How Habitat Features Shape Ground Squirrel (*Urocitellus beldingi*) Navigation

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The purpose of this investigation was to determine whether Belding's ground squirrels (*Urocitellus beldingi*) from areas rich in beacons perform differently in a task of spatial memory compared with squirrels from beacon-thin areas. To assess the role of environmental experience in spatial memory, wild-born squirrels with several days of experience in the field were compared with squirrels born in a lab and with no experience in their original habitat. Over two summers, squirrels captured from beacon-dense and beacon-thin areas were tested in a radial maze interspersed with beacons, using number of trials to criterion as a measure of spatial memory. To evaluate the effect of landmark navigation, in year 2 juveniles were prevented from seeing outside the maze area. In both years squirrels from beacon-dense populations reached criterion faster than squirrels from beacon-thin populations, and a weak rearing effect was present in 1 year. Despite sex differences in adult spatial skills, no differences were found between males and females in the maze. This demonstrates variation in the navigation strategies of young *U. beldingi*, and highlights the need to evaluate spatial preferences as a function of population or ecology in addition to species and sex.

Keywords: ground squirrels, development, spatial learning, beacons, sex differences

Charles Darwin emphasized the importance of habitat differences in the study of evolution. When he made his initial trip to the Galapagos Islands in 1836 he noticed that different habitats produced different varieties of finches, each well suited to the particular challenges of the islands they inhabited (Darwin, 1859; Grant & Grant, 1996; Grant, 1994). Since then, much work has examined how geographic and ecological processes that separate gene flow between conspecifics lead to speciation events (Bush, 1993; Mayr, 1963). Historically, morphological differences have been the most

common point of reference in studies of speciation; however, as we are gaining a better understanding of comparative animal behavior we are finding that behavioral changes are just as important when it comes to defining what makes a species distinct (Boggs, 2001; Peixoto, 2002). Within the realm of behavior, much of this work has focused on mate choice, communication and studies of cultural transmission (Baker, 2006; Koetz, Westcott, & Congdon, 2007; Mundinger, 1980; Nicholls & Goldizen, 2006; Peixoto, 2002). Nonsocial behaviors such as spatial memory, however, can also be fertile topics for the study of population differences within species (Pravosudov & Clayton, 2002).

For example, selection might operate directly upon navigation abilities, particularly when physical environments are complex or when animals travel at night or through media with poor visibility (Akamatsu, Hatakeyama, & Wang, 1996; Pack & Herman, 1995; Ruczyński, Kalko, & Siemers, 2009). With the difficulties associated with each environmental type comes diverse solutions as organisms are selected to use methods that best meet the challenges of their specific habitat (Dudchenko & Bruce, 2005; Dyer, 1987, 1996; Dyer & Dickinson, 1994; Gagliardo, Odetti, & Ioale, 2005; Gallistel, 1990; Scapini, Rossano, Marchetti, & Morgan, 2005; Wehner & Srinivasan, 1981). Species for which populations have multiple distinct habitat types provide behaviorists with a unique opportunity to study how direct exposure to specific environmental features shapes the development of navigation.

Many species can live in more than one habitat type and therefore individuals could utilize different navigational tactics to get around with the most efficiency. Despite the relative sense of this argument, few studies have looked at population-specific differences in navigation within a species to show habitat-related differences in capability and strategy as a function of environmental cues. In this study, we were interested in whether animals from

different population types use different methods of navigation that are specifically tailored to the physical environments they inhabit. One goal of this study was to evaluate conspecifics that inhabit different population types to see if they performed differently on a task that principally involved a method of navigation favoring one environment over another. The other goal was to examine the potential developmental mechanism for such differences by captive rearing some animals to eliminate experience with their natal environment. We were also interested in sex differences with regard to the use of specific navigation cue types.

The work of Pravosudov and Clayton (2002) has provided some insight into possible habitat-specific selection on landmark spatial navigation abilities in birds; however, they argued that the differing harshness of the conditions between two populations selected for improved spatial capacities in one population over another, not a selected "preference" for one method of navigation over another. Furthermore, there are many studies looking at the plasticity of navigational methods that have placed animals from the same population in different environments or conditions (including manipulation of environmental experience) and found that the animals can and do use different strategies (Dyer & Dickinson, 1994, 1996; Gould-Beierle & Kamil, 1999; Hurly & Healy, 1996; Sherry & Duff, 1996; Wiltschko & Balda, 1989).

There are many strategies used by animals for navigating (for a review see Shettleworth, 1998). Different tactics can be used in concert with each another giving an individual multiple methods of navigation (Shettleworth & Sutton, 2005; Wehner & Srinivasan, 1981). However, we are most concerned with allocentric navigation (using cues external to the body) and for purposes of this study have focused on navigation by beacons (cues at goals) and landmarks (cues distal from goals) (Shettleworth, 1998).

Beacons must be close to the goal (e.g., nest, foraging area, water source) and only one is required to derive both distance and directional information (Shettleworth, 1998). That is because beacon use is essentially an associative learning task (Morris, 1981; Shettleworth, 1998). The animal pairs or associates the object with the goal much the same way as a rat in a conditioning chamber pairs a bar press with a food reward. The beacon, like the bar, becomes synonymous with reward and the animal is drawn toward the beacon as it searches for water pools, food patches, or home burrows (Shettleworth, 1998). The usage of landmarks, however, is a spatial task because it requires hippocampal processing as the navigating animal is using more than one cue to localize itself relative to a configuration of objects in the environment (Leonard & McNaughton, 1990; Morris, 1981). Therefore, these cues do not need to be close to the "goal" when animals engage in landmark navigation. However, landmarks do not form associatively paired relationships with the goal and they are not approached as if they are rewarding but rather are used to help the animal understand where they are in their environment based on the configuration of cues relative to the navigator. Because beacons must maintain close proximity to the goal the scale of navigation we are interested in can be measured in a few meters rather than kilometers.

We use the terms beacons and landmarks rather than proximate/distal cues or local/global landmarks because our phrasing eliminates the confusion of whether the cues are relative to the navigator or the goal and highlights that these are really two distinct processes of navigation. In addition, Shettleworth (1998) does an excellent job emphasizing that these two types of allocentric cues are very distinct and not gradations of the same thing. Beacons and landmarks are not only neurologically distinct (Leonard & McNaughton, 1990) but cognitively and computationally distinct as well (Fraenkel & Gunn, 1961; Morris, 1981). Navigating by beacons is a conditioned associative learning task, whereas navigating by landmarks is a spatial memory task (Morris, 1981; Shettleworth, 1998). We will highlight in detail later on how this interpretation of allocentric cues helps us to understand the navigation of our study species.

The relative effectiveness of either type of allocentric cue is greatly dependent on the features abundant in the habitat, possibly resulting in individuals in some populations more focused on beacon cues whereas individuals in other populations remain more focused on the use of landmarks. Many species use multiple information sources when navigating (Dyer, 1987; Sherry & Duff, 1996, see below), but it is not always clear how the sources are weighted when searching for a 'goal.' Some studies have shown that animals prefer to use distal objects (either relative to the goal or to themselves) to orient rather than local ones (Bossema, 1979; Gould-Beierle & Kamil, 1996; Jacobs & Shiflett, 1999; Vander Wall, 1982; Vlasak, 2006). However, in other studies animals prefer cues close to the goal (Bennett, 1993; Cheng, Collett, Pickhard, & Wehner, 1987; Tinbergen & Kruyt, 1938/1972).

There is some evidence that the degree to which animals weigh beacon versus landmark information is partially species-specific. Studies on food-storing animals such as black-capped chickadees and Mongolian gerbils have found that these species weight spatial landmark cues more heavily than beacon cues when information from the two cue types conflict (Brodbeck, 1994; Ellard & Bigel, 1996). In contrast, nonfood storing animals like dark-eyed juncos seem to weight beacons and landmarks equally (Brodbeck & Shettleworth, 1995; see also Clayton & Krebs, 1994). Because food-storers rely on strong spatial skills to orient in the search for caches their preference to use landmark information is logical (Shettleworth, 1998). It is probable that the weighting of allocentric cues is dependent on both species type and individual experience (Cheng, 1995), but it may also function of population of origin.

Environments are heterogeneous, and as such not all have the same numbers of landmarks and beacons. It is therefore reasonable to hypothesize that evolution can shape individuals to be maximally responsive to the environment they inhabit. Because it has been shown that the processes of beacon and landmark use are indeed different in both evolution and development (Leonard & McNaughton, 1990; Morris, 1981; Shettleworth, 1998), perhaps there is differential proficiency in the use of these cues relative to the environment. What is missing, however, is an investigation within a species comparing populations that inhabit areas rich in beacons and areas lacking them. Belding's ground squirrels (*Urocitellus beldingi*; formerly *Spermophilus beldingi*; Helgen, Cole, Helgen, & Wilson, 2009) offer the possibility of studying this because they inhabit both forests and open meadows. For the duration of this paper we will refer to these groups as beacon-dense areas (living among trees and shrubs) and beacon-thin populations (living in relatively featureless high alpine meadows with views of distant mountains), respectively. We predict that beacon-dense populations will display more proficiency than beacon-thin populations in a test of beacon navigation.

It is unclear how Belding's ground squirrels specifically represent these cues in their environment; however, we do know two things about the nature of beacons that give us insight into how they may represent their world in habitat specific ways. The first is that beacons and landmarks are not only neurologically (Leonard & McNaughton, 1990) and developmentally (Nesterova, 2007; Rudy, Stadler-Morris, & Albert, 1987; Sutton, 2006) distinct, but are also distinct in how they are used (see above). The second is that young animals from our beacon-thin area have no real discernible beacons to use in navigation around their natal burrows. Their burrows are in open areas with no nearby rocks, trees, bushes, or human-made structures that they can use to find the goal. Population-type differences may be a function of sensory bias or experience with the environments (Gottlieb, 1976).

Method

Study Squirrels

Belding's ground squirrels (*Urocitellus beldingi*) are rodents found in the alpine regions of the western United States (Jenkins & Eshelman, 1984). They spend the majority of the year hibernating with active months between April and August. Females have only one litter each year of 5–8 offspring, which they rear in a natal burrow for about 4 weeks when the juveniles emerge nearly weaned (Sherman & Morton, 1984). Two to 3 months after natal emergence juveniles will disperse from the natal burrow, with females staying within 25 m and males migrating upward of 250–500 m from the mother's location (Holekamp, 1984b).

Belding's ground squirrels inhabit multiple burrow types throughout life, including a winter hibernaculum and active-season burrows as well as the aforementioned natal burrows which are 10–15 feet long and house a mother and her offspring for the summer (Sherman & Morton, 1987). *U. beldingi* also use single-entrance bolt holes throughout the habitat for rapid escape from predators. They prefer to enter multiple-entrance burrows when responding to trill alarm calls warning of terrestrial predators (which may follow them belowground), potentially bypassing a nearer single-entrance burrow, whereas the nearest burrow is preferred when responding to whistle alarm calls warning of aerial predators which attack extremely rapidly (Turner, 1973). Juvenile squirrels face difficulties upon natal emergence because they are becoming nutritionally independent and must find good sources of food (grass patches, seeds, insects, birds' eggs, small mammals, and carrion) and water relatively quickly (Sherman & Morton, 1984, 1987). Furthermore, they must develop a comprehension of where the safe burrows are located and how to get there quickly when hearing alarm calls. The importance of successful navigation at a young age cannot be overstated in Belding's ground squirrels as predation and infanticide pressures will lead to 30% mortality in the first 2 weeks above ground (Mateo, 1996, 2007; Mateo & Holmes, 1997, 1999).

Maximum size of home ranges for populations of ground squirrels we studied is not known, however, Sherman and Morton (1984) did not find adult animals migrating beyond 1.9 km from their main site in Tioga Pass which is closer than the distance between our two closest populations of study (7.6 km). Thus, given an animal's hibernaculum and summer burrows, burrows for refugia from predators, sources of food, water and nesting material,

and locations of friendly or agonistic conspecifics, *U. beldingi* need to learn and recall many locations within their environment.

Subjects and Squirrel Housing

This investigation was conducted over two summers in 2005 and 2006 at the Sierra Nevada Aquatic Research Laboratory (SNARL) near Mammoth Lakes, CA (37.649 N, 118.971 W; 2100 m). Subjects were either born and reared in the field or born and reared in a laboratory. Juveniles captured from the field were ~5 days past their natal emergence which occurs in June and July (depending on elevation of population). Lab-reared squirrels were born at a SNARL nursery to mothers that were trapped when pregnant in June (see Table 1). At the conclusion of this study, all squirrels were released back to the natal territories occupied by their mothers before capture or at their own site of capture. Captive-born young were released back to the wild with their mothers.

Squirrels were housed in an animal facility at SNARL on a 13:11 h light:dark cycle. The building was temperature regulated by the use of a heater and a portable air conditioner, and the temperature ranged from 10 °C at night to 32 °C during the day. Mothers (and their pups) were individually housed in a stainless steel cage (61 × 45 × 35 cm) which contained a wooden nest-box (28 × 20 × 20 cm) with a 6 cm diameter entry hole and wood shavings, dried grass, Nestlets (Ancare Co., Bellmore, NY) and strips of newspaper for bedding. Lab-born juveniles were separated from their mother and group-housed in the stainless steel cages with two other unrelated subjects when they were nutritionally independent (>27 days of age). Field-born squirrels were group-housed similarly. Squirrels started training when they were large enough to fit in the maze (>100 g). Each squirrel was fed four pellets daily of Purina mouse chow (#5015) with occasional supplements of dandelion heads, vegetables, and sunflower seeds. Water was available ad libitum. Squirrels were identified using metal tags (National Band and Tag, Newport, KY) placed on both ears. Most squirrels were around 100 g at the start of their participation in the study because of limitations of the testing apparatus.

Table 1

Numbers of Subjects by Population-of-Origin, Sex, and Rearing Condition in This Investigation of Juvenile Ground-Squirrel Navigation in a Radial-Arm Maze

	Field-born		Laboratory-born	
	Male	Female	Male	Female
2005				
SNARL*	2	0	0	0
Lundy*	1	4	2	3
East Fork*	0	0	3	3
Mono County Park**	3	2	1	0
Total	6	6	6	6
2006				
Lundy*	2	4	3	2
East Fork*	3	2	3	3
Mono County Park**	2	3	2	4
Total	7	9	8	9

* Indicates beacon-dense environments.   ** Indicates beacon-thin environment.

At the start of training (described below), squirrels from beacon-dense and beacon-thin population-types were an average of 38 and 42 days old, respectively, with an overall range of 34 to 48 days with one outlier of 54 days. On average, both lab and field born squirrels were 39 days old.

Collection Sites

Juveniles or their mothers were captured from various locations in the eastern Sierra of CA, including Mono County Park (MCP; 1,966 m), SNARL property (2,100 m), Lundy Campground (2,316 m), and East Fork (EF) Campground in Rock Creek Canyon (2,743 m). Locations were considered beacon-dense or beacon-thin. Lundy Campground, EF Campground, and SNARL were classified as beacon-dense because the two campgrounds are forested areas rich in trees as well as shrub vegetation and SNARL contains 10 one story and 2 two story buildings as well as other stationary human-made features and natural features: garden hoses, sprinklers, outdoor tables, nonmoving vehicles, scattered trees, and tall grass. On SNARL property, squirrels were trapped at burrows close to buildings and near other large features such as a permanently parked truck. MCP was categorized as a beacon-thin location because it is a large, open grass lawn. There are scattered trees and a very dense section of willows in the center of the park, with a few picnic tables and park swings in one quadrant; however, squirrels were only trapped from the centers of the lawns, at least 5 m from possible beacons.

Apparatus

To test visual spatial reference memory, we used a modified six-arm radial maze placed inside a large outdoor enclosure (9.7 × 9.7 × 1.6 m) the first year and a smaller but taller hexagonal enclosure the second year (each side 1.83 m across and 2.44 m tall). This unique maze was designed to train animals on beacon associations rather than landmark-based spatial navigation where the radial arm maze is typically used (Olton & Papas, 1979; Olton & Samuelson, 1976). Each arm of this maze had a directional beacon associated with it. For the subject to identify which arm would lead to reward he or she did not have to orient with respect to a configuration of cues in the environment, but rather just one object. The modular device consisted of a round center (80 cm diameter) with an aluminum base and a Plexiglas top and sides (10 cm high). Six evenly spaced, semicircular arms (2 m long, 8 cm diameter) extended from the center, and were composed of white rubber tubing for the bottom half and a double layer of 25.4 mm poultry netting for the top half. This design provided a stable, solid running surface with good traction and allowed squirrels to see cues outside the maze, while keeping juveniles over 100 g from escaping through the arms (subjects under that weight ran the risk of escaping through the poultry netting). A clean 3.79 L milk jug was attached to the end of each arm via an 8 cm hole on the side of the jug. Another 8 cm hole was cut into the adjacent side and a flap of double-layer poultry netting was attached to the hole with four thin wires (two above the hole and two below), which securely covered the open hole of five of the six jugs. The flap of the sixth "escape-jug" was attached with two wires above the hole and bent open so the squirrel could escape without injury. Two additional wires were attached to the bottom of the hole to keep visual cues constant across all jugs. As they moved through the maze subjects were unlikely to have seen the propped open flap because of the curvature of the arms and the obstruction provided by objects placed between maze arms as directional beacons. Regardless, had they seen the open flap from a distance this would not be a confound, but rather a visual cue that the subjects could use to learn the location of the escape jug.

In 2005, natural and human-made objects, including a yellow lawn sprinkler (30 × 10 × 12 cm), a wooden stump (40 cm diameter, 30 cm high), a propped wooden log (30 × 14 × 17 cm), a metal fence post propped by rocks (50 × 30 cm), a cinder block (20 × 20 × 40 cm), and a yellow rotary sprinkler (17 cm diameter, 15 cm high) were interspersed between maze arms to serve as directional beacons (see Figure 1). Because the objects were placed close to the entrance of the escape arm these cues can be defined as beacons, rather than landmarks because it is possible to orient to the goal using only one cue (Shettleworth, 1998).

The maze was placed in a plywood, four-wall open air enclosure (9.7 × 9.7 × 1.6 m) which included natural vegetation and a handful of rocks (about five per square meter). The wall of this seminatural environment limited the squirrels' visual fields to what they could see overhead or within the enclosure itself (mostly rocks no bigger than 30 cm). This prevented the use of extreme distal cues (such as mountains) in visual navigation and also muted (and probably redirected) the sounds of a road (~80 m away to the north) and a creek (~70 m to the south). However, it is possible that some distal cues could still be used as landmarks in 2005.

In 2006 we changed two elements of the maze. The first was the nature of the beacons. We used beacons that could easily be removed so that we could definitively show that it was the beacons
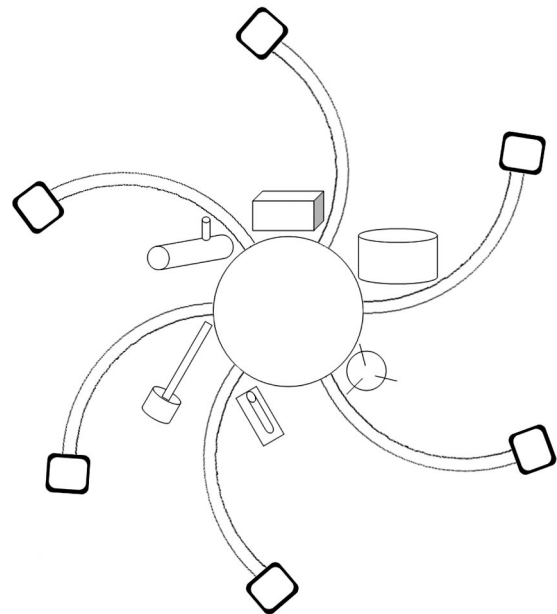

Figure 1. Top down view of radial arm maze used for Belding's ground squirrels, including a central start area, six tubular arms, and beacon objects between each arm (objects from bottom, clockwise: lawn sprinkler, metal pipe with PVC piping, log, cinderblock, stump, and rotary sprinkler). Squares at the end of each arm represent escape jugs.

the squirrels were using to navigate. We replaced the pile of rocks and the two yellow sprinklers with a 10 cm tall orange road cone, a round rock about 15 cm in diameter, and a metal step stool that was ~25.4 cm^3. After squirrels reached criterion on the maze task, we removed the beacons after to see how well they would perform without these cues.

Second, a 2.44 m tall hexagonal enclosure was built surrounding the maze and preventing the use of external landmarks in navigation. Each wall of this enclosure was covered with black single-layer plastic trash bags to provide visual uniformity across the walls. Three doors were placed in the hexagon enclosure at every other wall. This made it possible to enter at different locations and thus made it more difficult for subjects to use their point of entry into the hexagon as a cue for navigation. Squirrels were brought into the hexagon in an opaque canvas sack designed for handling squirrels to prevent the usage of path integration or external visual cues from where they entered the enclosure. It was not uncommon for experimenters entering the hexagon enclosure to themselves become lost with respect to direction.

Training Procedure

The squirrel facility was situated ~650 m from the maze. Squirrels were taken to the training site each day either on foot or by van in individual single-door Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, WI). Efforts were made to standardize this across all of the variables of interest; however, there was no discernable general trend in performance seen on days when the squirrels were transported by van rather than by foot. Once at the enclosure, squirrels were kept in traps in the shade (with an electric fan on warmer days) and provided with water bottles attached to traps. Each squirrel was kept in its trap both before and after each trial, for an average total time at the enclosure of 30–60 min.

Before training began, all squirrels were arbitrarily assigned to groups of four to five subjects, and then placed in the maze for three 20 min acclimation periods (one per day). The escape flap was closed during this portion of training. *U. beldingi* were acclimated as a group because they were reluctant to explore the maze when placed in it alone. Although we did not conduct systematic behavioral observations during this period, we did note that all squirrels moved about the entire apparatus during each acclimation session.

For each squirrel, the objective is to escape from the maze through an escape hole found only at the distal end of one arm. That is, only one arm is "baited" with the opportunity to escape. Escape was used as a reward rather than food, because all foods *U. beldingi* will eat have an odor, which would confound the use of visual cues. Consequently, the only universal reward identified for Belding's ground squirrels is escape (J. N. Bruck, unpublished data). Squirrels were run in the maze individually once a day until they met criterion, which was defined as exiting from the maze in <60 s on two trials in a row with one or zero errors. Subjects were trained either in the morning starting at around 7:30, or in the afternoon starting at 14:00. The running order was arbitrarily determined each day, but efforts were made to ensure that the same squirrels were not run at the same time of day frequently.

For each trial an assistant placed a squirrel in the maze from the top of the centerpiece using a funnel device, with the starting orientation rotated each day counterclockwise. This procedure lessened the effects of proprioception. Recording of movement began when all four feet of the juvenile were on the floor of the maze. We observed the subjects in real time via a remote video camera (closed-circuit generic security camera purchased at Sam's Club) while seated ~100 m away from the enclosure. We were not blind to which arm was the escape arm, because we needed to anticipate from where the squirrel would escape, but we did not know the squirrel's sex, age, or rearing condition. We recorded which arms each subject entered and their latency to exit the maze. Each entry into an arm (escape or closed) without escape was scored as an error. Recording ended when all four of the subject's feet left the maze through the escape jug or after 20 min had elapsed. The subject was then given 5 min of freedom within the enclosure. If it did not capture itself during that time, it was corralled into one of four traps placed in the corners of the enclosure.

After each trial, all parts were cleaned with Cide-all cleaning solution (Chemifax, Santa Fe Springs, CA) and water using a clean sponge attached to a 2 m flexible plastic tube for the arms, and a regular sponge was used for the other components, and allowed to air dry. The arms and jugs were arbitrarily reconfigured and the escape jug was placed on the correct arm for the next subject. In addition, the center piece of the maze was rotated arbitrarily. These measures assured that no subject could reliably use individual variation among the arms or possible remaining odors as a means of navigation. In 2006, after subjects met criterion twice in a row they were tested in the maze with the beacons completely removed. This was to assess the degree to which the squirrels were using the beacons provided.

Statistics

When data were not normally distributed (confirmed with Kolmogorov–Smirnov tests), log transformed values were used for all analyses on those variables. Analysis of variance tests (ANOVAs) were performed for most comparisons. A repeated measures ANOVA was used to evaluate performance after beacons were removed in 2006. A Pearson correlation matrix was used for the analyses of performance relative to body weight at the start of training and *t* tests were used in the analyses of latency data with respect to squirrel motivation to move through the maze. Because age data were not normal after log transformation, a Spearman's rho was used to analyze performance as a function of days old at start of testing. Possible interactions were evaluated using two-way ANOVAs. Most statistics were performed using Systat 11 statistical package (Wilkinson, 2004); however, the Spearman's rho was performed using SPSS 10.1.3. We include Cohen's *d* scores for all significant results.

Results

In 2005, juveniles from the beacon-dense population-type reached criterion in fewer trials than squirrels from the beacon-thin population type, $F(1, 22) = 7.94$, $p = .010$, $d = 1.42$; see Figure 2. There was no significant difference between those born in the lab and those born in the wild, $F(1, 22) = 0.42$, $p = .523$, or between sexes, $F(1, 22) = 0.08$, $p = .782$. A Pearson correlation matrix revealed that there was no significant association between weight at the start of training and the number of trials needed to reach
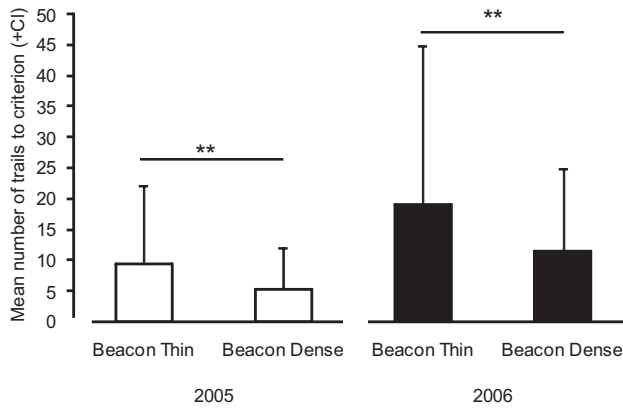
Figure 2. Mean number of trials to completion (+CI) in a radial-arm maze for juveniles from beacon-thin ($n = 6$) and beacon-dense ($n = 18$) population-types in 2005 (open columns) and 2006 (beacon-thin, $n = 11$; beacon dense $n = 22$; closed columns). Field-born and laboratory-born juveniles are combined within each population-type. Lines over columns indicate significant population differences based on ANOVA on log-transformed data (** $p < .001$).

criterion, beacon-dense and thin combined; $r(24) = 0.013$, $p = .952$. To establish that each of the visual cues were equally salient with regard to learning, the numbers of trials to criterion for each of the six escape arms were analyzed; no significant difference was found, $F(5, 18) = 0.75$, $p = .596$.

When just the juveniles from beacon-dense areas were analyzed separately ($n = 18$) there were no sex differences, $F(1, 16) = 0.30$, $p = .592$, or population differences, $F(2, 15) = 0.75$, $p = .490$ in the number of trials to criterion. There was a significant effect of rearing condition, $F(1, 16) = 4.58$, $p = .048$, $d = 1.04$, with lab-reared juveniles requiring more trials than those with a few days of experience in the field (see Figure 3). However, because these data were a subset the larger dataset which was also analyzed for rearing effects, a Bonferroni correction for multiple testing would be appropriate, and thus the results are no longer significant ($\alpha = .025$). A sample size of one prevented a similar analysis of beacon-thin juveniles.

In 2006, with the maze placed in a tall hexagonal enclosure, juveniles from beacon-thin environments again required more trials to reach criterion than squirrels from beacon-dense environments, $F(1, 31) = 7.152$, $p = .012$, $d = 0.950$; see Figure 2. There were no significant overall differences because of rearing condition, $F(1, 31) = 0.024$, $p = .878$, or sex, $F(1, 31) = 0.559$, $p = .460$. Body weight at the start of training was not associated with the rate of learning, $r(33) = 0.076$, $p = .674$. There was no significant difference in learning among the six arms, $F(5, 27) = 0.632$, $p = .677$. Overall, age was not a factor in maze performance for this study, $r_s(55) = 0.115$, $p = .396$.

Unlike in 2005, we found no effects of rearing for the beacon-dense population-type, $F(1, 20) = 0.222$, $p = .643$; see Figure 3. There was also no difference between field and lab rearing for the beacon-thin population type, $F(1, 9) = 0.012$, $p = .914$.

To examine the effect of removing the presence of landmark cues by using the hexagonal walls, we compared the 2006 and 2005 data. Squirrels in 2005 learned the maze task faster than squirrels in 2006, $F(1, 53) = 26.717$, $p < .001$, $d = 1.54$, with no

significant interaction with population-type, meaning no differential effect of year according to population-type, two-way ANOVA; $F(1, 53) = 0.339$, $p = .563$.

In 2006 we removed beacon cues as well as landmark cues after the squirrels met criterion to examine the degree to which the squirrels used these cues in navigation. Using latency to complete the maze as a dependent measurement we found that squirrels performed significantly worse on this test trial relative to their previous successful trial with the beacons present (repeated measures ANOVA; $F(1, 28) = 19.186$, $p < .0001$, $d = 0.85$). However, there was no significant difference in performance change between the two population types, $F(1, 28) = 0.150$, $p = .701$.

Finally, to test whether population-type differences in reaching criterion may be because of differences in motivation to move through and escape the maze, we measured both the latency to enter the first arm and the latency to enter the first jug each trial. We expected that if squirrels were less motivated to escape the maze they would have longer latencies to enter either the first arm or the first jug. For squirrels running in their first trial there were no significant difference between squirrels in beacon-thin or beacon-dense habitats in either their latency to enter the first arm, $t(1, 55) = 0.381$, $p = .705$, or their latency to enter the first jug, $t(1, 55) = 0.067$, $p = .947$. When averaged across all trials, there was also no significant difference for latency to enter first arm, $t(1, 55) = 0.115$, $p = .909$, or latency to enter first jug, $t(1, 55) = 0.279$, $p = .781$.

Discussion

In this study we sought to determine whether juvenile Belding ground squirrels from different habitat types would exhibit different navigation strategies in a spatial learning task. Specifically, we predicted that squirrels living in areas with many beacons near important areas (e.g., nest, foraging area) would learn faster in a
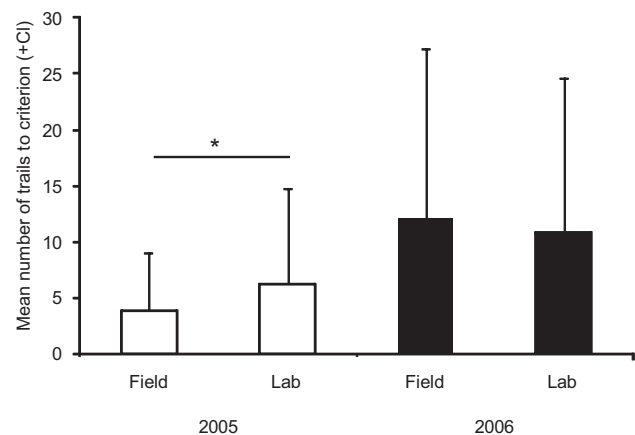
Figure 3. The effect of rearing condition (born in the field and brought to the laboratory after ~5 days of experience in the natural habitat, or born and reared in the laboratory) on mean number of trials to completion (+CI) for all beacon-dense subjects in the 2005 (field: $n = 7$; lab: $n = 11$) and 2006 (field: $n = 11$; lab: $n = 11$) data sets. Sample size was too small to analyze beacon-thin data ($n = 1$). Lines over columns indicate significant rearing group differences based on ANOVA on log-transformed data before Bonferroni correction (* $p < .05$).

radial maze which was interspersed with objects acting as beacons, compared with squirrels living in areas lacking beacons. The results demonstrated that squirrels from beacon-rich areas learned the maze in significantly fewer trials than squirrels from beacon-thin population-type (see Figure 2). There was very weak evidence that developmental experience with the environment impacted maze performance (see Figure 3); however, we did not find differences associated with sex or any of the control variables (start weight, motivation, beacon salience, age, or population differences within beacon-dense group). Finally, the removal of landmarks and beacons led to poorer maze performance overall in both beacon-thin and beacon-dense population-types.

Population-Type Differences

Juveniles from Mono County Park, a site with large open lawns and few beacons, required more trials to reach criterion than juveniles from sites with abundant beacons, indicating that habitat type influences performance in this radial arm maze. Navigating by beacons requires that a squirrel learn associations between desired locations and the features near them. In the maze used here, squirrels can take advantage of the objects between the arms by using them as beacons, therefore associating these unique items with the featureless arms they come to represent. Although squirrels could have processed the configuration of multiple objects as landmarks, it would be faster and easier for them to use the objects as beacons, and pair the conditioned stimulus (CS; the object placed between the maze arms) with the unconditioned stimulus (US), the "correct" arm/escape jug.

From neurological, cognitive, and theoretical standpoints, the use of beacons is a much simpler task than the use of landmarks (Fraenkel & Gunn, 1961; Leonard & McNaughton, 1990; Rudy et al., 1987; Shettleworth, 1998). The use of landmarks involves orienting relative to a configuration of stimuli (that must be perceived accurately) as well as greater neurological processing (because of hippocampal recruitment), and thus is more error-prone and time consuming (Leonard & McNaughton, 1990; Shettleworth, 1998). Furthermore, in some species the competent use of beacons occurs earlier in development than landmark cue usage, further attesting to the relative difficulty of the two modes of navigation (Nesterova, 2007; Rudy et al., 1987; Sutton, 2006). Data from *U. columbianus* are consistent with the idea that a given individual may prefer to weigh certain allocentric information more heavily than other allocentric information, as juveniles appear to use local cues more proficiently than adults in a task that eliminates distant landmarks, whereas adults are better at using distal cues than juveniles in a global landmark task (Nesterova, 2007).

Alternative Explanation and Control Measures

The increased latency to complete the maze task when the beacons were removed in 2006 (after squirrels reached criterion) demonstrates that these squirrels were using these cues to navigate. Both beacon-thin and beacon-dense groups did worse on the task when the beacons were removed, which would be expected because the nature of the task relied on the use of beacons. The fact that beacon-dense squirrels seemed to do better relative to beacon-thin squirrels when these cues were removed is interesting, but

only highlights the fact that these beacon-dense squirrels might be better at identifying the propped open escape door as a beacon in much the same way as rats identified a raised platform in Morris's (1981) water maze study.

The fact that there were no discernable population-type differences in how the squirrels moved in the maze from the centerpiece to the first arm, then to the first jug on either the first trial or across all trials indicates, as best as we can measure, no population-type differences in motivation to explore or to escape. If squirrels were not interested in escaping the maze then they might simply remain in the centerpiece or move into a jug and "hide-out." No squirrel stayed in any jug for more than 30 s and when squirrels did enter a jug they would often be seen scratching at the plastic. It is not very likely that differences in maze performance were the result of differential motivation to escape. That all squirrels eventually did reach criterion suggests that once the squirrels did learn to escape and run about the enclosure, that was the place they preferred to be.

Although it is reasonable to conclude that habitat influences the weighting of allocentric cues when navigating in population-specific ways, other factors may have contributed to the results reported here. Heritable differences in learning potential may exist among the populations such that any associative learning task could produce similar results. For example, an operant task involving a conditioning chamber could reveal whether the poor maze performance by MCP juveniles was because of reduced beacon exposure or because of a generalized learning deficiency. In addition, if pesticides or fertilizers were used on the lawn at MCP, these potential teratogens could result in population-wide impairments in learning (Calas et al., 2008; Heise & Hudson, 1985).

Finally, stress hormones are known to affect learning and memory, including spatial learning (Williams et al., 2003), and population-type differences in basal cortisol are known for juvenile *U. beldingi* (Mateo, 2006). Cortisol is lower at Lundy Canyon than at MCP (juveniles at East Fork and SNARL have not been sampled), and highly elevated cortisol can impair spatial learning by juveniles (Mateo, 2008), but it is unknown whether the levels at MCP are high enough to interfere with learning. Only by testing other beacon-thin population-types would one be able to determine if the performance of MCP juveniles is because of their specific location or to general features of beacon-thin environments. We note that MCP juveniles might do very well in tasks with landmarks only, in which case squirrels from beacon-dense environments might do relatively poorly.

Sex Differences

No sex differences were observed in maze performance. This finding is of note because it is in direct contrast with other studies showing that male rodents such as rats, deer mice, and meadow voles are the more proficient sex in spatial tasks (see Bimonte & Denenberg, 2000; Galea, Kavaliers, & Ossenkopp, 1996; Gaulin & FitzGerald, 1986; Gaulin, FitzGerald, & Wartell, 1990; Jonasson, 2005; Juraska, Henderson, & Mueller, 1984; Voyer, Voyer, & Bryden, 1995). Here juveniles were tested several weeks before the age of natal dispersal, and 1 (females) or 2 (males) years before sexual maturity (Jenkins & Eshelman, 1984), and thus according to life-history patterns there is no a priori reason to expect sex differences at this age. Had juveniles been tested at later ages, such

as during the process of natal dispersal, sex differences in maze learning may have been evident.

It is possible that sex differences in Belding's ground squirrel spatial abilities are present in older individuals because male *U. beldingi* disperse further from natal burrows and range greater distances during the mating season in search of estrous females (Holekamp, 1984a, 1984b; Holekamp & Sherman, 1989; Sherman & Morton, 1984; J. M. Mateo, personal observations). Another possible explanation for the lack of sex differences may be the nonspatial nature of the task. As mentioned before beacon navigation is not a "spatial" task when compared with other forms of orientation that require specific spatial processing (Fraenkel & Gunn, 1961; Leonard & McNaughton, 1990; Shettleworth, 1998). A beacon learning task is fundamentally an associative learning task (Morris, 1981). As such the sex difference may not be present because the squirrels may not be using parts of the brain that are potentially sexually differentiated. This is corroborated by Mateo (1996, 2008) which found no ground squirrel sex differences in other learning tasks (mostly associative in nature).

Cue Weighting

In 2005 juveniles required significantly fewer trials to reach criterion than in 2006, when a hexagon enclosure surrounded the maze (see Figure 2). The likely explanation for the difference in maze performance is the elimination of any possible landmark cues or cues from the distant walls of the enclosure. The learning impairment in 2006 suggests that either both beacon-thin and beacon-dense population-types use landmarks to some degree, or that addition of the hexagon enclosure added a degree of artificiality that somehow interfered with learning. It is probable that both population-types use landmarks in some contexts. This is consistent with the many studies that have shown that squirrels prefer to use distal objects, sometimes at the exclusion of more local cues (Gould-Beierle & Kamil, 1996, 1999; Jacobs & Shiflett, 1999; Vlasak, 2006). Because beacons are not always readily evident as a squirrel first begins to seek a goal it makes perfect sense that landmarks might be the first thing a squirrel looks for.

Notwithstanding, there are studies suggesting that squirrels actually prefer cues closer to the goal to navigate (Bennett, 1993; Cheng et al., 1987; Tinbergen & Kruyt, 1938/1972). The question at hand is what are the relative weights each squirrel gives to landmark information versus beacon information? It has been argued that the degree to which squirrels weigh the different types of orientation information is largely based on species and individual experience which would seem to make sense given the conflicted findings of the studies that have looked at allocentric cue preference (Cheng, 1995). Our data provide some evidence that population of origin also affects the weighting of landmark and beacon information. This explains why the beacon-dense squirrels were less influenced by the complete removal of landmark information in 2006, because they were weighted more toward the use of beacons in their overall combination of cues (Shettleworth, 1998). Differential weighting would permit significant adaptive plasticity in navigation strategies within a species, according to an individual's habitat type.

Rearing Condition

Before a Bonferroni correction there was a significant effect of rearing condition in 2005 but not 2006 (see Figure 3). This finding may not be very significant and these results should be interpreted with some degree of caution. Let us assume, that in the first year, beacon-dense juveniles learned the maze faster if they were born in the field and had a few days of experience in that environment before capture, relative to those born in the lab. The 2005 data support an equal potential/canalization view of beacon navigation (Gottlieb, 1981, 1991). Although this tabula rasa explanation is often viewed in contrast with the heritable differences perspective (Crusio & Schwegler, 2005), the components of learning may be quite heritable as shown in early rodent maze studies (see Gottlieb, 1976; Tolman, 1924; Tryon, 1929). Canalization could make sense, however, as squirrels within even the same population may inhabit very different physical environments, and plasticity in the use of whatever allocentric cues are available is a good solution to the problem of unpredictable environments. A ground squirrel born in an open field at Mono County Park may rely less on beacons than one born at a natal burrow near a tree. Evolutionarily, the heterogeneity of squirrel environments should favor an equal potential followed by a specialization strategy with regard to beacon navigation. Sample size was too small to analyze data from beacon-thin juveniles in 2005 because one group had an $N = 1$.

It is unclear why rearing condition had even less of an effect in 2006. It is possible that the hexagon enclosure attenuated the advantages associated with experience with beacons in the field (if there are any). However, if the 2006 data more accurately represent *U. beldingi* learning, then early experience with microhabitat features have little effect on beacon-based navigation. Therefore, if rearing effects are not found and these beacon-thin/beacon-dense strategies are in fact highly heritable, and resistant to the influence of environmental input, then we might have an example of divergent evolution with respect to navigation preferences. These populations are not known to interbreed (J. M. Mateo, personal observations), and it is possible that selection has favored weighting toward beacon use when cues are combined in beacon-dense population-types. However, insights from Gould-Beierle and Kamil (1999), Hurly and Healy (1996), and Hermer and Spelke (1996) suggest that organisms from the same population can often rely on multiple or different strategies when faced with conflicting cue information or unique experimental conditions. Further studies looking at the assimilation of landmark and solar navigation have further demonstrated how experience with the environment shapes navigation (Dyer & Dickinson, 1994, 1996; Sherry & Duff, 1996; Wiltschko & Balda, 1989) As a result, there is some evidence from other species of plasticity in methods of navigation. Additional research with larger sample sizes of *U. beldingi* is needed to better understand the influence of rearing conditions on their spatial learning, but as it stands these data do support a heritable-differences explanation over an equal potential/canalization view of beacon navigation.

Concluding Remarks

When Darwin first proposed the concept of speciation through selection his focus was on morphological traits (Darwin, 1859). However, as selection acts on behavior as well as morphology, it

should come as no surprise that different populations within a species can express different behavioral phenotypes if they live in divergent habitats. Clearly, this is no surprise to those familiar with the study of animal culture and animal communication. Orcas maintain completely different communication systems, diets, and social structures simply as a function of the population into which they are born (Ford, Ellis, & Balcomb, 2000; Ford et al., 1998). Similar findings have been made in the study of bird (Baptista, 1974, 1975; Kroodsma, 2004; Wright, Dahlin, & Salinas-Melgoza, 2008) and bat dialects (Davidson & Wilkinson, 2002). In addition, cultural differences and the transmission of alternate strategies in the use of tools have been found in experiments with chimpanzees (Whiten et al., 2007).

Our study contributes to the growing number of studies on intraspecific population differences in behavior, here showing differential weighting of beacon cues which directly match onto habitat type. Furthermore, ambiguity related to the nature of the heritability of these spatial traits may offer evidence to suggest that divergent evolution is taking place with respect to Belding's ground squirrels in the eastern Sierra. This is in contrast to the more common mode of learned cultural transmission found in other studies of population specific traits.

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