (J.A. Devenport & L.D. Devenport, field observations). It is between these two species that the strongest cognitive differences have been observed.

Eastern chipmunks not only physically control feeding sites but have larger cheek pouches than *T.minimus* allowing them to remove more food from a patch. While this could put least chipmunks at an initial disadvantage, they, unlike their large competitor, tend to hull their seeds. Hulling seeds reduces their size which doubles pouch capacity (Devenport, Devenport, & Kokesh, 1999; Jenkins & Devenport, 2 014). Once these hulled seeds have been added to their cheek pouches, least chipmunks seem uniquely able to make boli (Devenport, et al., 1999; Jenkins & Devenport). These are clumps of seeds held together by adhesive properties of their saliva. Both hulling and the salivary secretions greatly slows the formation of mold on these seeds when cultured in the laboratory (Devenport, 2012). Further, caches consisting of boli have been shown to be harder to locate using olfaction compared to caches made of either hulled or, especially, unhulled seeds (Jenkins & Devenport, 2014). By creating caches made of these boli, least chipmunks are able to reduce pilferage of their stores.

T.minimus further protect their caches by preferring to make many scatter-caches of these unhulled boli in dry substrates away from potential beacons (Devenport et al., in prep; Jenkins & Devenport, 2014; Penner & Devenport, 2011). Each of these behaviors by itself should reduce the rate of cache pilferage. By engaging in all of these behaviors, *T.minimus* should be successfully hiding their caches from potential thieves. Given the lack of olfactory cues and beacons that guide retrieval of caches, *T.minimus* would also be unsuccessful in relocating their own caches unless they had the ability to create complex cognitive maps (Devenport & Devenport, 1994a; Devenport et al., 1998). In addition to this, knowledge of the exact location of their own caches frees search time to systematically steal from others.

Conversely, *T. striatus* typically exhibit fewer anti-theft tactics preferring to cache unhulled seeds in wet substrates and near objects (Devenport et al., in prep; Penner & Devenport, 2011). This preference for wet substrates and local landmarks suggest that they may rely more on external cues for cache retrieval such as olfactory cues and beacons rather than relying on detailed spatial memory for cache sites (Devenport et al., in prep; Penner & Devenport, 2011). In addition, *T.striatus* does not engage in systematic robbery of competitors to the degree seen in *T.minimus* showing no preference for either their own or other caches (Devenport et al., in prep; Penner & Devenport, 2011). These differences suggest that eastern chipmunks do not have the cognitive adaptations seen in *T.minimus* and instead gain foraging advantages by their physical dominance alone.

Least chipmunks are typically found in populations that are under strong asymmetric competition. If they are to survive, they must employ strategies that compensate for their initial foraging disadvantage. The current study attempts to compare spatial memory between least chipmunks and a larger competitor, *T.striatus*. Additionally, it will examine whether these spatial memory differences are correlated with differences in foraging efficiencies. It is expected that least chipmunks will have better spatial memory which allows them to forage more efficiently.

Hypotheses

Devenport and Devenport (1994a) reported that rather than relying on beacons, least chipmunks used cognitive maps to relocate caches. *T.minimus* has further been shown to systematically avoid landmarks when making caches, but *T.striatus* did not (Penner & Devenport, 2011). These studies suggests that for successful cache recovery, least chipmunks rely on internal representations of spatial memory while easterns use external cues for cache retrieval. My first experiment tests this hypothesis in a well-validated, ecologically-independent measure of spatial mapping, the Morris water maze (Brandeis, Brandys, & Yehuda, 1989; D'Hooge, & De Deyn, 2001; Morris, 1984; Vorhees & Williams, 2006; Devenport Stidham, & Hale, 1989). This measure has become the standard mapping assessment tool for rodents. During this task, animals must learn, if possible, the location of a hidden platform using either a beacon or distal relational cues. Animals are trained to swim to a platform that is alternately visible or hidden over several days. When the platform is visible, it serves as a beacon, clearly indicating its location. In order to successfully find the platform when it is hidden, each animal must be able to navigate to the platform using the relationships of extra-maze (distal) cues that are placed at a distance from the water tank rather than relying on the beacon (i.e., the platform) for navigation. Because the animals are started from varying positions in the tank, they cannot solve the problem by simply swimming in a constant direction relative to the edge of the tank. Those that are able to integrate these distal cues should take faster, more direct routes to the platform across trials. Animals that are unable to successfully map the location of the platform using distal cues will be slower to locate the platform likely due to reliance on random search. To fully test whether an animal has successfully mapped the location of the platform, it is necessary to have a testing condition where the platform is shifted from its learned location. Those that have successfully mapped its location will spend more time swimming near the learned position, while those that have not will engage in a random search (Devenport et al., 1989; Morris, 1982; Vorhees & Williams, 2006). I hypothesize that least chipmunks will perform better in the invisible platform condition, indicating that they are able to create complex cognitive maps using distal relational cues and as such will exhibit shorter swimming routes to the platform and spend more time searching for the platform in its learned quadrant following its removal. Conversely, I hypothesize that eastern chipmunks will be poorer at using distal relational cues and will take longer routes to the platform and engage in more random search. When a beacon is available (e.g., when the water is clear), the species should not differ.

Since both species engage in scatter-hoarding, spatial memory differences should also be observed in cache placement behaviors. Those that do best at creating complex maps should choose to hyperdisperse their caches and place them farther from landmarks. Species that cannot create these maps should cluster their caches more and place them closer to beacons, where they are more easily found. Least chipmunks have been previously shown to avoid landmarks when making caches while easterns choose locations near these objects (Penner & Devenport, 2011). Thus, I hypothesize that *T.minimus* will continue to display evidence for detailed spatial mapping by hyperdispersing caches and avoiding landmarks when caching, and that the degree to which they do so is likely to correlate with their individual mapping success as observed in the water maze study. In contrast, I hypothesize that eastern chipmunks will show poorer overall spatial memory by exhibiting a greater reliance on local landmarks when choosing caching locations, consistent with expectations about their water maze behavior. However, individual differences in spatial navigation in the water maze should correlate with the extent of cache dispersal.

T.minimus is at a distinct competitive disadvantage due to its size and cannot compete directly with heterospecifics. Cache protection resulting from detailed spatial memory is one method that may allow them to compete, but they may also engage in more pilfering behaviors to indirectly enhance their competitive success. This species may be able to engage in more theft primarily because their stores are well-hidden needing little protection from thieves while their large competitors' caches are poorly placed making them easy targets. For species like *T.striatus* who make poorer cache placement decisions, recovering one's own caches provides the maximum benefit as they will likely be easily stolen if left unattended. I will assess pilfering by allowing individuals to make caches and then give them the option to either recover their own stores or pilfer from a competitor. Animals could display one of three preferences: recovering more of their own stores, no recovery preference for either own or competitor stores, or recovering more of the competitor's caches. Recovering one's own stores requires the least amount of energy of the behavioral options as only memory for cache location is needed to find food successfully. But, if they are in the presence of competitor caches, animals may prefer to rob them and retain their own stores (Penner & Devenport, 2011). On the other hand, animals might display no preference for pilfering which could be an indication that they have difficulty finding the competitor's caches. For small species like *T.minimus* engaging in pilfering may be a necessary strategy when faced with strong asymmetrical competition. I hypothesize that least chipmunks will further increase their competitiveness by engaging in more pilfering than easterns.

In summary, I expect least chipmunks to form more complex cognitive maps. I expect this ability to correlate with greater success in the spatial concealment of caches and, because their memory allows for easy to relocation, more time spent pilfering. Conversely animals with the poorer spatial memory should preferentially place caches near landmarks, engage in more local area searching, and spend less time pilfering.

Methods

Species

Subjects for these studies were 8 eastern chipmunks and 8 least chipmunks. These species overlap extensively in the Great Lakes region and are frequently found together, though *T.striatus* tends to favor slightly damper hardwood forests, and *T.minimus* tends to occupy drier conifer forests (Forbes, 1966; Jackson, 1961). Both species forage on the same food types preferring to eat seeds, nuts, berries, and invertebrates, and both engage in larder and scatter-hoarding (Criddle, 1943; Elliot, 1978; Verts & Caraway, 2000).

Ten animals were drawn from populations captured in the upper peninsula of Michigan in the summers of 2010, 2011, and 2012 using Sherman live traps. Once they were trapped, they were sexed, marked for identification, and dusted with Sevin to kill any external parasites. After receiving professional health certification, animals were transported from Michigan to Oklahoma under permits from the Oklahoma Department of Wildlife and the University of Oklahoma Animal Care and Use Committee and housed in the Animal Cognition Laboratory. The other six animals were born to females that had been previously imported to the laboratory.

Once in the lab, chipmunks were placed in one of two 1.5 m x 2.5 m semi-naturalistic enclosures with conspecifics. These enclosures consisted of a bed of hardwood chips and mounds of lava rocks for nesting and retreat. A number of projecting sticks, logs, ropes, and running wheels were installed for sensory enrichment and exercise. In order to maintain normal circannual rhythms, animals were kept on a natural light:dark cycle that reflected the seasonal changes such that animals received a maximum of 14 hours of light in the spring and a minimum of 10 hours in the winter. Chipmunks were given access to fresh water within the enclosures and were fed daily. For feedings, rodent chow was alternated with fresh fruits and vegetables.

General Methods

Animals were removed from the free-living enclosures and placed in individual polystyrene cages measuring 46 cm x 24 cm x 20 cm with litter and an artificial nesting burrow. The purpose of caging prior to behavioral sessions was to monitor the animal's weight and diet and to ease their capture for test sessions. Except for water maze sessions, diet was limited to 1-2 pellets of rodent chow daily to reduce body weight by approximately 10%. All sessions were recorded using a video camera located above the testing arena. Following testing, the animals were returned to their free-living quarters.

Water Maze

The water maze was a 1.83 m diameter steel stock tank divided into four quadrants, visible by markings on its outside edge (i.e., visible only to researchers). A water tank heating element was mounted deep inside the tank to allow for temperature adjustments. Extra-maze cues of various shapes and colors were placed on the walls and ceiling of the testing room which acted as relational cues (Morris, 1984). Animals were required to learn the location of a 33.2 cm tall, 16 cm diameter concrete cylinder that was located 2 cm below the surface of the water in the center of a randomly assigned quadrant. This training occurred during the two training sessions given each day. Each session comprised four trials that had starting points in each of the quadrants. Starting points were determined using a random number generator and were sampled without replacement. This was done so animals could learn the location of the platform regardless of starting position. Morning sessions consisted of clear conditions where the platform was visible. During these sessions, the platform should be a beacon leading animals to have no difficulty locating it. Animals experienced opaque conditions in the afternoon. In opaque conditions, the platform was no longer visible and extra maze cues would be necessary to orient to the location of the platform. The ability to use these distal cues requires the use of a cognitive map. Most water maze studies use powdered milk to cloud the water for trials where the platform needs to remain hidden (e.g., Morris, 1984). However, powdered milk quickly sours and does not settle forcing experimenters to repeatedly change tank water. Instead, I mixed a suspension of 7 kg of magnesium hydroxide into the water. Magnesium hydroxide is practically insoluble in water and settles out to the tank bottom after a few hours, allowing clear and opaque trials to be run the same day and in the same tank. For opaque sessions, the magnesium hydroxide was stirred up in the tank eliminating platform visibility and forcing the animals to rely on cognitive mapping to relocate it (after Devenport, et al., 1989). To further reduce visibility, the platform was painted white to match the color of the water during opaque trials.

During each trial, animals either successfully located the platform on their own during the allotted amount of time or were guided through the water to the platform which they, then, either crawled onto or were placed on by experimenters. Animals were guided through the water rather than simply placed on the platform because it has been suggested that the middle portion of the swim path is important for learning (Sutherland, Chew, Baker, & Linggard, 1987). Once on the platform, animals were required to wait on it for 10 seconds. This allowed animals to observe their surroundings and take note of the position of extra-maze cues in relation to the platform. Following removal from the platform, they were placed in a polystyrene box that contained aspen bedding for 60 seconds between trials. To prevent hypothermia, the box was placed on a heating pad and partially under a heat lamp.

Pilot study

While the Morris water maze is commonly used to test spatial memory in rodents, it has not been previously used for chipmunks. For that reason, this measure was piloted using 2 animals of each species prior to formal experimental testing. Chipmunks swam to the platform’s location across 2 training sessions, morning and afternoon. Each session comprised four trials that each lasted a maximum of 120 seconds. During the pilot study trials, it became evident that each species reacted differently to the water maze. Eastern chipmunks did not display any behaviors suggesting difficulty with the conditions of the task. Least chipmunks, however, were not able to swim for the full 120 seconds if they did not find the platform. This was evidenced by a clear struggle to stay afloat indicating a potential risk for drowning. Pilot trials for *T.minimus* were consistently terminated early to prevent exhaustion. Further, due to their small size, *T.minimus* visibly reacted to the room temperature water by staying immobile and shivering once removed from the maze. This reaction resulted in longer recovery times between trials. Following initial trials, water temperature was kept between 20-22° Celsius for eastern chipmunks and 25-27°C for least chipmunks, using the immersion heater. Importantly, test sessions were shortened to 60 seconds for both species. Following these changes, *T.minimus* no longer displayed visible signs of stress.

Experimental Sessions

Experimental training sessions were conducted using methods developed in the pilot trials. Training sessions occurred twice a day for 6 days resulting in a total of 12 sessions. During training sessions, an animal was determined to have learned the position of the platform if they were able to successfully locate it in two consecutive opaque trials within the time allowed. Following each training session, video data were reviewed, and the amount of time it took to locate the platform for each trial was recorded. Additionally, the path taken to the platform was recorded on a representative maze. These paths were later traced using a digital opsimometer to record distance swum. Both time and distance were averaged across the four trials for each session. Following the training sessions, the platform was moved into a quadrant 180° from the training position and one additional opaque test session occurred. This ensured that the platform was indeed hidden during the opaque trials and successfully locating it could only occur through mapping. Animals that successfully mapped the platform location with respect to extra maze cues should spend significantly more time swimming in the previously learned quadrant compared to chance (.25). Animals unable to map the location of the platform should engage in a random search. To assess mapping ability, I recorded total distance swum before reaching the platform. Then, I examined the proportion of their swimming distance that occurred in the previously learned quadrant. Rather than averaging distance swum across all four trials in the session, I averaged only the first two trials. This was done because animals capable of doing so would begin mapping the platform's new location quickly.

Swimming motivation

As discussed above, pilot testing indicated that training trials needed to be shortened for least chipmunks to prevent undue stress. However, there were no indications that this was necessary for *T.striatus*. The stress experienced by least chipmunks could have led them to be more motivated to find the platform while eastern chipmunks lacked this urgency. To rule out whether observed differences were due to differences in motivation, a follow-up study was conducted to explore whether motivation was related to the results obtained. To do this, I manipulated the appeal swimming might have for each species by exploring whether motivational differences were temperature-dependent using the assumption that colder temperatures would result in more motivation to find the platform.

This task was performed in the same tank used for the water maze. To prevent cognitive mapping differences from affecting the results, the platform was made clearly visible by painting it black and keeping it 1 cm above the surface of the water. Animals were placed in the tank for six swimming sessions, two at each of three temperatures. Water temperatures were set at 20, 18, and 16°C for eastern chipmunks and 27, 29, and 31°C for least chipmunks. Temperatures for least chipmunks were controlled by the thermostatic heating element while colder temperatures resulted from adding ice and allowing it to melt. A subsequent follow-up measure for eastern chipmunks added two new temperature points, 21 and 10°C. For all testing sessions, animals were given four separate trials that lasted 60 seconds for leasts and 120 seconds for easterns. *T.striatus* trials were lengthened due to a concern that the shorter time resulted in a ceiling effect restricting the observable species differences. To assess motivation, I measured latency and route to the platform, the amount of time spent on the platform, and the number of times the animal chose to swim rather than stand on the platform.

Cache placement

Caching tests took place in a 1.5 m x 2.5 m room that was filled with sand to a depth of 6-8 cm. Immediately prior to these tests, animals were given a 20 minute habituation to the full testing room. For testing sessions, an aluminum dish was filled two-thirds with black sunflower seeds and placed in the center of the room. Four landmarks (two logs and two rocks) were semi-randomly placed within the room. Animals were given up to three hours to make six caches. If fewer than six caches were made, the trial was discontinued and the animal was returned to its living quarters. After caches were made, sand above each cache was carefully removed such that only the very top of each cache was exposed. Following this, I measured cache distance to the closest landmark or wall, the distance to the next closest object, the distance between those objects, the distance between caches, and the distance between caches and the food source (after Devenport, et al., 2000; Penner & Devenport, 2011). I, further examined whether each species evenly dispersed their caches throughout the testing arena. Using the food source as the central location, I measured the angles between each cache and the next successive cache. I, then, averaged these angles and compared that average to 90° (after Devenport et al., 2000). As the environment fills, the angles between successive caches should not differ from 90° (in either direction). After all testing sessions, any debris or excrement was removed from the testing location, and surfaces were cleaned with a 10% alcohol solution.

Pilfering

Caching and pilfering trials occurred in the same testing arenas as cache placement trials. Before trials took place, animals were allowed to habituate to the room for 20 minutes. For caching trials, a clear Plexiglas partition was used to bisect the testing arena. An aluminum dish filled two-thirds with black sunflower seeds was placed in the middle of one half of the testing arena. Test animals were allowed to make 6-8 caches on their side of the partition. These caches were subsequently excavated and the depth and number of seeds were recorded. The caches were then reburied at an average depth used by each species, (*T.striatus* in dry substrate, 3 cm; *T.minimus*, 1.5 cm, (Penner & Devenport 2011; Devenport et al., in prep.).

Burying the caches involved using a small piece of PVC pipe 4 cm in diameter that had internal markings indicating pipe depth. This pipe was placed at a cache site and pressed into the sand until the sand filled the pipe to the top-most marking (1.5 cm from the edge of the PVC pipe). Sand was removed from the pipe until the appropriate marking indicating the depth was reached. Seeds were placed in the center of the pipe such that the top of the seeds were 1.5 or 3 cm below the surface. These depths are based on averages used by each species (least and eastern, respectively) (Devenport et al., in prep). Sand was then layered on top of the seeds until it was at the original level. Finally, the PVC pipe was carefully removed using a steady twisting motion.

Experimental caches matched for size, depth, and location were made on the opposite side of the partition using the same method. Caches sat untouched for at least 24 hours to reduce extraneous odor cues. Following this, the caches were covered with coarse mesh (framed half-inch hardware cloth) and a conspecific was allowed to explore “its” side of the room (i.e., where we placed the experimental caches) for 1 hour. Chipmunks newly introduced to an area explore virtually all parts of the compartment, leaving their scent as the predominant odor associated with the experimental caches. It was assumed that from the forager’s point of view, those caches would be associated with the competitor. The mesh was used to prevent animals from removing any of the experimental caches.   Conspecifics were chosen as “competitors” because previous work (Devenport et al., in prep; Penner & Devenport, 2011) has shown that both eastern and least chipmunks pilfer from hetero- and conspecifics at the same rates suggesting that competitor species does not influence robbery behaviors.

Following the introduction of the conspecific's scent, the mesh and arena partition were removed. The sand was gently raked over in order to remove any visual cues to cache location. The test animal, which was immediately allowed to forage for 1 hour, was thus presented with a room in which half contained the scent of a competitor and experimental caches while the other half held their own caches. This gave test animals the choice between recovering their own caches and stealing from a competitor. The behavior of interest for this measure was the proportion of competitor caches that were pilfered out of the total number of caches from which seeds were taken. Following the test trial, caches were dug up by the experimenters and any cache remains were recorded.

Results

Water maze

A 2 x 2 x 6 mixed repeated measures ANOVA (species x condition x session) was used to analyze whether least chipmunks were able to take a shorter route to the platform compared to easterns and whether routes varied as a result of platform visibility. As shown in Figure 1, both *T.minimus and T.striatus* learned to swim to the position of the platform, taking shorter routes to reach the it across both clear and opaque training sessions (*F* (5,70) = 33.57, *p* < .01). Although both species took shorter routes to reach the platform in clear compared to cloudy conditions (*F* (1,14) = 19.16, *p* < .01), eastern chipmunks always swam longer distances before reaching the platform regardless of condition (*F* (1,14) = 15.40, *p* <.01) (see Fig. 1). Further, as seen in Figure 2, *T.striatus* required twice the number of trials to learn the position of the platform in opaque conditions compared to least chipmunks (*t* (14) = 2.35, *p* =.03). As least chipmunks are approximately half the size of easterns, it was possible that some observed differences could have resulted simply due to a difference in swimming speed. However, analyses showed that swimming speed (distance swum divided by time) did not differ between species (*F* (1,14) = 2.66, *p* = ns).

Separate analyses examined mapping differences during the platform-shifted trial. For these analyses, the proportion of swimming distance in the previously learned quadrant was compared to chance levels (.25). The amount that *T.striatus* swam in the trained quadrant did not significantly differ from chance (.25) of the total distance swum (*M* = 0.27, *t* (7) = .44, *p* = ns). Conversely, *T.minimus* demonstrated accurate memory for the location of the platform and swam much more in the previously trained quadrant (*M* = 0.43, *t* (7) = 2.94, *p* = .02) (see Fig. 3).

Swimming motivation

Water maze analyses showed that time spent swimming was highly correlated with the amount of time spent trying to find the platform with correlation values between .71 and .94 at the *p* < .01 level indicating that either could be used for analyses. For this reason, all motivation analyses were conducted using swimming time rather than distance. As in the water maze trials, least chipmunks remained faster at reaching the platform than easterns regardless of temperature (*F* (1,14) = 7.18, *p* = .02) (see Fig. 4) and across days (*F* (2,26) = 4.71, *p* = .02). However, the amount of time taken to reach the platform did not differ across temperature (*F* (2,26) =1.13, *p* = ns). To ensure that the temperature points served as a sufficiently strong stimuli for easterns, I repeated testing with but measured their behavior with water temperatures of 21° and 10° C. This analysis was conducted using 7 data points as one animal died before being retested at these temperatures. The amount of time they spent finding the platform continued to show no effect of temperature (*F* (1,6) = 1.1, *p* = ns).

Cache placement

To assess how closely animals placed caches to objects, I examined the correlations between each cache and the nearest object, next nearest object, and the inter-object distance. Contrary to previous research (Penner & Devenport, 2011), eastern chipmunks showed an active avoidance of objects when placing caches, exhibiting significant correlations between the inter-object distance and the nearest object (*r* (46) = .42, *p* <.01) and next nearest object (*r* (46) =.83, *p* <.01). Further, least chipmunks did not show an avoidance of objects, choosing instead to place caches closer to one object as inter-object distances lengthened, (nearest object *r* (46) = .15, *p* = ns; next-nearest object (*r* (46) = .84, *p* <.01). To examine whether animals were treating the food source as a landmark, the distance caches were placed from the food dish out of the total distance available was compared to the expected proportion of the distance used if the food dish was treated as another landmark to avoid (.50). Both least and easterns showed a distinct avoidance of the food source choosing to place caches closer to the walls of the testing arena (least *M* =.76, *t* (7) = 4.44, *p* =.003; easterns *M* =.80, *t* (7) = 8.37, *p* <.01). To examine how caches were dispersed throughout the arena, I compared the average angle between caches to 90°. *T.striatus* spread their six caches evenly throughout the testing arena (*M* = 83.33, *t* (7) = -.84, *p* = ns). Least chipmunks, on the other hand, tended to selectively place their caches close together (*M* = 68.08, *t* (7) = -2.2, *p* =.06).

Pilfering

Data could only be collected for 7 of the 8 least chipmunks for this measure as the final animal would not make the required number of caches. As seen in Figure 5, analyses revealed that least chipmunks had no preference for taking seeds from either their own or their "competitor's" caches, although, there was a trend in that direction (t (6) = 1.81, p = .12). Additional analyses showed that least chipmunks did not preferentially sniff or dig at either their own or other's caches (t (6) = -0.89, p = .41). When given the option of pilfering from others' caches, eastern chipmunks did not exhibit a preference for either their own or other caches (t (7) = 1.56, p =.16). As with *T.minimus*, there was no preference for sniffing or digging at either their own or other's caches. There was a slight trend toward visiting, but not taking seeds, from their own caches (M = 58.25%, SD = 23.38, t (7) = -1.68, p = .14)

Suite of correlated behaviors

Pilfering in *T.minimus* was marginally correlated with the number of trials required to learn the position of the hidden platform in the water maze study. Those that pilfered more found the platform more quickly (r (8) = -.74, p =.06). There were no significant correlations between eastern behaviors in any of the tested measures.

Discussion

Asymmetrical competition could force small species to adopt new behavioral strategies or risk exclusion at shared foraging sites (Bowers & Brown, 1982; MacArthur, 1984). This study investigated whether competition has guided a cognitive adaptation in a small species (*T. minimus*) and whether this adaptation has led to differences in observed foraging behaviors. Previous research (Devenport, 2012;

Devenport, et al., 1999; Devenport et al., in prep; Jenkins & Devenport, 2014; Penner & Devenport, 2011) has suggested that least chipmunks employ multiple foraging strategies that their larger counterparts do not use. For instance, *T.minimus* protects its scatter-caches better from theft by suppressing odor signals (e.g., hulling of seeds, Jenkins & Devenport, 2014) and avoiding beacons (Penner & Devenport, 2011) when making caches. This type of cache protection should make it more difficult for other animals to locate these stores, but implies that least chipmunks must possess more accurate cognitive mapping of cache locations so cache owners alone can retrieve them (Devenport & Devenport, 1994). Using a standard, controlled laboratory test, this study examined whether such complex mapping occurs and if it differs between the competing species.

This study successfully showed that least chipmunks are faster and better at forming complex spatial maps compared to their larger counterparts. Analyses of the water maze data indicated that least chipmunks required half the number of trials to successfully locate the hidden platform and consistently took shorter routes to it compared to easterns. If least and eastern chipmunks were equally adept at using use extra maze cues to navigate to the platform, there should have been no difference in route length or the number of trials needed to find the platform. These results suggest that least chipmunks were not only forming more detailed spatial maps, but were doing so much more quickly than their larger counterparts. While eastern chipmunks were slower than least to locate the platform during training sessions, it should be noted that they were able to learn the location of the platform. However, when the platform was shifted 180°, *T.striatus* searched in the previously learned quadrant at chance levels suggesting that they were only able to locate the platform through random search. This suggests that while eastern chipmunks can use spatial memory, as all scatter-caching species must, their maps are not as accurate as least chipmunks with *T.striatus* less able to use distal cues and relying more on general direction and random search. *T.minimus,* however, swam in the previously correct quadrant at levels that were significantly higher than chance showing that they had an accurate cognitive map of the testing arena and knew where the platform should have been located. Moreover, these differences were observed even when eastern chipmunks should have been highly motivated to locate the platform. This suggests that motivation did not lead to the observed differences, but rather, it was due to a difference in underlying mapping ability. These data also support the hypothesis that when compared to eastern chipmunks, *T.minimus* relies more on distal relational cues when forming complex spatial maps. It is this ability that allowed them to more easily navigate to the unseen platform. It is possible that due to the necessity of shortening the trial length during the water maze, a ceiling effect was created for the easterns. Had trials not been shortened, a species x condition interaction may have been seen wherein easterns would have performed even worse in the opaque conditions if their trials lasted longer. Though, it should be noted that following the first day of testing (1 clear and 1 opaque session) most *T.striatus* found the platform before the 60 second time limit; so while the measure lost some sensitivity by introducing a ceiling to *T.striatus* behavior, the loss was not extreme.

Previous studies (Penner & Devenport, 2011) have implied that *T.minimus* may have better cognitive mapping abilities than *T.striatus* due to observed differences in cache placement, but this is the first research to use a well-validated laboratory measure to demonstrate strong interspecific differences. This finding is important because this cognitive trait is of broad value for not only relocating caches or patches of food, it implies better memory for predator locales, the territories of potential mates, as well as easy, time-saving (short-cut) returns to these places and back to their burrows. Further, unlike other behaviors (e.g., cache placement), the ability to create a detailed map based on distal cues rather than local landmarks cannot be learned and should not be affected by any environmental factors. For example, an animal may change its scatter-hoarding behaviors due to competition (e.g., *D. merriami*, Preston & Jacobs 2001, 2005), but it cannot change its underlying spatial mapping adaptation. It still either can or cannot make complex spatial maps. In this study, *T.minimus* demonstrated that they are capable of making detailed spatial maps on which they rely for later navigation while *T.striatus* did not display an ability to use these internal representations suggesting that they do not possess this cognitive adaptation.

Importantly, these strong spatial memory differences were unrelated to motivational factors. Despite very cold temperatures, *T.striatus* did not decrease their swim time even though the platform was visible during these trials. It is still possible that altering the water temperature did not serve as a strong enough motivator for *T.striatus*; however, it would be difficult to vary motivation using the Morris water maze using any other variable. To further exclude potential motivational differences between the species, performance on a secondary measure of cognitive mapping like a radial arm maze would need to be used compared for these two species.

Water maze analyses indicate that least chipmunks are more successful at creating complex spatial maps than eastern chipmunks in a non-ecological setting. It is important to explore whether these differences are directly correlated with observed caching differences, as was done here. Scatter-caching animals should need more detailed maps if they place their caches away from landmarks which is why it was hypothesized that, as with prior research (Devenport et al., in prep; Penner & Devenport, 2011), least chipmunks would avoid landmarks more than easterns. If least chipmunks did not engage in avoidance of landmarks, they would have no need for this adaptation. Eastern chipmunks' poor ability to use distal relational cues to create cognitive maps suggest that they lack the adaptation seen in least chipmunks, and they should exhibit a preference for placing caches near landmarks as seen previously (Penner & Devenport, 2011). However, the species differences did not hold when landmark avoidance was examined in this study.

Leasts were hypothesized to display these scatter-caching behaviors due to pressure from asymmetric competition; however, in a laboratory setting competitive influence diminishes. Animals lived in free-range habitats with only other conspecifics and were supplied with food on a daily basis. Additionally, the least chipmunks used in this study had been in the lab between 2-5 years, further removing them from asymmetrical competition. It is possible that when competition is minimized for several years, least chipmunks correspondingly shift their caching behaviors away from what would be beneficial under strong asymmetrical competition conditions. While leasts frequently scatter-hoard in the wild, in the lab, they are forced to live in relatively close quarters with conspecifics. Under these conditions, scatter-hoarding would be significantly less beneficial as others could watch for caching and steal stores soon thereafter. It may be these changes from a natural competitive environment that prevented replication of previous findings.

Similarly, eastern chipmunks were hypothesized to avoid landmarks when caching as seen previously (Penner & Devenport, 2011). They, instead, avoided objects when making caches and hyperdispersed their caches throughout the testing arena. This result was unexpected since they did not display an ability to learn the geometric relationship between multiple cues during the water maze. The ability to create detailed spatial maps should have been necessary if they were to later recover these stores; though, they were not given the option to do so. A follow-up session allowing eastern chipmunks to attempt cache retrieval would be necessary to better understand why they were observed avoiding landmarks when caching. It is possible that they may have experienced difficulties relocating the caches.

It was hypothesized that the small *T.minimus* would increase their competitive ability by engaging in not just better cache protection strategies, but also greater amounts of theft while *T.striatus* would not display these behaviors. Consistent with previous work on eastern chipmunks (Penner & Devenport, 2011; Devenport et al., in prep), no preference was found for either own or other caches during a cache recovery session. This finding is consistent with the hypothesis that eastern chipmunks may need to rely less on pilfering as they can physically dominate competitors at food sources. Least chipmunk data, however, were not consistent with previous findings as no preference for either own or others' caches was observed.

The discrepancy between prior research and observed pilfering in *T.minimus* may have been due to a selection bias. The same chipmunks were used for each measure to better explore how underlying complex mapping was directly correlated to observed foraging behaviors. However, it did result in a non-random sampling of the laboratory population. During pilot studies for the water maze, it became clear that not all *T.minimus* could endure the swim equally well. Only animals that could endure were selected for the water maze and were, thus, used for the other measures as well. Of the 16 least chipmunks that were available in the laboratory population, only 8 proved to be able to swim with no stressful side effects. As the hypotheses for this study required using the same animals for each measure, only those that could complete each phase successfully could be sampled for this study. It is possible if a random sampling of least chipmunks could have been used, the preference for robbery would have been replicated. Further, of the 8 *T.minimus* that could swim, only 7 successfully completed the caching and pilfering test. The final animal did not cache despite being tested over the course of several months. Due to a closure of the lab, testing needed to be ceased before the caching data could be collected for this particular animal. It may be that due to a biased sample population that was nonrandomly chosen, many of the previous *T.minimus* results were not replicated.

When using populations consisting of both wild caught and lab-born animals, it is important to consider whether their origin affected their behavioral decisions. Lab-born chipmunks tend to habituate to testing procedures and experimenter handling more quickly than their wild-caught. Conversely, wild caught animals tend to remain highly reactive throughout their time in the lab (personal observations). Lab-born animals also never experience aggressive interspecific competition as they are kept separate from heterospecifics. Due to this, these animals may not need to display the range of behaviors seen in wild populations. For this study, half of the *T.minimus* sample were wild caught and half were born in the laboratory. It should be noted that lab-born animals in this study were all first generation preventing domestication from being an issue. Any phenotypic differences between the two groups could have been the result of differences in learning experiences rather than differences in cognitive adaptation. As there were only 4 lab born animals and 3 wild caught, there were too few to conduct a valid statistical test to examine these possibilities. Although, it did appear that lab born animals may be engaging in more pilfering. A larger sample size must be used to determine whether there are differences between wild-caught and lab-born chipmunks in their caching and pilfering behaviors.

This study sought to examine whether owing to better memory structure, least chipmunks would be able to display a suite of correlated behaviors resulting in the potential easing of asymmetrical competition. However, only one marginal correlation was found for *T.minimus* where pilferers learned the position of the hidden platform in the water maze trials more quickly. The quickness with which an animal learned the location of the platform was an important aspect of the water maze trial as it could indicate mapping speed, but it does not give a complete picture of spatial mapping ability. As these pilferers did not take shorter distances to the platform during trials, it cannot be concluded that they were actually faster at making cognitive maps. As with observed pilfering differences, it did appear that lab-born least chipmunks required fewer trials suggesting that these differences may have been the result of differing characteristics between lab-born and wild caught animals rather than spatial mapping differences.

It is possible that the reason many of the results of this study failed to replicate previous work was due to the lab setting. Ziv et al. (1993) reported shifts in the foraging behaviors of small species only when competitors were present, but Preston and Jacobs (2001, 2005) reported shifts only when it competitors were paired with pilfering. As previously mentioned, least chipmunks did not need to compete with easterns while living in their semi-naturalistic enclosures. The only potential competition they experienced was with conspecifics. However, even this competition was lessened as food that was readily available on a daily basis, and *T.minimus* tend to be more tolerant of conspecifics when sharing a food source (field observation). Likely, there was little scatter-caching occurring in these settings due to the high rate of pilfering that would occur. The animals used in this study were either lab-born or had been living in this setting for years and had not experienced strong foraging competition recently. It may have been this release of competition that prevented many of the observed behavioral differences in the current study. It is also possible that in the caching and pilfering measures, animals were unaware of potential competitors. “Competitors” were allowed to run in the arena during pilfering trials, but perhaps this cue was not strong enough to elicit active searches for another’s caches.

While the expected behavioral adaptations may not have been present due to several years of diminished competition, the observed differences in the Morris water maze remain impressive particularly as neither species had previous experience with this task unlike the caching studies. As has been shown in multiple studies (Brandeis, Brandys, & Yehuda, 1989; D’Hooge, & De Deyn, 2001; Morris, 1984; Vorhees & Williams, 2006; Devenport Stidham, & Hale, 1989), the ability to navigate to a platform using multiple distal cues reflects the underlying spatial memory capabilities of each species. Least chipmunks showed a strong ability to use these cues as a navigational tool while eastern chipmunks could not. If there is flexibility in hoarding behaviors, which would be expected in species that both larder and scatter-hoard, environmental and laboratory conditions may have altered the natural behaviors of these species during the ecological measures. While this study was unable to show that cognitive mapping is directly correlated to foraging preferences, it is possible that using a different population of animals or ones currently experiencing natural environmental conditions, these advantageous behaviors would be expressed.

Future considerations should investigate the possible facultative nature of these interspecies differences. If these differences are the result of character displacement, a small animal may need to recognize the presence of a large competitor. It may be that asymmetrical competition effects on behavior could only be observed soon after animals are brought into a laboratory setting. This would ensure that they have not yet become exposed to a lack of strong competition. Additionally, their reaction to these dominant animals may change as a function of age or dominance status. Changes in intraspecies competition as an individual ages (becoming more or less dominant) could have effects on its need to compete in an indirect manner. It may be that younger animals engage in the most amount of indirect competition because they are unable to compete against large competitors and dominant conspecifics. Asymmetrical competition forces small species to adopt alternative strategies, but these behaviors may change as the degree of competition fluctuates. In order to better explore these possibilities, it is important that future laboratory research uses freshly caught wild animals and improves on the current methodology to help substantiate whether these individual characteristics could influence observed foraging behaviors.

By using these fresh animals, researchers could further examine the advantages that could be gained by having better spatial memory than a competitor. The superior spatial memory exhibited by the least chipmunks should enhance their ability to perform a range behaviors (e.g., returning to the best patches, remembering predator locales). If their spatial memory is better than that of their large competitors, future research should also find species differences in other spatially-related behaviors which may suggest that *T.minimus*' spatial memory capabilities has resulted in wide-spread foraging advantages allowing them to effectively compete despite their size.

Summary

When two species directly compete for the same resources like least and eastern chipmunks, one species must change its behavior or be outcompeted. Eastern chipmunks are able to physically dominate resources and do not need to shift their behaviors, but least chipmunks must use alternate foraging strategies to remain in the area. Previous work has found multiple behavioral adaptations that differ between *T.minimus* and *T.striatus* (Devenport et al., in prep; Devenport et al., 1998; Jenkins & Devenport, 2014; Penner & Devenport, 2011). While some of these differences were not observed in the current study, clear cognitive differences were detected. Least chipmunks were faster and better at creating complex cognitive maps than their large competitors. It is likely that this underlying mechanism allows for many of the previously observed behavioral differences between these species. These complex cognitive maps may allow small least chipmunks to better protect their own stores from theft while giving them the opportunity to actively steal from the poorly placed caches of their dominant congenerics. By engaging in these covert tactics, non-dominant species may be able to effectively level the foraging playing field with a larger competitor facilitating the coexistence of these sympatric populations.

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Figure Captions

Figure 1. Comparison of the distance swum in meters by least and eastern chipmunks before locating the platform. Data is separated by species as well as condition (clear and opaque) and represents the mean distance swum ± SEM in each of the six sessions per condition.

Figure 2. Comparison of the mean number of trials ± SEM each species required before the platform was successfully located twice in opaque conditions. Least chipmunks needed significantly fewer trials to learn the platform location.

Figure 3. For test sessions, the mean proportion ± SEM of total swim distance spent in the previously learned quadrant was measured for both eastern and least chipmunks. This was compared the proportion expected by a random search (.25). Differences from .25 are indicated.

Figure 4. Values represent the average time swum ± SEM until research the platform by both species across three temperatures. Temperatures ranged from cold (easterns 16°C, least 27°C) to moderate (easterns 18°C, least 29°C) to warm (easterns 20°C, least 31°C). Least were consistently faster than *T.striatus* but there was no effect of temperature on swim time.

Figure 5. Values represent the average ± SEM proportion of “competitor” caches from out of the total number of caches from which seeds were recovered during pilfering sessions.

Figure 1.

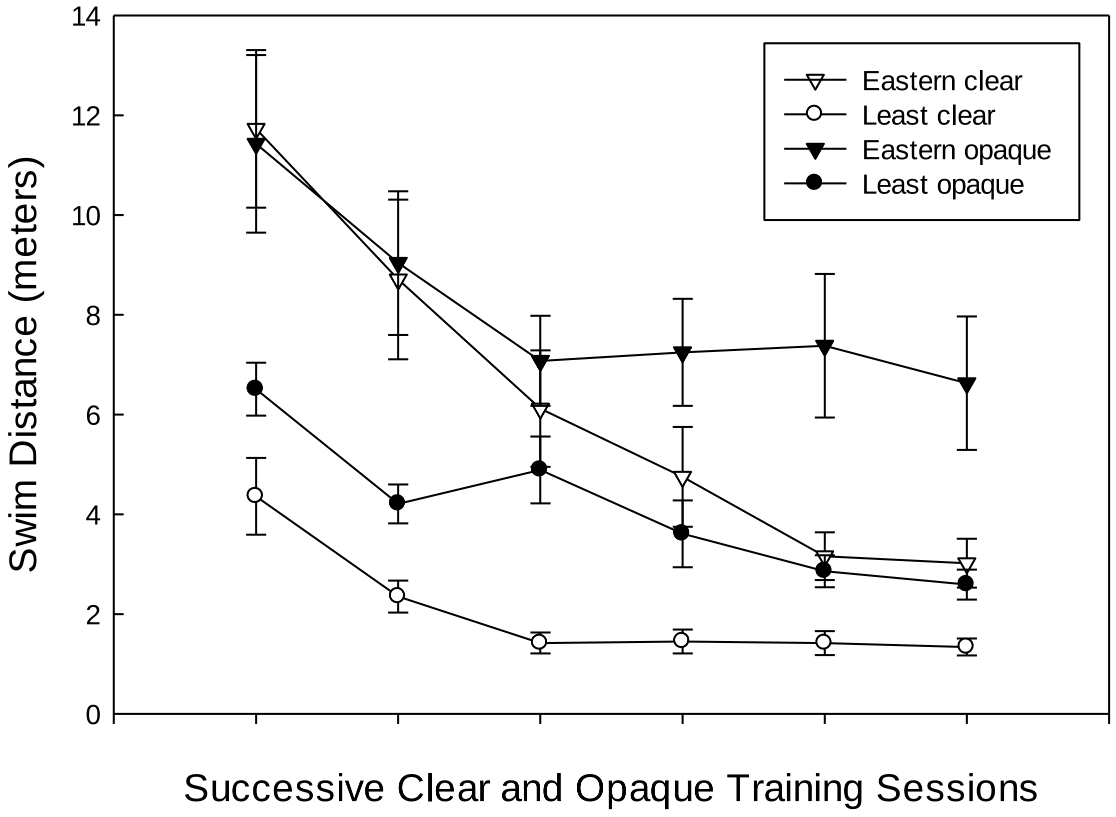
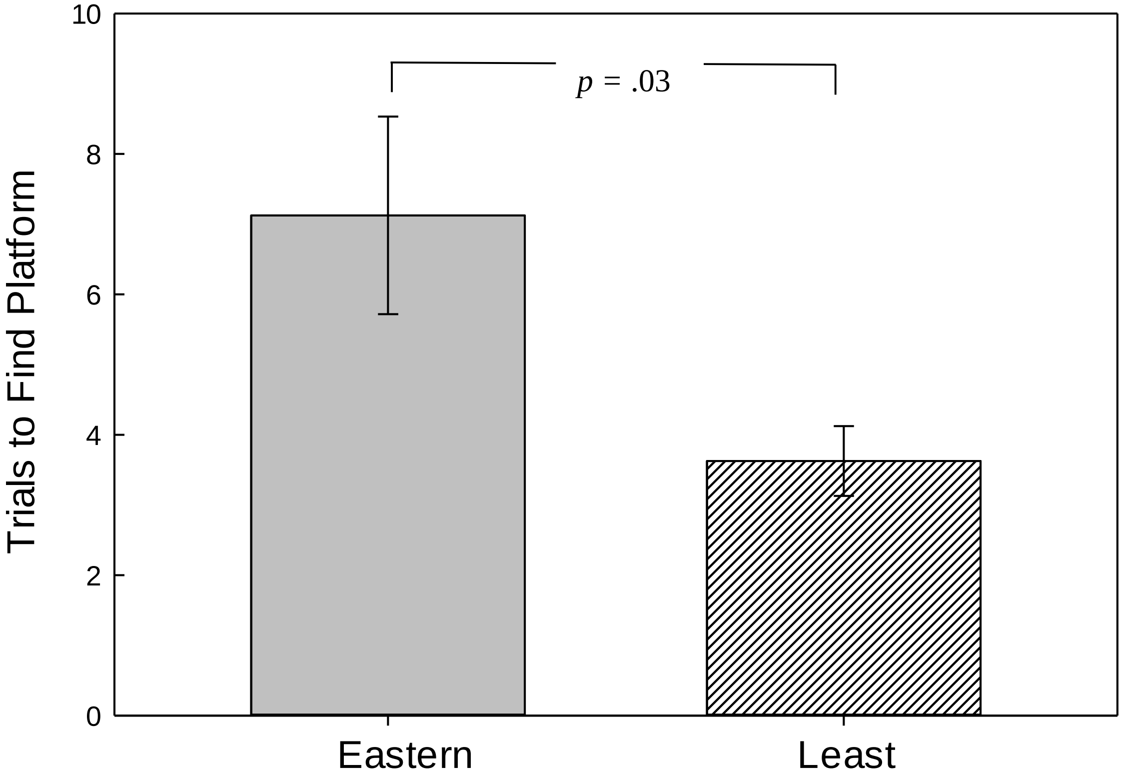

14
12
10
8
6
4
2
0
Swim Distance (meters)
Successive Clear and Opaque Training Sessions
Eastern clear
Least clear
Eastern opaque
Least opaque

Figure 2.



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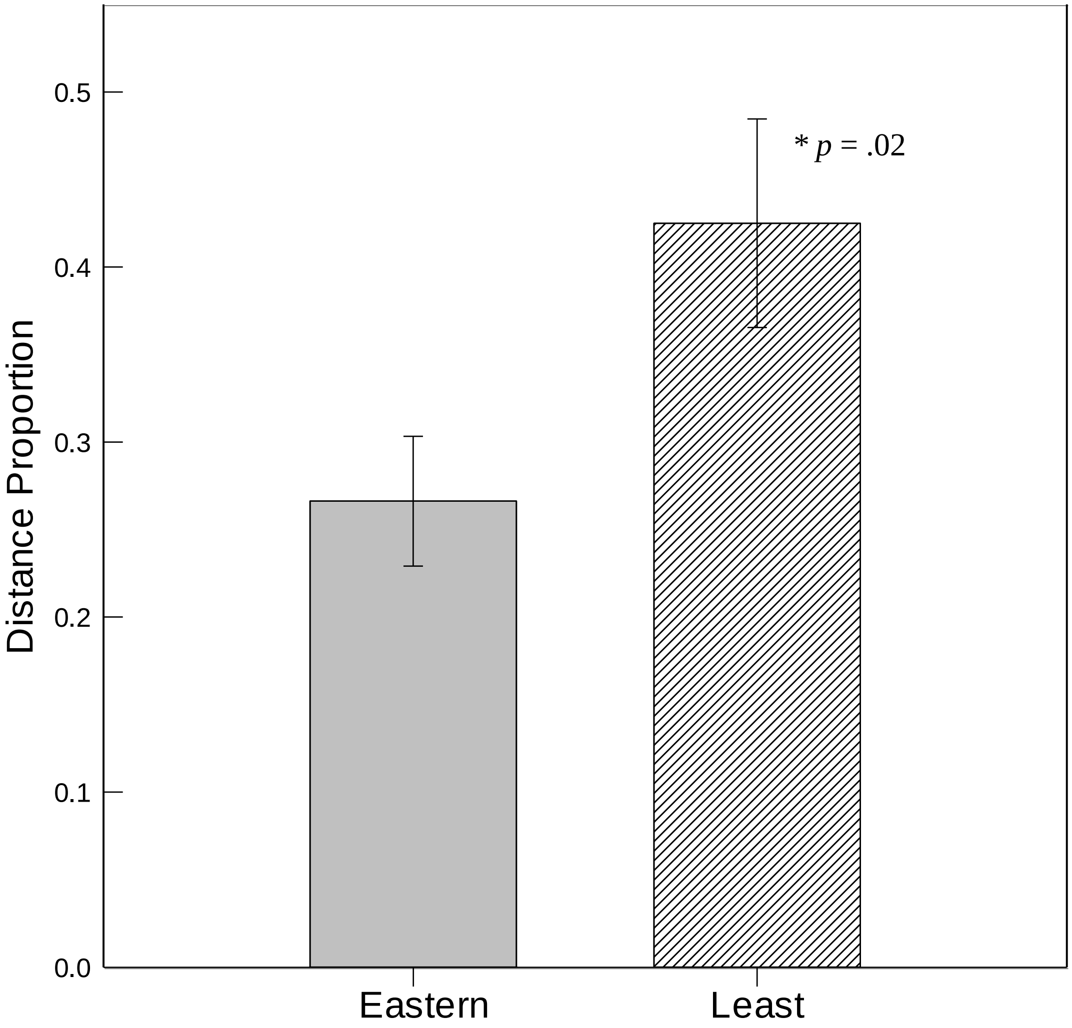


Figure 4.

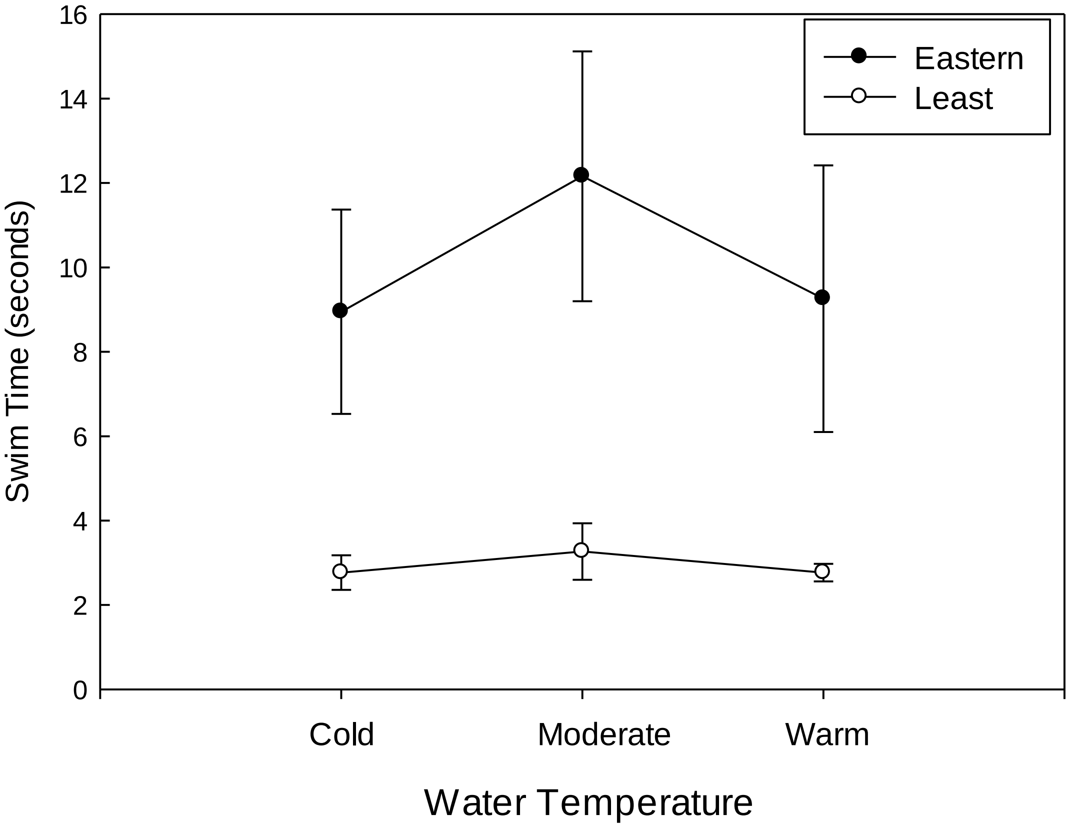
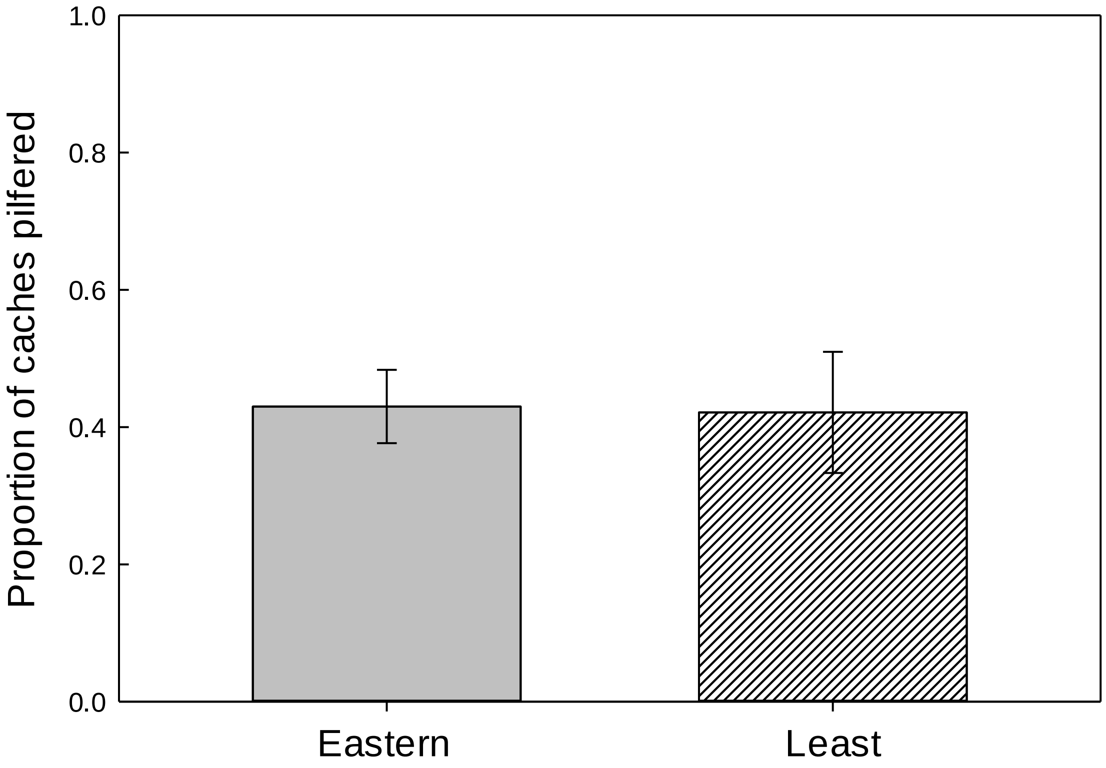

16
14
12
10
8
6
4
2
0
Swim Time (seconds)
Eastern
Least
Cold
Moderate
Warm
Water Temperature

Figure 5.



Proportion of caches pilfered
1.0
0.8
0.6
0.4
0.2
0.0
Eastern
Least