Is landmark use by rock pigeons (*Columba livia*) and pinyon jays (*Gymnorhinus cyanocephalus*) affected by environmental clutter when learning about a goal location?

by

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Abstract

In this thesis, I explored whether and how environmental clutter affects the process in which an animal searches for a goal. Previous research on the spatial learning of birds has suggested that to consistently locate a goal, animals encode specific properties of landmarks. How uninformative objects, or *clutter*, in the search space impacts this landmark-based goal calculation needs further investigation. I examined this topic using rock pigeons (*Columba livia*) and pinyon jays (*Gymnorhinus cyanocephalus*), chosen for their pronounced spatial abilities.

Rock pigeons can return to their loft site when released several hundred kilometers away. and they scatter forage for food. In contrast, pinyon jays move mainly within their home range of approximately 21 square kilometers and are a food-storing bird. Pigeons do not need to remember thousands of locations across seasons, as is the case with the pinyon jays, which rely on accurate spatial abilities to retrieve food hidden several weeks to months earlier. I hypothesized these two species would differ in their use of spatial information when learning the location of a goal site. Specifically, pigeons would use absolute distance information between the goal and surrounding landmarks, whereas pinyon jays would use both absolute and relative distance information. I also hypothesized that pigeons would be more affected than pinyon jays by modifications to the color of landmarks as well as changes in the presence or absence of environmental clutter. The need for pinyon jays to encode spatial information when engaged in food-storing and recovery across seasons, would support the need for a flexible spatial representation, whereas for pigeons, this would not be necessary. I trained the birds to find a goal using an array of four distinctively colored landmarks. For each species, I assigned birds to one of two groups. Whereas the search space for *Group Open* contained just the landmarks and the goal, the search space for *Group Clutter* also contained a set of uninformative objects to simulate environmental clutter. Across training trials, the goal-landmark array rotated and moved across the search space, so that only the landmarks can consistently inform the goal location. Following training, I manipulated experimental parameters using three tests—an expansion of the landmark array (*Expansion test*), removal of the distinctive landmark colors (*Geometry test*), and the addition or removal of environmental clutter (*Reversal test*). I videorecorded where the birds searched for the goal during these test trials to measure their search errors for each experimental manipulation. After training and before testing, the two species in both the open and the cluttered environment searched with similar accuracy. Results from the Expansion test showed that when learning about the goal location, neither species used relative metrics, or to search at the *center* of the landmark array. Instead, rock pigeons searched at a location that interpolated the absolute and relative metrics from adjacent landmarks, in both environments. Moreover, rock pigeons in the cluttered environment used absolute metrics from single landmarks. Pinyon jays exclusively used the absolute metrics from single landmarks in both open and cluttered environments. Results from the Geometry test showed that when the distinctive color information was removed from the landmarks, rock pigeons but not pinyon jays searched with more error in both environments. Results from the Reversal test showed that, for both species, adding clutter to the open environment increased search error, whereas removing clutter from the cluttered environment decreased search error. Findings from the present study suggest that rock pigeons and pinyon jays use different metrics to encode goal-landmark relations, pigeons are more affected by changing the landmarks' color information than pinyon jays, and the abrupt change in environmental clutter impacts search error for both species.

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Chapter 1: General Introduction

Animals need to find food, water, and shelter. To find the location of these essential resources (i.e. a *goal location*), mobile animals must calculate spatial relationships between the goal and stable objects or surfaces of an environment. This process is called *spatial learning*. These objects, referred to as *landmarks*, may have distinctive properties that can be encoded to allow for the reliable and consistent relocation of the desired goal.

Generally, landmark properties can be defined by two categories—*features* and *geometry* (see review by Tommasi *et al.* 2012). Featural information includes the color or texture of an object or surface. For example, a tree may be remembered as a landmark for its red maple leaves. Geometric information includes metrics such as distance, direction, and shape. The relationship among landmarks or between a landmark(s) and a goal can be encoded using *absolute* or *relative* metrics. Using *absolute* metrics would involve learning a compass direction and the Euclidean distance between a goal and a landmark(s). For instance, the location of a food source can be remembered as being 2 m south-west of a particular tree. In the case where multiple landmarks are present, *relative* metrics can also be used to find the goal. Relative metrics involve the spatial relationship between the goal location and the configuration of multiple landmarks (*landmark array*). For example, when four trees are configured in a square shape, and a food source is within the shape and equidistant from each tree, the relative metric of "center" can be used to define the goal from the four trees. Compared to relying on a single landmark, a landmark array may be more informative in locating a goal because multiple vectors informing the goal from different positions can cancel some of the estimation errors that results from each individual landmark. For example, some animals use both a sun-based compass and one or more landmarks to return to a goal (Kelly *et al.* 2019; Wiltschko and Balda 1989). A small amount of error in the compass would increase the error of the directional information from a single landmark (Kamil and Cheng 2001). If the only way the goal was encoded was using a single landmark, then the precision needed to find a small goal would be greatly reduced. If the goal location was encoded using multiple landmarks, then the combined use of landmark configural information and the absolute distance and directional information from each landmark would provide much more information to resist against compass error. Thus, error from using a sun compass can result in a significant decrease in search accuracy when only one landmark is used to encode a goal, but not when multiple landmarks are used to encode a goal (Kamil and Cheng 2001; Kelly *et al.* 2019). Kamil and Cheng (2001) suggested that the redundancy of encoding a goal from multiple landmarks could be a form of adaptation against environmental variation, especially the potential change in landmark availability. If one landmark or a subset of landmarks was removed or rendering uninformative, some spatial information from the remaining landmarks could still be used to find a goal. When learning a goal location, animals can use absolute metrics from individual landmarks and relative metrics from an array of landmarks. The differential use of landmarks may depend on the nature of the spatial task and the environment in which the task is completed.

The environment in which animals must find essential resources is constantly changing. Whether it is due to seasonal shifts (e.g. snowfall) or anthropogenic events (e.g. logging), animals may need to repeat a spatial task in a visually different environment. A *search space* is any section of an environment where an animal can search for a goal using landmarks, such as a laboratory room or a part of the forest floor. For this study, a barren search space that contained only landmarks and a goal was referred to as an *open environment*. In contrast, a search space can also contain other stimuli that does not provide any reliable information about the goal location. For this study, objects that do not provide any information as to the goal location are referred to as *clutter*. Any environment that contains many uninformative objects is referred to as a *cluttered environment*. Although many studies have investigated the use of landmarks during spatial search, few have examined the influence of clutter. Thus, it is unclear whether animals change their landmark-based searching strategies depending on the amount of clutter in their immediate environment. In nature, flexibility in encoding landmarks may be an adaptation to environmental fluctuations over time. Anthropogenic alterations to natural habitats are occurring at a rapid rate, and objects within an environment may be abruptly added, removed, displaced or their characteristics modified. Controlled laboratory conditions provide the opportunity to examine the specific effects of environmental clutter and its fluctuations on the spatial encoding of animals. Insights from studying environmental clutter and spatial information change in controlled settings can support future field studies that aim to inform policy about landscape management. Furthermore, examining two species using the same experimental paradigm helps to resolve whether different results are due to true species differences or experimental differences. Understanding whether and how particular species can sufficiently adapt to rapid environmental changes is important for wildlife management and conservation efforts.

The objective of my thesis is to better understand the influence of environmental clutter on animals' use of landmarks. To do so, I investigated how two species', with differing natural history traits, use of landmarks in an open environment and a cluttered environment. Birds need to repeatedly find food and water sources, as well as nest sites. Pinyon jays rely mostly on the activity of storing and recovering thousands of seeds in various locations. Relocating these *caches* at a later date requires great spatial precision of a few centimeters. Rock pigeons do not store food, rather the food for which they forage is often visually salient (e.g. seed and crop spillage from silos). Both rock pigeons and pinyon jays live in large, long-term flocks of up to thousands of members, and nests are established close together within the colony (rock pigeons: Murton *et al*. 1972; pinyon jays: Balda and Bateman, 1971). Both rock pigeons and pinyon jays must identify and return to their own nest among many nearby nests, and thus each species encodes some form of spatial information to consistently arrive home. Although spatial information such as the position of the sun in the sky coupled with the time of day, can be used to navigate at a broader spatial scale, landmarks can inform navigation at a local spatial scale. While rock pigeons demonstrate superb search accuracy when needing to relocate to a single loft site, pinyon jays achieve extraordinary search accuracy when needing to relocate hundreds of cache sites Therefore, it is possible that spatial tasks performed by rock pigeons in the real world do not require as much precision as the cache-recovery tasks performed by pinyon jays.

I trained individual birds to find a goal using a four-landmark array. Once the birds were accurately and consistently locating the goal, I tested them with trials during which some property of the landmarks or the environment was transformed. I hypothesized that environmental clutter increases birds' error in estimating the goal using landmarks. I also hypothesized that rock pigeons encode absolute metrics from single landmarks as it is a parsimonious strategy for a non-caching species. For the food-caching pinyon jays, I hypothesize that they use both absolute and relative metrics from a configuration of landmarks to encode their numerous cache sites. Lastly I hypothesize that pigeons These hypotheses were generated based on the findings of existing spatial learning research, many of which studied landmark use in birds (Cheng 1988, 1989; Spetch *et al.* 1997; Kamil and Jones 1997; Kamil and Cheng 2001; Jones *et al.* 2002; Kelly *et al.* 2008). The next chapter summarizes the findings from some of these studies as they relate to the current investigation.

Chapter 2: Literature Review

Many previous studies have paved the way for examining the contextual use of landmark properties, using rock pigeons (*Columba livia*) and food-storing corvids (species of the *Corvidae* family). One general paradigm used to understand the mechanism of landmark use is the *spatial search task*, which typically consists of three overall procedural steps (Cheng, 1988; Kelly *et al.* 2008; Spetch *et al*. 1997). First, the subject is trained to search for a food reward at a location that bears a constant spatial relationship to one or more landmarks. The rewarded location is referred to as the *goal*. Second, once the subject is readily approaching and consuming the food reward, this goal is gradually concealed (usually buried or covered), requiring the subject to use surrounding landmarks to relocate it, thus, shifting from the use of visual cues of the food itself, to the use of the spatial relationship between the landmark(s) and the position of the now hidden goal. This is used as a baseline to compare against subsequent tests, the control condition consists of the same landmark set-up as used during training, but without any food reward present. Removing the food reward on control and test trials prevents the use of food-related cues, such as odor, during search. Third, the subject is presented with occasional non-rewarded test trials, in which the food reward is removed and some property of the landmark(s) or environment is changed. The places where the subject searches on these test trials are recorded. The search patterns observed in the control condition (no landmark/environment change) are compared against those in the test condition (with landmark change). The application of this paradigm offers insight into the landmark properties that are used in spatial navigation.

Using this type of landmark manipulation paradigm, Cheng (1988) investigated whether each goal-landmark relationship is encoded when a bird is presented with a multiple landmark array, or if the overall configuration of landmarks is used to determine the goal location. These two possibilities were derived from earlier studies examining landmark use by rodents (Cheng 1986 and Collett *et al.* 1986). Cheng addressed this issue using rock pigeons as they are adept spatial navigators (Keeton 1974; Sasaki and Biro 2017; Collet *et al.* 2021) and have been used in many spatial cognition studies (see review by Cheng *et al.* 2006). First, rock pigeons were trained to find a small well containing food within a wooden box. The goal was hidden underneath a layer of substrate, which required the subject to shift through the substrate to search for the reward. Inside the experimental box, a blue strip of cardboard was attached to the wall nearest the goal. In addition to this landmark, the box's entrance and furniture that occupied the room alongside the box also served as landmarks (Figure 1). In the control condition, the goal did not contain any food reward, and the blue strip remained in the same position as during training. On occasional test trials, the blue strip was moved a specific distance and direction from its original position (10 cm or 30 cm, to the left or the right). When comparing where the rock pigeons concentrated their search between the control and test conditions, Cheng found that rock pigeons shifted their search in the same direction that the blue landmark was moved. During the trials where the blue landmark was displaced at larger distances, the rock pigeons searched at an intermediate position between the goal location as defined by the displaced blue landmark and the goal location as defined by remaining unmoved landmarks. These findings supported the *vector sum model*, which predicted that the animals encoded the location of the goal by computing vectors from the landmarks to the goal. Each vector was recorded from each landmark, with a distance and a direction component. When a landmark shifted, the same distance and direction vector from the landmark as learned during training directed the bird to a location that differed from training, as well as from the location directed by the goal-landmark vectors from the unshifted landmarks. As a result, the three rock pigeons calculated that the goal was positioned between the original location according to the unmoved landmarks and the location according to the shifted landmark. Moreover, the author suggested that the weight given to each landmark-to-goal vector varies among individual birds. In the study, each of the three rock pigeons provided a different pattern of search distribution along the left-right axis as a function of the distance that the blue landmark shifted (10 cm or 30 cm, left or right). One bird shifted its search in a linear pattern with the shifted distance of the landmark up to 10 cm, after which the bird searched at the same position regardless of how far the landmark has shifted. In contrast, the other two birds shifted their search position in a linear pattern with the shifted distance of the landmark until the furthest distance at 30 cm. Furthermore, the latter two birds differed in their slope of shifted position of search as a function of shifted distance of the landmark from the training position. This suggests that individual differences can exist within a species' overall pattern of searching using landmarks.

Figure 1: Layout of the experimental room used in Cheng (1988)

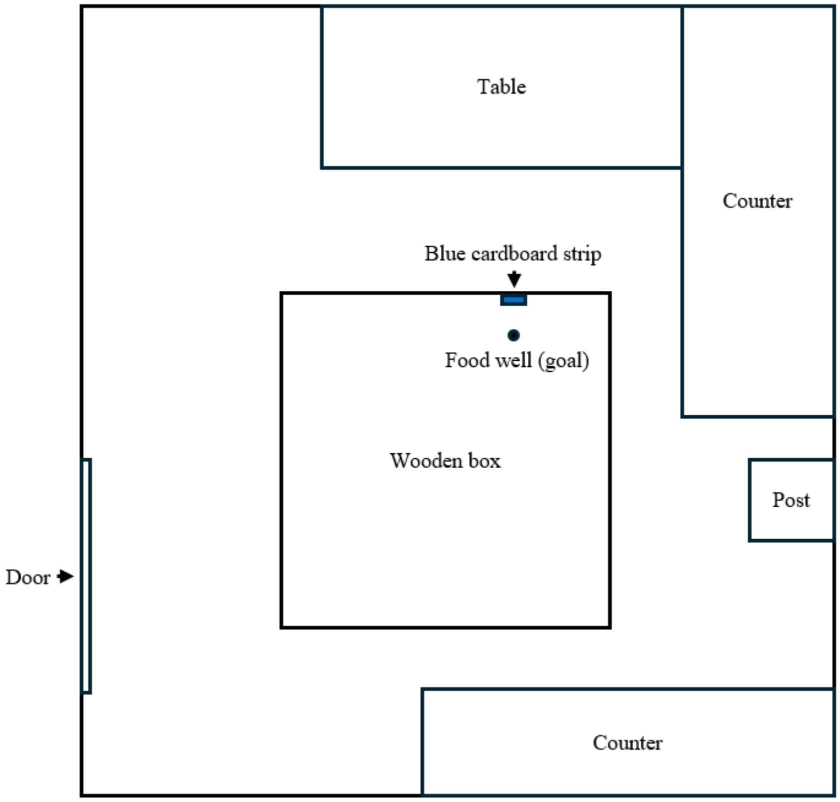


Figure 1: Layout of the experimental room used in Cheng (1988), adapted from the paper.

In a subsequent study, Cheng (1989) provided further evidence of rock pigeons' use of landmark vectors to find a goal. Specifically, the author assessed if each landmark in the array was weighted differently when encoding a goal location, and whether the weighing of a landmark is a function of its distance to the goal. In the study, rock pigeons were trained to find a goal positioned between two distinct landmarks, with one landmark closer to the goal than the other landmark (see Training panel in Figure 2). During landmark-shift tests, both landmarks were moved away from the goal, at the same displaced distance but in opposite directions. The rock pigeons shifted their search along the direction in which the nearer landmark was displaced. However, the distance of the rock pigeons’ shift in searching suggested three strategies were being used. The rock pigeons searched: 1) using only the nearer landmark, 2) by summing the goal-landmark vectors from both landmarks, or 3) at an intermediary position between the two previous strategies (Figure 2). Overall, Cheng found that the rock pigeons encoded the landmarks as independent vectors, which could be used together or separately to locate the goal. Rock pigeons tended to give more weight to the nearer landmark than the farther landmark when searching for the goal, but the weight given to any landmark was flexible to change. The author suggested that animals can use landmarks flexibly, which could be advantageous in situations where any landmark can become less informative or become unavailable due to unexpected changes in the search space.

Figure 2 Illustration of experimental set up in Cheng (1989) during the training, control, and test conditions.

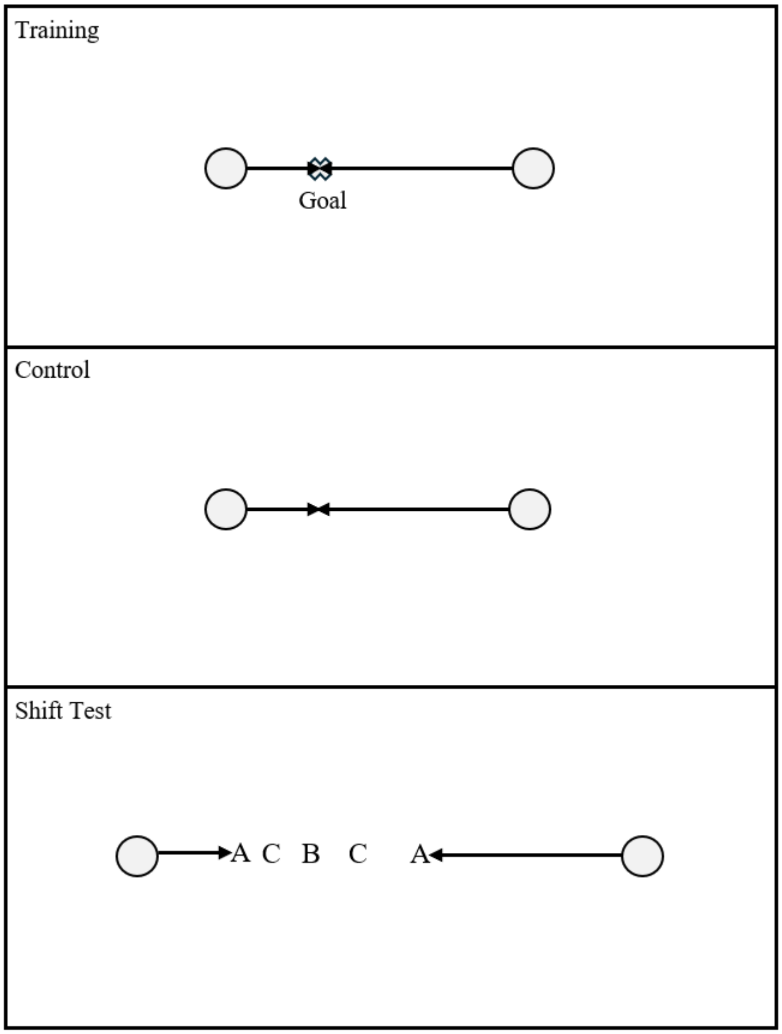


Figure 2. Illustration of experimental set up in Cheng (1989) during the training, control, and test conditions. The circles represent the landmarks. The “X” shape represents the rewarded goal position during training. The arrows represent the goal-landmark vector that can be encoded from each landmark. The letters represent the possible search distributions. “A” represents the search positions informed solely by either landmark. “B” represents the search position informed by the

vector summing of both landmarks. "C" represents the intermediary search positions between using one landmark and using vector summing of both landmarks.

To examine whether rock pigeons use an array of landmarks as an overall configuration, Spetch *et al.* (1997) designed a spatial search task in which a goal was positioned to maintain a fixed spatial relationship with regard to an array of four identical landmarks. The goal was positioned at the center of a hypothetical square formed by four landmarks equidistant from each other. The arrangement of landmarks in the square array made the distance of each landmark to the goal equal, from different cardinal directions. Across training trials, the position of the goal-landmark array varied within the search space. This approach required the rock pigeons to establish the direction of the goal using multiple landmarks from the array, rather than depending on only a single landmark or any external stimuli. To establish the distance of the goal, the rock pigeons could use the absolute distance from one of the landmarks in the array or use the relative distance of the configuration of the landmark array (Figure 3). To parse out which strategy the rock pigeons were using, Spetch and colleagues presented the birds with an *array expansion* test. During this test, the four landmarks were moved the same distance apart from one another. If the rock pigeons used the landmark configuration to derive both its distance and direction to the goal, their search would be concentrated at the center of the array. However, if the rock pigeons used an absolute distance-direction vector from one of the landmarks (or multiple landmarks independently), their search would be concentrated at a location defined by this vector. If multiple independent distance-direction vectors were learned from multiple landmarks, the birds would search at multiple locations defined by this training distance-direction vector. Spetch et al. found that during the test trials, the rock pigeons did not search at the center of the expanded array, suggesting that they did not encode the goal using relative metric information from the configuration of landmarks. Instead, they searched in positions that preserved the absolute training distance from individual landmarks within the landmark array. Findings from this study suggest that when the absolute direction from a single landmark cannot reliably inform the goal, rock pigeons can use multiple landmarks to find the relative direction of a goal. When both absolute and relative metrics can be used to estimate the distance to a goal, rock pigeons prefer to search using the absolute distance from individual landmarks.

Figure 3. Illustration of the experimental arrays used in Spetch et al. (1997).

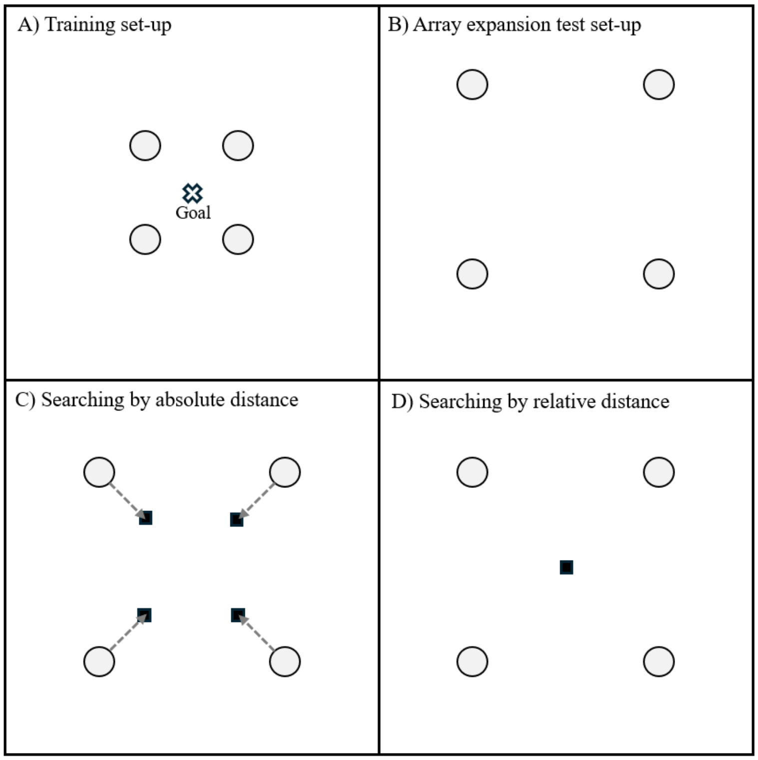


Figure 3. Illustration of the experimental arrays used in Spetch et al. (1997). The circles represent the landmarks. Panel A depicts the landmark array set-up used during training. The "X" represents the rewarded goal location. Panel B depicts the landmark array used during an array expansion test. The black squares in Panels C and D represent hypothetical search concentrations. Panel C depicts the search concentration that results from using the absolute distance from individual landmarks in the array. Panel D depicts the search concentration that results from using the relative distance from the configuration of the landmark array.

Although they have different life history traits to the non-food-storing rock pigeons, species of food-storing birds also demonstrate superb spatial abilities. Food-storing animals have been well-studied for their strong reliance on landmark-based spatial learning, as they make *caches* (hidden sites where the animals have stored their food) during times with plenty of food to provision during times of food scarcity. Clark's nutcrackers are a species of corvid that search for thousands of their caches with high accuracy (Tomback 1980). The birds can consistently find a cache of a few pine seeds, using their slim beaks to accurately locate this hidden target with incredible precision. To find such a small goal, the nutcrackers must make no more than a few centimeters of error. Under laboratory settings, Vander Wall (1982) reported that the nutcrackers can use landmarks to accurately find their goal.

To understand whether the corvid Clark's nutcracker is capable of using relative metric information from multiple landmarks, which might explain their accurate encoding of large numbers of cache locations, Kamil and Jones (1997) trained Clark's nutcrackers (*Nucifraga columbiana*) to find a goal hidden halfway between two landmarks. During training, the goal was always hidden at the halfway point of the hypothetical line connecting two landmarks. However, the inter-landmark distance changed across trials, which forced the birds to use relative distance to locate consistently the goal at the midpoint. Encoding the absolute distance from any single landmark to the goal would not allow the birds to reliably locate the goal across trials. The nutcrackers learned to consistently find the goal, thus demonstrating their encoding of relative distance from the landmark array. When presented with novel inter-landmark distances during test trials, the birds continued to search at the halfway point of the two landmarks. This study suggested that, when absolute metrics cannot be used to find a goal, animals can learn an abstract geometric relationship to establish relative distance. To replicate the Kamil and Jones study and assess the performance of rock pigeons, Jones *et al.* (2002) used a similar two-landmark task that varied the inter-landmark distance across trials and compared the spatial performance of rock pigeons and Clark’s nutcrackers. Both species learned to represent the goal as halfway (a relative metric) between the landmarks. However, the rock pigeons searched with greater error than the nutcrackers, suggesting a species difference in spatial search accuracy.

Kamil and Cheng (2001) presented the *Multiple Bearings Hypothesis* to explain mechanisms that enable Clark’s nutcrackers to achieve such high search accuracy. Specifically, the hypothesis proposed that search precision varies as a function of the number of landmarks and their geometric arrangement. When a goal can be represented by its spatial relationship to multiple landmarks, the directional component of each landmark vector predicts the goal with higher accuracy (less error) than its distance component. Moreover, search precision increases as more landmarks are used to encode the goal. To test the hypothesis, the authors used a computer simulation to test how a 1% or 2% random error (e.g. from a compass) impacts search accuracy. The authors set the independent variable as the number of available landmarks (two, three, or four) that was used to estimate the goal. The results of the simulation indicated that encoding the goal with four landmarks in a square shape reduces search error more than encoding with two or three landmarks.

To see if Clark's nutcrackers would use relative bearings (as reported in Kamil and Jones, 1997) in a different spatial task, Kelly *et al.* (2008) employed a four landmark array similar to the rock pigeon study by Spetch *et al.* (1997). In the study, nutcrackers were trained to search for food hidden at the center of a square landmark array of four landmarks. The goal-landmark array moved across trials, which required the nutcrackers to search using the array configuration. To solve the task, the birds could use both absolute distance information provided by any landmark and relative distance information provided by the landmark array. When presented with an array expansion test (similar to that used by Spetch *et al.* 1997) the researchers found that the birds did not search at the center of the array. The nutcrackers concentrated their searching in positions that preserved the absolute distance from at least one landmark. The findings from this study suggest that when both absolute and relative distance information can be used, Clark's nutcrackers prefer to search by the absolute distance from individual landmarks. This pattern of landmark use contrasts with the pattern shown in (Kamil and Jones, 1997), which demonstrate that Clark's nutcrackers can solve different spatial tasks by using landmarks flexibly. Moreover, when the task can be solved by a simpler rule (i.e. the distance and direction from one landmark) as compared to the more abstract halfway rule, nutcrackers show similar patterns of search to rock pigeons.

Like Clark's nutcrackers, pinyon jays (*Gymnorhinus cyanocephalus*) also remember their cache sites for several months (Ligon 1978). Vander Wall and Balda (1981) observed that pinyon jays cache approximately 20, 000 pine seeds in the pinyon-juniper woodland during the autumn, across their home range of approximately 21 square kilometers (Balda and Bateman 1971).

Throughout the winter and early spring, Ligon (1978) reported that pinyon jays rely heavily on their cached seeds to feed themselves and their young, retrieving up to 90% of their caches. Thus, spatial learning is a biologically important task for the pinyon jays, similar to that of Clark's nutcrackers. Balda and Kamil (1989) compared cache recovery by Clark's nutcrackers and pinyon jays in the laboratory. When the birds were provided seeds to cache in a select number of locations, both species later return to their cache locations with high accuracy. However, changing the number of caching locations affected each species differently. When the number of holes available for caching decreased from 90 to 15, the birds were forced to cache in sites that were further apart from one another. As a result, while recovering their caches in the 15-hole condition, the pinyon jays decreased in their overall search accuracy to a greater degree than the Clark's nutcrackers. The authors suggested that the pinyon jays may be using a different spatial strategy from the nutcrackers to achieve a high search accuracy. For instance, pinyon jays make caches that are closer together than those made by Clark's nutcrackers. Pinyon jays might encode the caches within a cluster by several absolute vectors from a single nearby landmark. In contrast, Clark's nutcrackers tend to distribute their caches more broadly than pinyon jays, so they may encode each cache by its nearest landmark, and the cache sites may be encoded by absolute metrics from different landmarks. During array expansion tests (similar to that used by Spetch *et al.* 1997), the pinyon jays' searching may concentrate in an area associated with the absolute distance of one landmark, whereas the nutcrackers may search in more than one area where each maintains the absolute distance from a different landmark. Currently, little research has been conducted to examine how pinyon jays encode spatial information, particularly how they use properties of an array of landmarks to search.

Landscapes vary in visual complexity because of seasonal changes (e.g. snowfall, new growth in springtime) and anthropogenic events (e.g. infrastructure construction, logging). Most of the previous research used relatively barren (*open*) arenas, which contained just a landmark or a few landmarks and a goal. It is unclear whether the conclusions of landmark-use patterns in these studies would transfer to cluttered search spaces. Within a cluttered search space, animals may need to process many distance-direction vectors from uninformative objects, which may distract from their encoding of the goal with the vectors from informative objects. Moreover, learning multiple landmarks may be advantageous because any single landmark could become less useful (e.g. by displacement) or absent (Kamil and Cheng 2001). Moreover, the geometric stability of landmarks is important to representing a hidden goal by spatial relationships (Biegler and Morris 1993).

The present study explores the effect of environmental cluttering on landmark-based spatial searching strategies. I used rock pigeons and pinyon jays as subjects. Comparing the spatial performance of a food-storing bird (pinyon jay) and a non-storing bird (rock pigeon) may provide insight into the variance between species that employ landmark-based spatial learning for different purposes. Examining how environmental clutter may affect rock pigeons' learning of landmarks can extend the current research on rock pigeons' spatial cognition. Moreover, studying pinyon jays' spatial performance may contribute and update the existing generalizations about specialized food-storing corvids, which are based mostly upon findings in Clark's nutcrackers. In terms of experimental design, Kelly *et al.* (2008) studied Clark's nutcrackers by replicating the paradigm used in the rock pigeon study by Spetch *et al.* (1997). Both studies were able to identify distinctive landmark-based search patterns, which suggests that the approximate parameters used in the two studies can provide adequate resolution to detect the distinctive search pattern of both rock pigeons and pinyon jays. Thus, I replicated this experimental set-up for the current study. I trained the birds to search for a hidden goal using a stable four-landmark array. To measure the effect of clutter on landmark use, I trained one group of birds with clutter (i.e. PVC pipes differing in color from landmarks, whose positions are pseudo-randomized across trials) present in the search space, and another group without.

After the birds learned to consistently find the goal using the landmarks, I presented the birds with a series of tests that altered either the property of the landmarks or the environment. The first was an expanded array test, similar to the methods used in Spetch *et al.* (1997) and Kelly *et al.* (2008). This test identified the overall landmark-based strategies used by each species to encode the goal in each type of environment. The second test removed the distinctive color of each landmark, and tested whether the birds can search accurately using just the geometric configuration of the landmark array. The final test added or removed clutter from the search space, depending on the training condition of each bird. The birds trained in the open environment subsequently searched in the cluttered environment. In contrast, the birds trained in a cluttered environment searched in the open environment. From these tests, I documented the locations searched by each bird as coordinate data and compared the search pattern and search error for differences between species (rock pigeon and pinyon jay) and environmental condition (open or cluttered). I tested five hypotheses: 1) environmental clutter increases the error in estimating the goal using landmarks; 2) pigeons encode absolute distance metrics from a landmark array; 3) pinyon jays encode both absolute and relative distance metrics from a landmark array; 4) pigeons are more affected in search accuracy than pinyon jays by the removal of color information; 5) pigeons are more affected in search accuracy than pinyon jays by abrupt environmental changes.

Chapter 3: Methods

Subjects

Four wild-caught adult pinyon jays (*Gymnorhinus cyanocephalus*; two females and two males) and four adult rock pigeons (*Columba livia*; two females and two males) served as subjects. The pinyon jays were captured as adults with at least one season of caching experience from Arizona, USA, with an estimated age range of 15 – 28 years, and the rock pigeons were bred from racing pigeons in Saskatchewan as well as Manitoba Canada, with an age range of 2 – 10 years. None of the pigeons had any outdoor experience. The sex and age of the birds per group was balanced, but these were not considered as variables in the present study. All birds had previous experience with unrelated tasks but were naïve to spatial search tasks (e.g., pinyon jays: Vernouillet and Kelly 2020; Kelly *et al.* 2023; rock pigeons: Meier *et al.* 2021, Shabro *et al.* 2022). All birds were housed individually in large cages (60 cm × 60 cm × 38 cm, length × width × height) and in two species-specific colony rooms at the University of Manitoba. Both colonies were kept on a 12-hour light/dark cycle with the lights on at 0700 (local time) and maintained at 22°C. This photoperiod reflects spring and autumn for pinyon jays in Arizona and pigeons in Saskatchewan. The birds were maintained at 90% of their ad-lib body weight. The pinyon jays were provided a regular diet consisting of parrot pellets, turkey starter, sunflower seeds, mealworms, peanuts, oyster shells, and a vitamin supplement Prime®. The rock pigeons were provided a regular diet consisting of green peas, yellow peas, millet, milo, oat groat, and corn. All birds had free access to water and grit in their home cage. During the experimental procedures, each species received a different food reinforcement according to their natural diet, pinyon jays were rewarded with pine nuts and rock pigeons with maple peas. This research was approved by University of Manitoba's Animal Care Committee (protocol #F18-042) and has adhered to the guidelines set by the Canadian Council on Animal Care.

Apparatus

To facilitate a direct comparison to the results in Spetch *et al.* (1997), I replicated the size of the arena, landmarks, and landmark array dimensions of that study as closely as possible. Pinyon jays and rock pigeons completed the experiment in two species-specific experimental rooms. These rooms had identical dimensions (3.35 × 3.22 m, length × width) and were illuminated by LED lights controlled from outside of the room. A door (2.18 × 0.92 m, length × width) allowed the experimenter access into the room. Each room contained an opaque sliding window with a 0.65 m^2 opening to give the birds access into the room. Outside of each experimental room, a holding cage was placed flush against the sliding window. Birds were trained to move between the holding cage and the experimental room using this window. The experimental arena within the room was positioned against the corner of the room farthest from the door to allow the experimenter's door to fully open. The arena consisted of a square plywood floor (2.25 × 2.25 m, length × width) and 50 cm high walls made from corrugated plastic. Birds searched across the floor of this arena, which was divided into four equal quadrants to counterbalance the location of the reinforcement: North-West, South-West, North-East, and South-East. Sixty-four crosshairs were evenly marked across the floor, spaced 25 cm apart to serve as reference points for the experimenter to set up the landmarks and the goal in the 8 × 8 matrix (Figure 4). The location of the landmarks and the goal were defined by the 8 rows and 8 columns of the matrix. The floor was covered by a layer of aspen chips (approximately 2 cm thick). Birds used their beaks to sweep through this aspen chip in search of hidden food rewards (when available).

Figure 4: Schematic representation of the experimental arena.

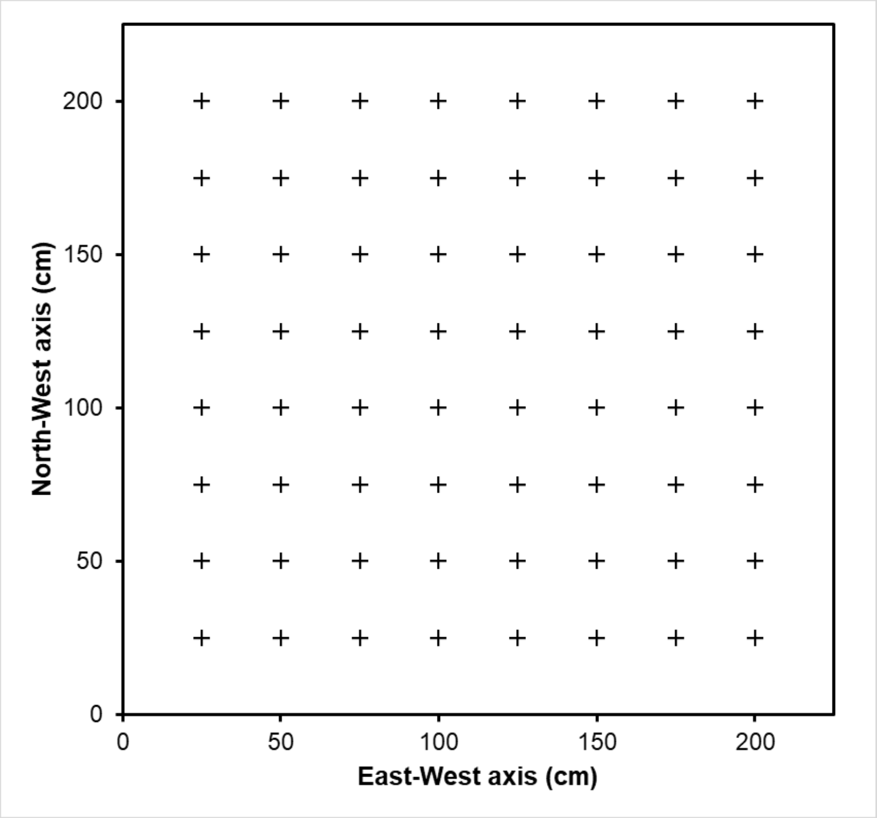


Figure 4. Schematic representation of the experimental arena. The crosshairs (+) depict the possible landmark coordinates.

Four polyvinyl chloride (PVC) pipes (41 cm length, 2.5 cm diameter) served as landmarks. The PVC pipes were spray painted such that one was blue, one yellow, one black, one green, and one gray (see Training section below). Eight additional identical PVC pipes (41 cm length, 2.5 cm diameter) painted dark brown. The location of these identical PVC pipes was variable across trials and therefore did not provide stable spatial information.

A Sony SSC-M393 video camera was mounted in the ceiling above the center of each arena floor. An opening in the ceiling exposed only the camera's lens to the arena. The camera was connected to a monitor and computer located outside of the experimental room from which all experimental sessions were monitored and recorded.

General procedures

Birds were divided into two groups: *group Open* (n = 2 for pinyon jays; n = 2 for rock pigeons) and *group Clutter* (n = 2 for pinyon jays; n = 2 for rock pigeons). For group Open, only the landmark array and the goal was presented in the arena (Figure 5), whereas for group Clutter, the landmark array and the goal was accompanied by seven uninformative cues within the array (Figure 5). Within each group, the birds were tested in three conditions: Expansion, Geometry, and Reversal (see Testing section below). Group Open was trained, and then tested with the Expansion test and Geometry test, without the uninformative cues. During the Reversal test, the birds in group Open were exposed to an identical set-up as the training condition for group Clutter; i.e. the uninformative cues were present in the arena. Group Clutter was trained and tested with the Expansion test and Geometry test, with the uninformative cues present. During the Reversal test, birds in group Clutter experienced the same set-up as the training condition for group Open; i.e. the uninformative cues were not present.

Figure 5. Schematic of the training set-up for group Open and group Clutter

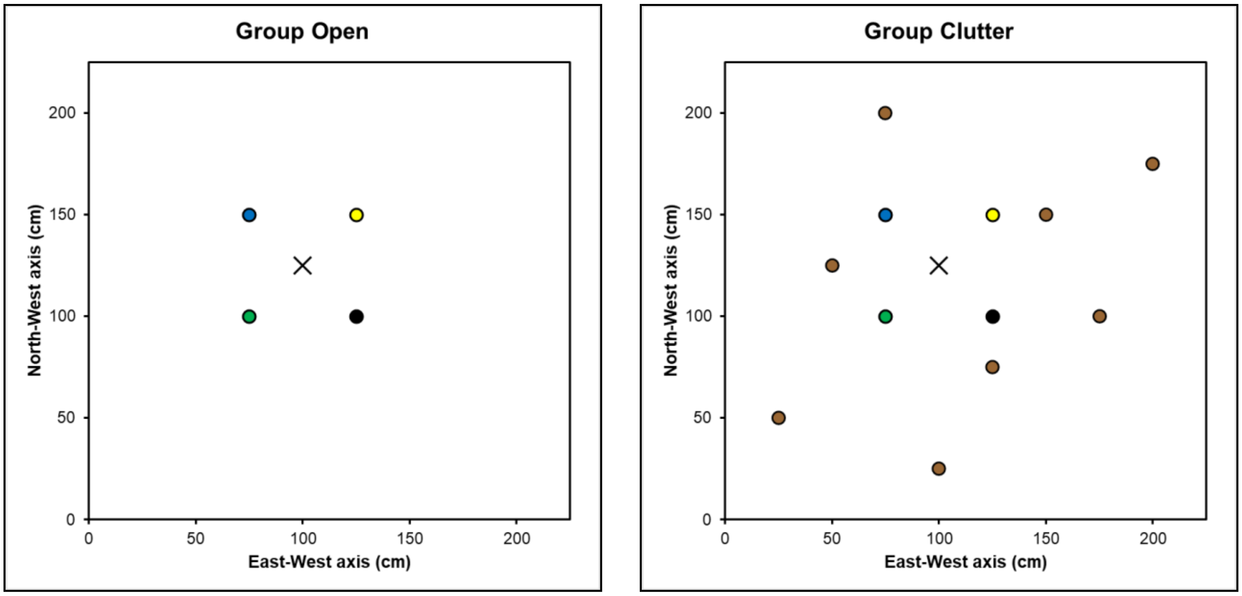


Figure 5. Schematic of the arena set-up for group Open and group Clutter (left and right panel, respectively). In each panel, the blue, yellow, black, and green circles represent the four landmarks. The brown circles (right panel) represent the uninformative cues in Clutter training. The schematics show only one example of a training set-up, as the landmark array was in different positions and rotations throughout the arena across trials. The arrangement of the uninformative cues, when present, differed across sessions.

Birds were transported between their home cage and the experimental room using an opaque ventilated box. Once in the experimental room, the bird was moved into the holding cage which was illuminated by a lamp. Before each trial, all uninformative cues and the goal were placed in predetermined locations, except for during the Familiarization phase in which neither landmarks nor uninformative cues were present (see *Familiarization phase* below). With the spatial relationship of the landmark array and the goal location held constant throughout training and reinforced test trials, the absolute goal location within the room was selected from the 36 possible positions and changed for each trial. The location of the goal was counterbalanced amongst the four quadrants. Moving the landmark array around the room ensured that the subjects could not use geomagnetic or external landmark cues (e.g. experimental room door, fire alarm) to encode the goal location. The landmark array was also rotated on its origin for each trial (the four possible rotations were counterbalanced for each session), but the relative order of the landmarks was fixed. Clockwise, the order of the landmarks was blue, yellow, black, and green. Rotating the landmarks (while maintaining the same color sequence within the array) across trials ensured that the birds cannot exclusively use the absolute distance and direction vectors from a single landmark to reliably locate the goal. To maintain a similar distribution of uninformative cues across sessions, the positions of uninformative cues were determined pseudo-randomly so that there are always two uninformative cues occupying each quadrant and there is never more than one uninformative cue occupying the same row or the same column. The locations of the uninformative cues remained the same across trials within the same session, counterbalanced across sessions and selected without replacement.

Familiarization Phase

To familiarize the birds to the experimental room before training, they were given two familiarization sessions, with two trials per session, one session per day. A bottle cap containing twenty unshelled pine nuts or maples peas was placed on a plate on top of the aspen chip bedding within the arena. The position of this plate was counterbalanced across sessions to ensure an even distribution amongst the four quadrants. No landmarks nor uninformative cues were present during these trials. Each trial ended when the bird retrieved all of the pine nuts or until 20 minutes have elapsed since the start of the trial, whichever occurred first.

Training Phase

The birds were given ten trials per session, one session per day, five days per week. During training, the landmarks were placed 50 cm apart from one another to form a square array with a bottle cap (4 cm diameter) containing two pine nuts or maple peas (herein referred to collectively as the *goal*) depending on species (pinyon jays or rock pigeons, respectively), at the center of the array. Birds were trained to search for the hidden goal using a shaping procedure. During initial stages, the goal was completely visible, but with successive trials the aspen chip bedding will gradually occlude the goal, such that the birds needed to rely on spatial memory to locate its position.

When a bird located the goal within a minute during at least eight out of the ten trials for two consecutive sessions, non-reinforced trials were introduced in the following session. During non-reinforced trials, the goal was absent. Training the birds to search without reinforcement ensured that only the landmarks guided their search, rather than food-related cues such as odor. The birds completed two sessions containing two non-reinforced trials within each session and then two sessions containing four non-reinforced trials within each session. The first trial of each session was always reinforced, and the non-reinforced trials never occurred consecutively. For the purposes of the current study, a *peck* was defined as the location where a bird’s beak contacted the substrate within the arena. Each non-reinforced trial ended when a bird made 20 pecks or 5 minutes elapsed, whichever occurred first. When a bird made a peck within 5 minutes of every trial within one session, for two consecutive sessions, testing began on the following day. The number of training sessions required for each bird to meet these learning criteria were counted.

Testing Phase

Testing was conducted in the same arena as during training. The array location, landmark rotation, and the positions of the uninformative cues changed across trials and was determined in the same manner as during training. Each test session consisted of ten trials. Two of the ten trials were non-reinforced test trials. Two of the ten trials were non-reinforced control trials, which were identical to the non-reinforced training trials. The non-reinforced control and test trials ended when the bird made twenty sweeps or five minutes elapsed, whichever occurred first, by turning off the lights. Six of these ten trials were reinforced and identical to the final training phase (i.e., the rewarded goal was completely buried). The reinforced trials ended when the bird found the food or five minutes elapsed, whichever occurred first. The order in which a bird experienced the trials within a session was determined to ensure that the first and last trial in each test session were always reinforced and that the test and control trials never occurred consecutively. To examine how manipulating the landmark or environmental variables affected searching, a control condition was used as a baseline to compare search performance during the test conditions. The control condition for all three tests consists of the same array was set up as in training, without food reward present.

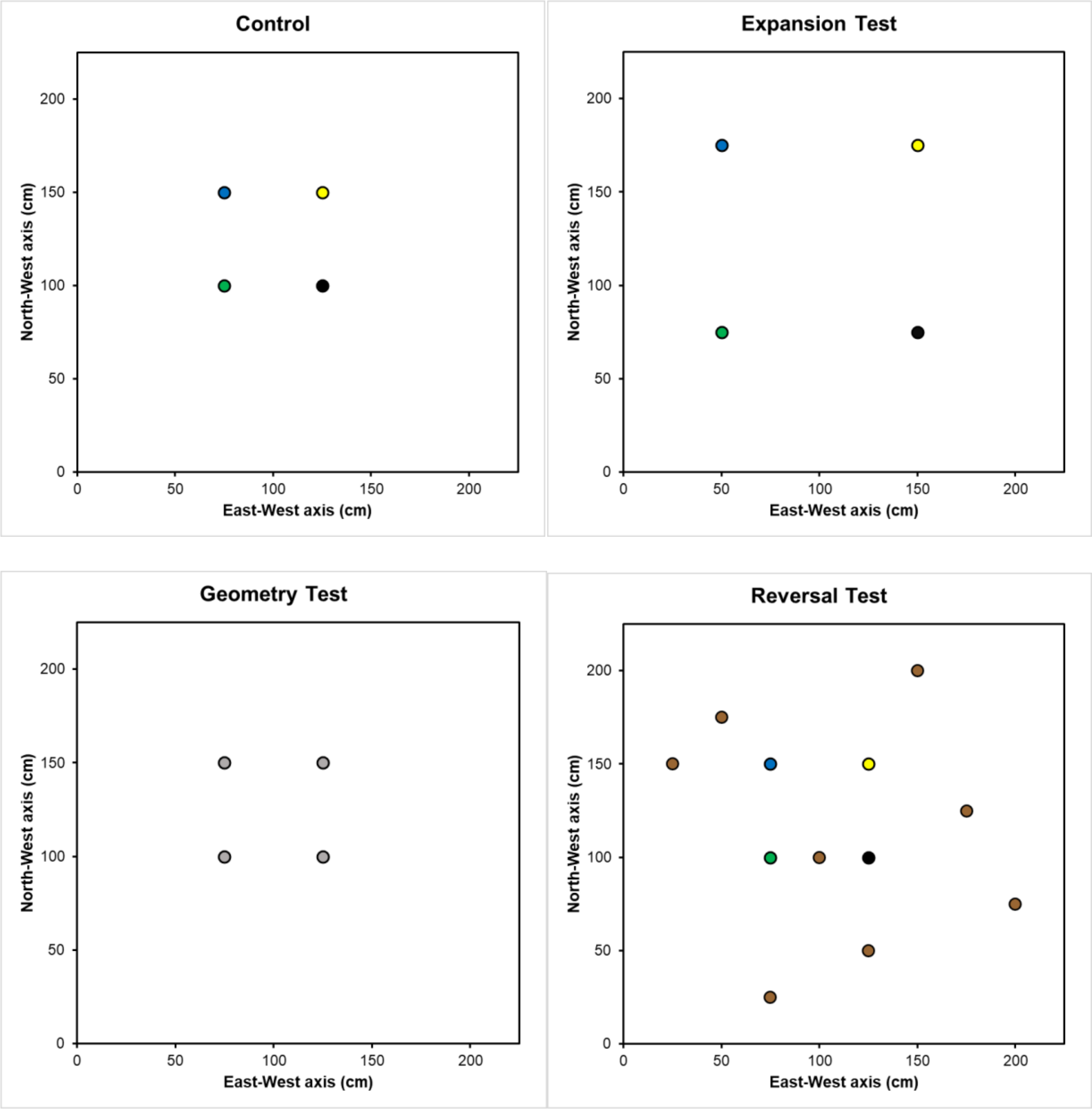
The birds completed the Expansion test, the Geometry test, and the Reversal test in a blocked order. A blocked order of tests with the Expansion test completed first ensured that any search patterns generated during the Expansion test could only be attributed to what the birds have learned about the absolute and relative landmark properties during training. If the Geometry and Reversal tests were completed first, possible learning from the changes to the arena and landmark set-up during these tests could confound the interpretation of their learning from training. The birds completed ten sessions of each test, and each test block was interspersed with two non-reinforced baseline sessions to further reduce the effect of the previous experience on the birds' searching decision in the following test.

During the Expansion test, the birds searched within the arena using the same landmarks but the inter-landmark distance was doubled in the North-South and East-West directions simultaneously in comparison to the training inter-landmark distance (i.e. 100 × 100 cm; Figure 6). The square shape of the landmark array was preserved. This manipulation allowed us to determine the landmark-based metric strategies used by each species.

During the Geometry test, the birds searched within the arena using a landmark array that was the same as the training array, except all four landmarks were uniformly pale gray (Figure 6), to remove the informative featural cues. This manipulation assessed whether the bird has encoded the geometry of the landmark array in the presence of featural cues.

During the Reversal test, the birds searched within the arena that is set up with the opposite condition from training (i.e., a bird that was trained in the open condition will search in the clutter condition, and *vice versa*; Figure 6). During this test, the landmark colors and inter-landmark distances remained identical to that of training, as only the presence or absence of uninformative cues were manipulated. This manipulation simulates abrupt environmental changes resulting increasingly frequently from anthropogenic alterations (e.g. logging), and permitted us to examine the effect of abrupt changes in environmental variability on birds' searching accuracy and overall behavior.

Figure 6: Schematic representations of the landmarks and uninformative cues for group Open



Control

Expansion Test

Geometry Test

Reversal Test

Figure 6. Schematic representations of the landmarks and uninformative cues (if present) in the control condition and each test condition for group Open. In the panels depicting the Control, Expansion, and Reversal conditions, the blue, yellow, black, and green circles represent the four landmarks. The gray circles in the Geometry test (bottom left panel) represent the uniformly colored landmarks. The brown circles in the Reversal test (bottom right panel) represent the uninformative cues. Only one example is shown for each test condition, as the location of the

landmark array changed throughout the arena across trials and the location of uninformative cues (when present) changed across sessions.

Figure 7: Schematic representations of the landmarks and uninformative cues for group Clutter

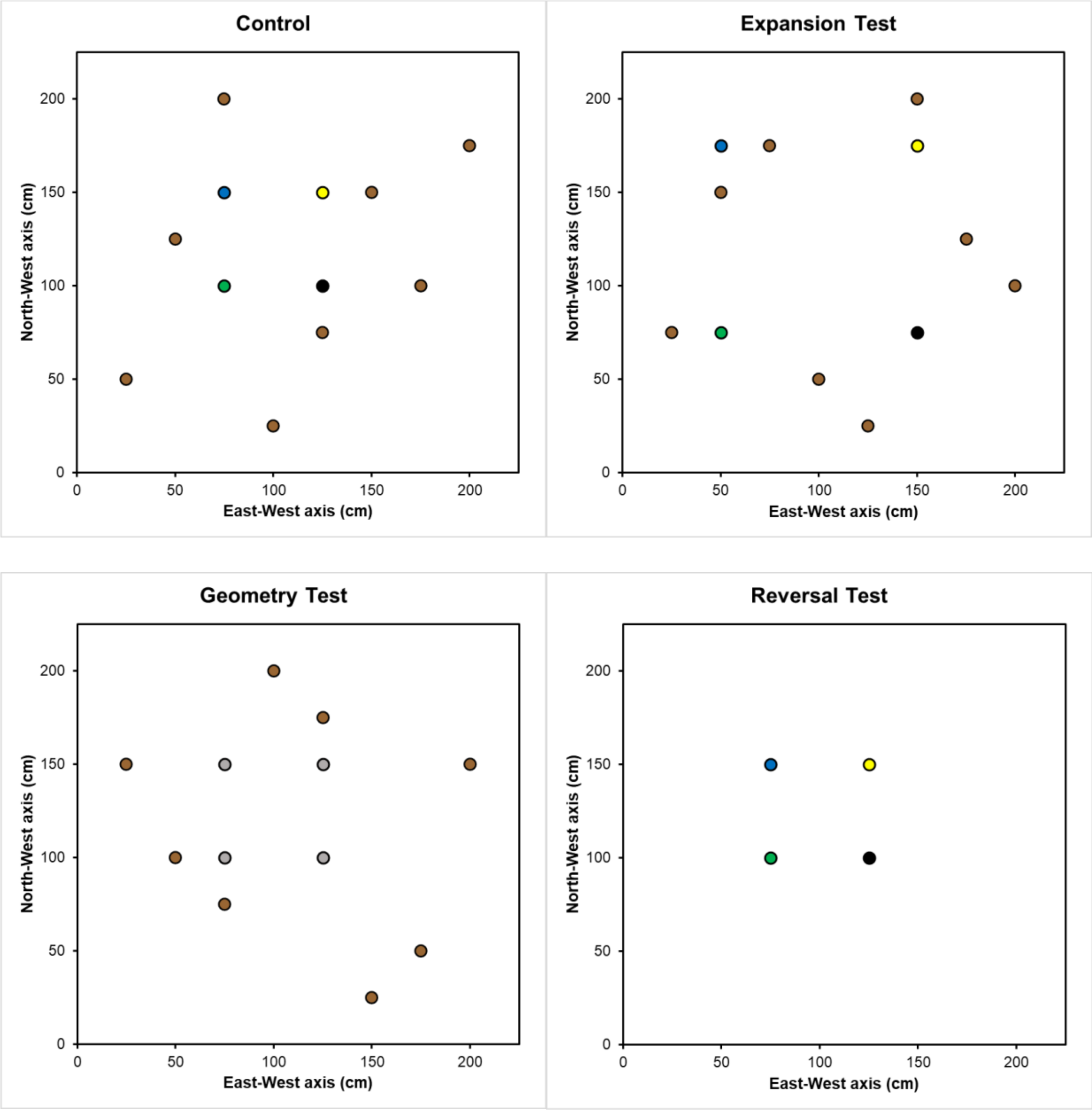


Figure 7. Schematic representations of the landmarks and uninformative cues (if present) in the control condition and each test condition for group Clutter. In the panels depicting the Control,

Expansion, and Reversal conditions, the blue, yellow, black, and green circles represent the four landmarks. In the panels depicting the Control, Expansion, and Geometry conditions, the brown circles represent the uninformative cues. The gray circles in the Geometry test (bottom left panel) represent the uniformly colored landmarks. Only one example is shown for each testing condition, as the location of the landmark array changed throughout the arena across trials and the location of uninformative cues (when present) changed across sessions.

Data recording and analysis

The videos from the testing trials were digitized, and a bitmap was created for each of the first ten probes a bird made in search of the goal. The positions of the probe, the landmarks, the center of the landmark array were converted into x-y coordinates using the application ImageJ. The coordinates were corrected to scale using the representational fraction of the pixel distance to the distance in centimeters on the ground.

For the Expansion Test, the spatial information learned to complete the training task, for which four places of search would correctly preserve the absolute distance from each individual landmark, and preserve the relative direction informed by the landmark array. Thus, the distance of each peck to multiple reference points were required to identify the search patterns. A matrix of 25 reference points, including the landmark coordinates, were evenly distributed across the expanded landmark array (Figure 8: Panel A). For each peck coordinate, the nearest reference point was identified by finding the smallest absolute distance among all the reference points. Pecks are grouped by the nearest reference point and counted. The binomial probability of the number of pecks within each region was calculated, testing against the chance proportion of 0.04

(1/25). If the subjects were systematically searching based on absolute, relative, or interpolated metrics, one or more search patterns should be seen. Figure 8 shows hypothetical areas of search concentration if the birds were using the center of the landmark array, the absolute distance from any one individual landmark within the array, the middle of two adjacent landmarks, or an interpolation of the two-landmark middle rule and the four-landmark center rule (see panels B, C, D and E, respectively). For regions in which subjects searched above chance, the total search error from the reference point was averaged for each bird, and the reference regions that contain above-chance searching were compared within each group.

To examine search accuracy within each of hypothesized regions of concentrated searching, the recorded pecks were first grouped based on the nearest reference point to each peck (see Figure 8 in the Methods section). Then, the total search error was calculated for each peck from the reference point and averaged for each trial. A Kruskal-Wallis one-way ANOVA was used to compare search accuracy across the four groups, for the absolute regions (Figure 9; Panel C), the center region (Panel B), and the interpolated regions (Panel E). The assumptions of the Kruskal-Wallis test are the following: 1) the dependent variable is a continuous measurement, 2) the independent variable consists of two or more independent, categorical groups, and 3) the distribution of each group is similar in shape. The search error data had met all the Kruskal-Wallis test assumptions. Dwass-Steel-Critchlow-Fligner (DSCF) pairwise comparisons were used to further examine the significant results.

Figure 8: Schematic representation of the hypothetical search concentrations within the expanded array of the Expansion Test

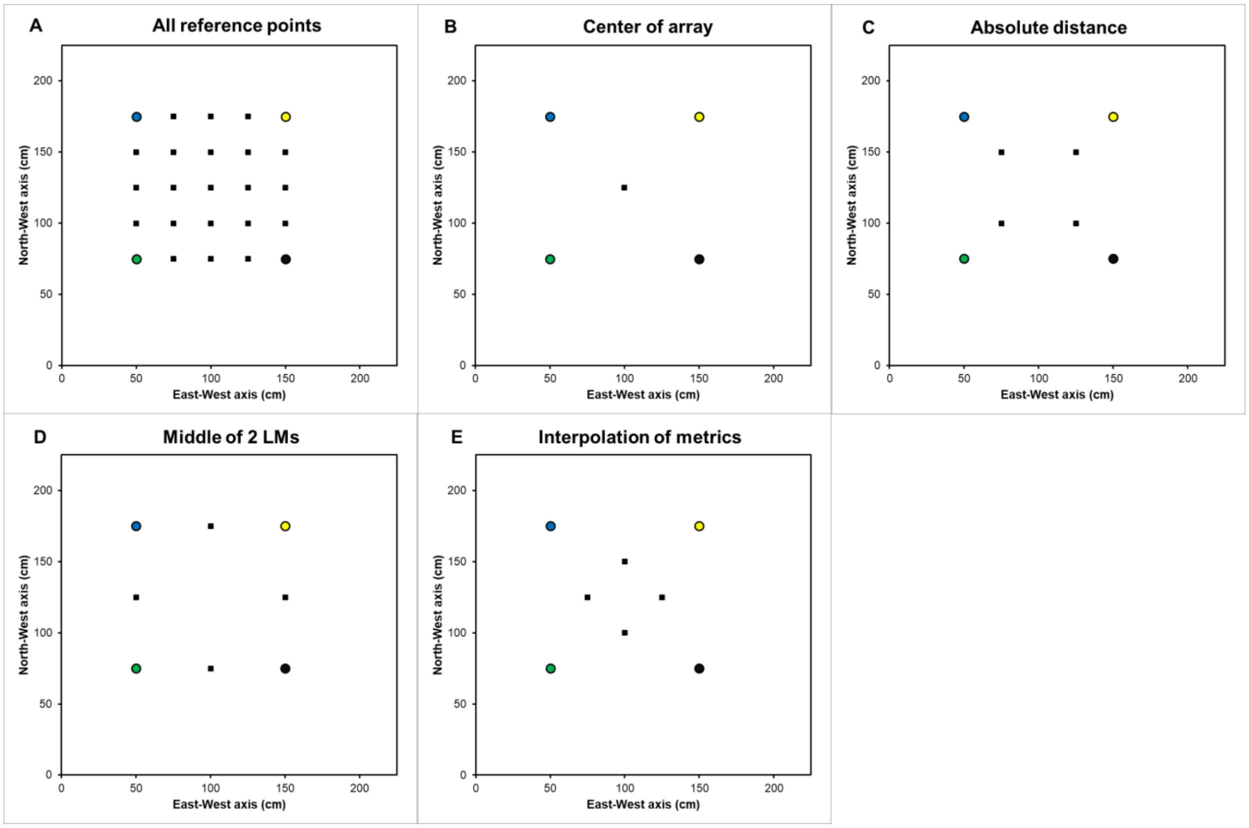


Figure 8. Schematic representation of the hypothetical search concentrations within the expanded array presented on the Expansion test. In Panel A, the smaller black squares represent the reference points from which the distance from each peck is calculated. Subsequent panels depict the patterns if search was governed by the relative center (Panel B), the absolute training distances from individual landmarks within the array (Panel C), the relative middle between two adjacent landmarks (Panel D), and the interpolation of middle and center relationships between the landmarks (Panel E).

The Expansion Test is evaluated differently than the Control condition, as well as the Geometry and Reversal tests. The Expansion Test puts the absolute and relative metrics in conflict, and each metric predicts the goal to be in a different position than the other. Therefore, instead of a single reference point, search accuracy must be examined relative to multiple reference points in the Expansion Test. In contrast, the landmark metrics in the Control condition, Geometry Test, and Reversal Test unanimously predict the goal to be in a single position. Thus, search accuracy was examined relative to one reference point.

For each Control trial, as well as for the Geometry and Reversal test trials, the absolute distance of the first 10 probes from the arena center was calculated using error along the horizontal axis and error along the vertical axis as variables in Pythagorean's theorem (Figure 9). These absolute distances were then averaged for each trial and each group to represent the total search error. Non-parametric Kruskal-Wallis analysis of variance was used to analyze the total search error between groups for each condition (Control and Test) and for the Geometry and Reversal test condition. All significance testing was conducted at $\alpha = .05$.

Figure 9: The calculation of total search error using Pythagorean's theorem

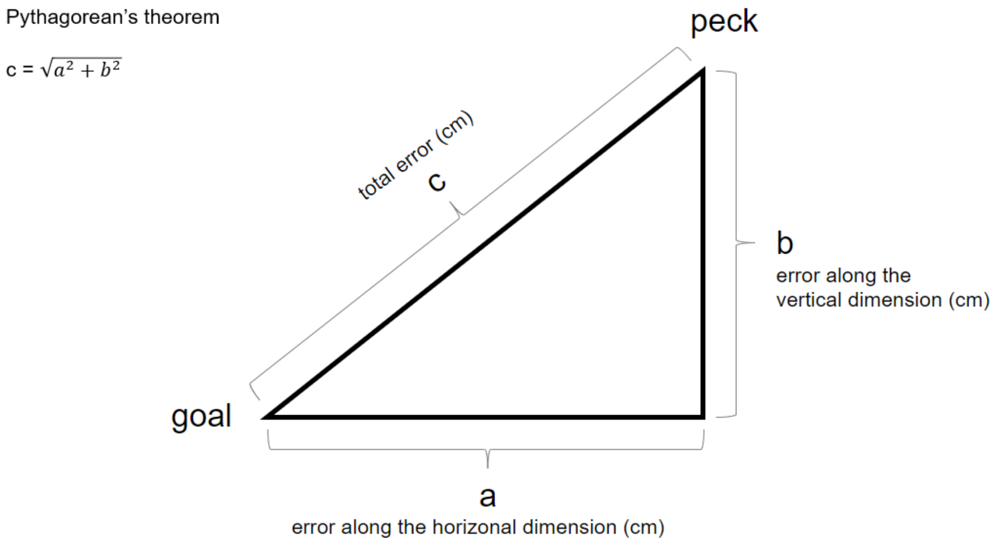


Figure 9. The calculation of total search error using Pythagorean’s theorem.

Chapter 4: Results

Training

The number of sessions to reach training criteria was summed for each subject. The two pinyon jays in group Open required 24 and 48 sessions, whereas the two pinyon jays in group Clutter required 26 and 73 sessions. The two rock pigeons in group Open required 26 and 43 sessions, whereas the two rock pigeons in group Clutter needed 16 and 89 sessions. For all the groups, the large variation in the number of training sessions required to meet criterion offers a preliminary suggestion of individual differences in learning the spatial memory task for this experiment.

To compare search accuracy at the end of training, the non-reinforced trials during the last two training sessions were examined ($n = 8$ non-reinforced trials). For each trial, total error was calculated for each peck using the location of the peck and the goal (i.e. center of the landmark array; Panel B in Figure 8) and then the average of the ten pecks per trial was calculated. Figure 10 shows total error for each group and species. A Kruskal-Wallis non-parametric one-way ANOVA did not detect a difference in total error among the species and groups ($\chi^2 = 4.46$, $df = 3$, $p = 0.216$).

Figure 10: Mean total error during the final non-reinforced training trials

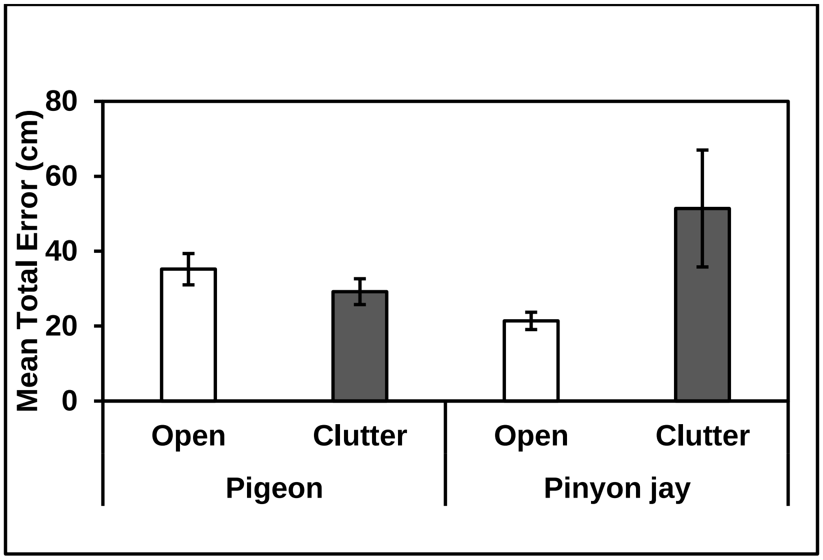


Figure 10. Mean total error during the final non-reinforced training trials by rock pigeons and pinyon jays for groups Open and group Clutter.

Expansion Test

The Expansion Test presented a conflict of absolute and relative metrics in estimating the location of the goal. Figure 11 shows the searched locations of each bird during the test, categorized by group and species. Out of the all the recorded pecks (capping at 10 pecks per trial, 20 trials per bird; (*n* = 200 per bird), most of the searches were in the Interpolated and Absolute regions. The rock pigeons in group Open searched 43% in the Interpolated regions, 20% in the Absolute regions, and 0.07% in the Center region (top left panel; Figure 11). The rock pigeons in group Clutter searched 45% in the Interpolated regions, 36% in the Absolute regions, and 11% in the Center region (top right panel; Figure 11). The pinyon jays in group Open searched 37% in the Absolute regions, 25% in the Interpolated regions, and 4% in the Center region (bottom left panel; Figure 11). The pinyon jays in group Clutter searched 35% in the Absolute regions, 10% in the Interpolated regions, and 3% in the Center region (bottom right panel; Figure 11).

A Kruskal-Wallis one-way ANOVA was used to compare search accuracy across the four groups, for the absolute regions (Figure 9; Panel C), the center region (Panel B), and the interpolated regions (Panel E). Within the absolute regions, a group effect was detected for the mean total error ($\chi^2 = 15.10$, $df = 3$, $p = 0.002$; Figure 12). Subsequent Dwass-Steel-Critchlow-Fligner (DSCF) pairwise comparisons did not find any significant differences between the two groups of rock pigeons (group Open: $M = 22.1 \pm 0.855$; group Clutter: $M = 22.4 \pm 0.846$; $W = 0.178$, $p = 0.999$) nor between the two groups of pinyon jays (group Open: $M = 18.5 \pm 0.876$; group Clutter: $M = 18.8 \pm 0.892$; $W = 0.632$, $p = 0.970$). However, the comparisons showed that the rock pigeons in group Open searched with greater total error than the pinyon jays in group Open ($W = -3.824$, $p = 0.035$). From the visual representation in Figure 8, the rock pigeons in group Open also seemed to search with greater error as compared to the pinyon jays in group Clutter, but this difference failed to meet statistical significance ($W = -3.470$, $p = 0.067$). The rock pigeons in group Clutter searched with greater error than the pinyon jays in group Open ($W = -4.207$, $p = 0.016$) and group Clutter ($W = -3.910$, $p = 0.029$).

Figure 11: Peck frequency on the Expansion Test for each bird.

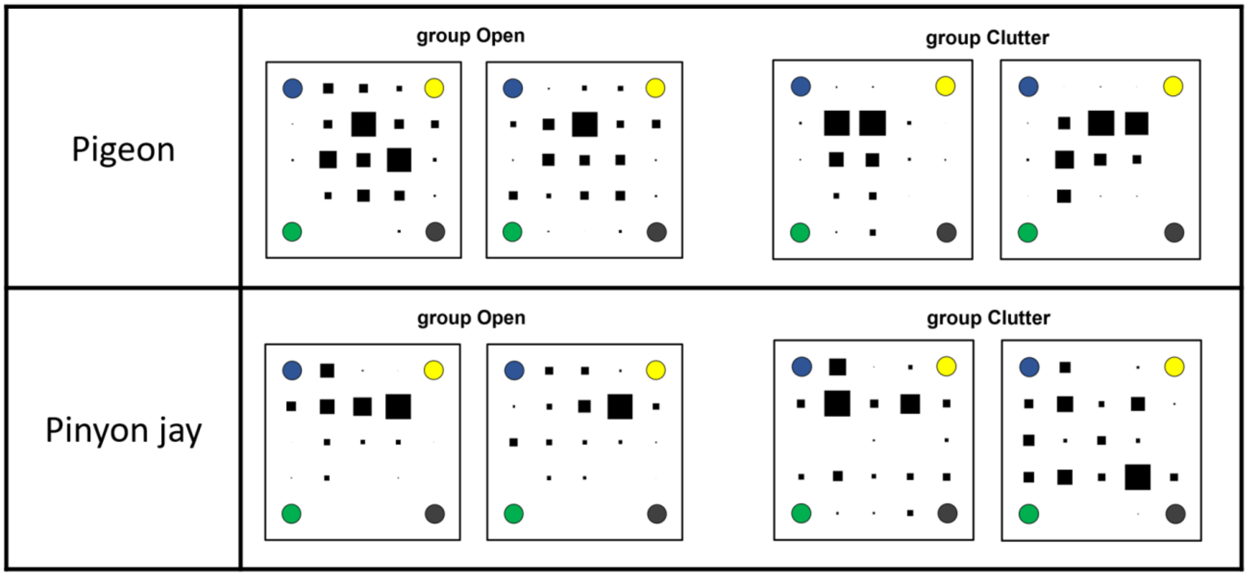


Figure 11. Peck frequency on the Expansion Test for each bird. The circles represent the location of landmarks. The width of the black filled squares is proportional to the instances that each bird pecked within each reference area.

Within the interpolated regions, the two groups of rock pigeons (*Ms* ± *SD* = 19.8 ± 0.61 and 22.4 ± 0.81 for groups Open and Clutter, respectively) did not differ in search accuracy from the two groups of pinyon jays (*Ms* ± *SD* = 20.8 ± 1.02 and 21.1 ± 1.64 for groups Open and Clutter respectively; $\chi^2 = 6.00$, $df = 3$, $p = 0.112$). Within the center region, no differences were found across the four groups (rock pigeons: *Ms* ± *SD* = 20 ± 1.45 and 17.8 ± 2.00 for groups Open and Clutter, respectively, and pinyon jays: 21.9 ± 1.28 and 26.6 ± 2.05 for groups Open and Clutter respectively; $\chi^2 = 6.79$, $df = 3$, $p = 0.079$).

In summary, results from the Expansion test show that, on the one hand, rock pigeons encode both absolute information from distinct landmarks and interpolate absolute and relative metric information to guide their search. On the other hand, pinyon jays seem to rely more on absolute information from distinct landmarks than on relative information. When using only absolute distance from landmarks, the rock pigeons generally searched with more error than the pinyon jays.

Figure 12: Mean total search error made by each group and species within the regions associated with the hypothetical places of search.

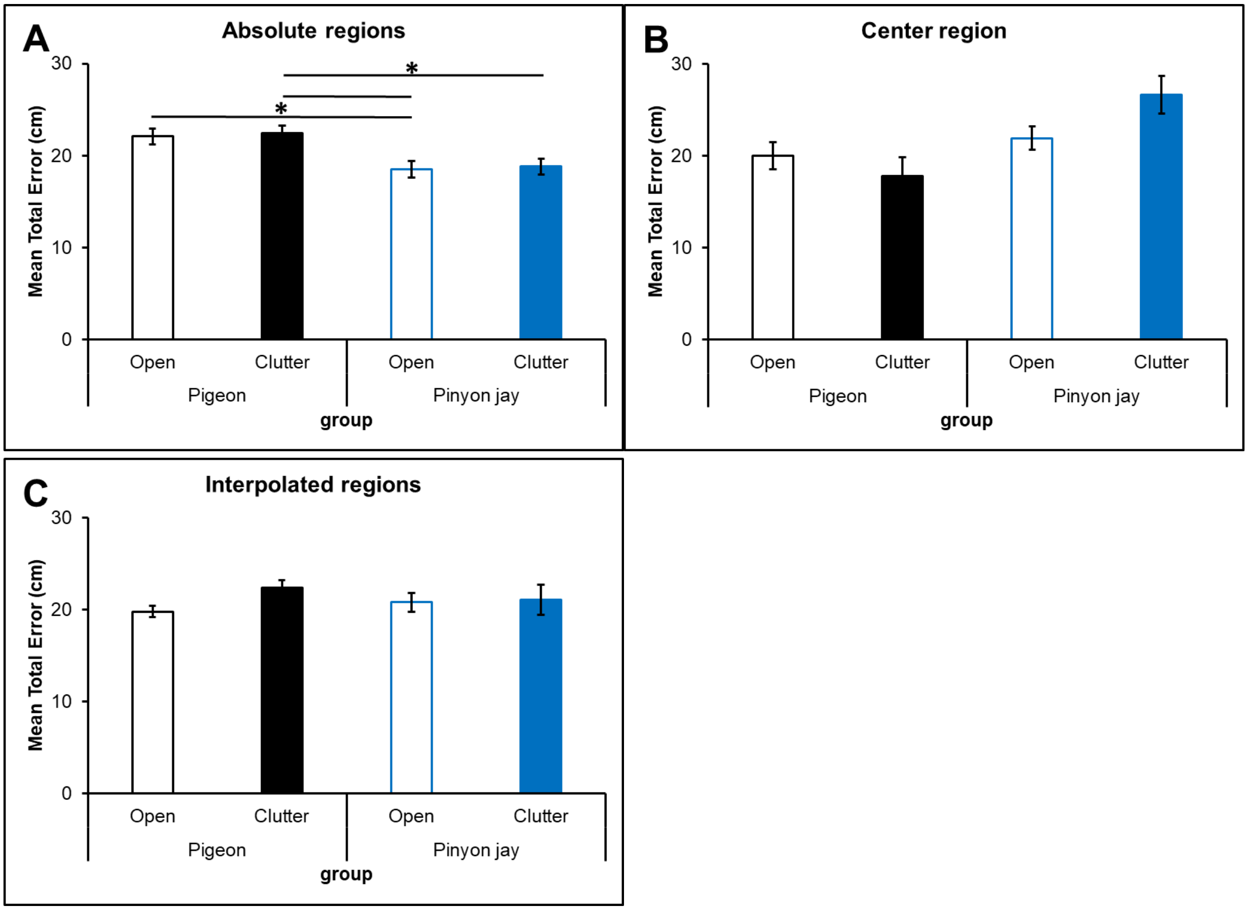


Figure 12. Mean total search error made by each group and species within the search region(s) as predicted by the absolute training distance (A), the relative center rule (B), and the interpolation of the absolute training distance and the middle of two landmarks (C). Statistical significance is indicated by an *.

Geometry Test

The Geometry Test assessed whether the subjects encoded the geometric properties of the landmark array during training. The straight-line distance between the place of search and the center of the array was measured for each peck to represent the total search error (Figure 9). Figure 13 shows within-group comparisons between the control and testing conditions. The Wilcoxon signed-rank test for each group shows that when color information is absent, rock pigeons in group Open ($Ms \pm SD = 50.6 \pm 4.77$) and group Clutter ($Ms \pm SD = 54.9 \pm 5.22$) had significantly greater search error compared to the Control condition when the landmarks had distinctive colors (Open: $Ms \pm SD = 29.2 \pm 2.83$, $W = 175$, $p = 0.001$; Clutter: $Ms \pm SD = 22.4 \pm 2.37$; $W = 66$, $p < 0.001$). In contrast, pinyon jays in both groups did not show significant differences in total search error between the control (Open: $Ms \pm SD = 32 \pm 4.42$; Clutter: $Ms \pm SD = 50.9 \pm 7.1$) and testing conditions (Open: $Ms \pm SD = 23.3 \pm 3.24$; $W = 515$, $p = 0.162$; Clutter: $Ms \pm SD = 69.2 \pm 11.9$; $W = 299$, $p = 0.307$).

Figure 13: The mean total error made during the Geometry Test

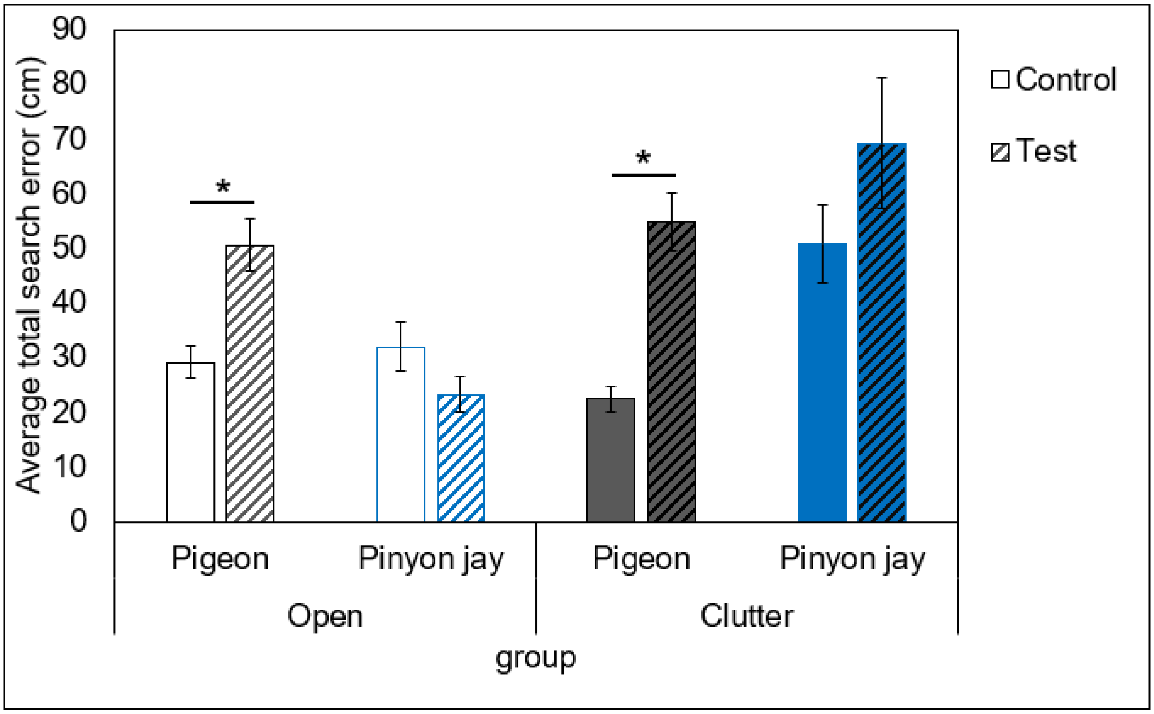


Figure 13. The average total error made during the Geometry Test for the Control condition (landmarks with distinctive colors and the Geometry Test condition (landmarks are all uniformly colored) for each species in each group. Significance level $p \leq 0.05$.

Reversal Test

The Reversal test examined whether the birds would be affected by adding or removing uninformative cues (clutter) within the search space. Figure 14 shows within-group comparisons between the control and testing conditions. The Wilcoxon signed-rank test detected a significant difference in total search error between species and groups. Rock pigeons (*Ms* ± *SD* = 52.8 ± 5.42) and pinyon jays (*Ms* ± *SD* = 69.3 ± 10.98) in group Open made more errors when searching in a cluttered arena as compared to their search in the open arena (Control; Rock pigeons: $Ms \pm SD = 26.3 \pm 2.72$, $W = 117$, $p < 0.001$; Pinyon jays: $Ms \pm SD = 23.8 \pm 2.92$, $W = 105$, $p < 0.001$). In contrast, rock pigeons ($Ms \pm SD = 18.6 \pm 3.67$) and pinyon jays ($Ms \pm SD = 26.7 \pm 3.38$) in group Clutter searched more accurately when tested in an open arena as compared to their searching in the cluttered arena (Control; Rock pigeons: $Ms \pm SD = 23.3 \pm 2.81$, $W = 521$, $p = 0.01$; Pinyon jays: $Ms \pm SD = 57.7 \pm 3.38$; $W = 480$, $p < 0.001$).

Figure 14: The mean total error made during the Reversal Test

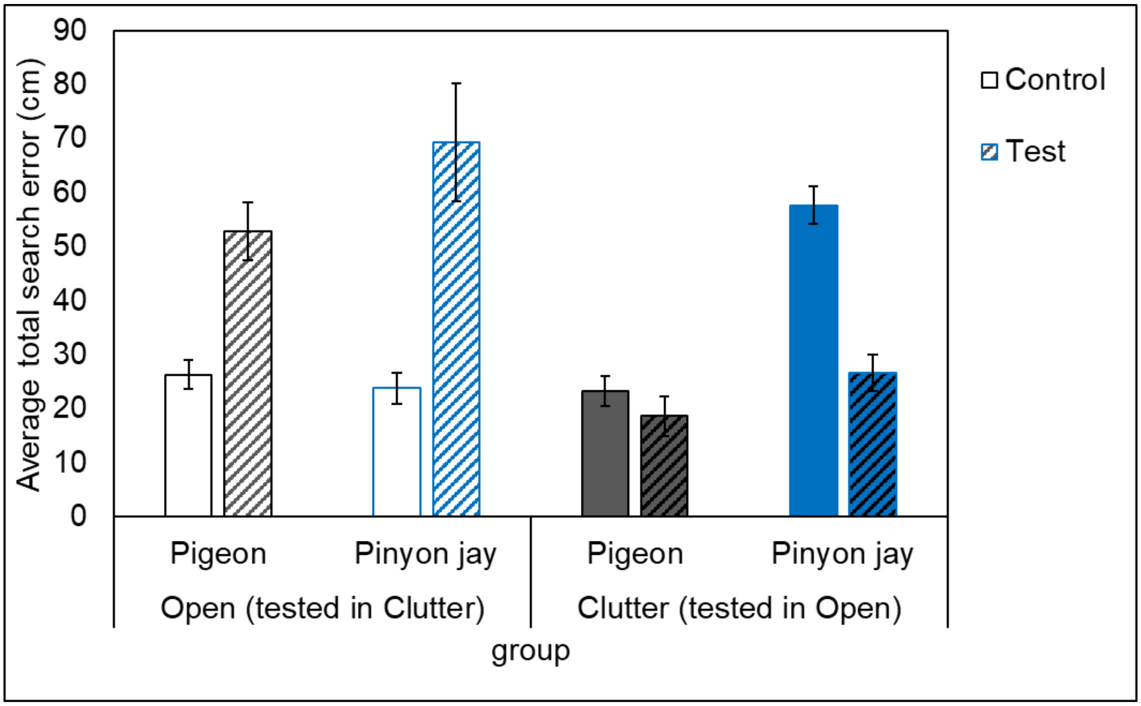


Figure 14. The average total search error made during the Reversal Test. During the Reversal test, the Open group was presented with all the clutter objects surrounding the landmark array, whereas the Clutter group had all the clutter objects removed during these test sessions. The presence or absence of the clutter during Control condition was as in training (i.e., The Open group did not have an extra clutter objects present, whereas the Clutter group had extra cludder objects present) and these trials were non-reinforced. Significance level $p \leq 0.05$.

Chapter 5: Discussion

I examined the effect of environmental clutter on the search strategy and accuracy of the non-caching rock pigeons and caching pinyon jays when learning the location of a goal within a four-landmark array. I also examined whether search accuracy is affected by a change in the color information provided on the landmarks themselves, and by abrupt changes to the environment from the absence of clutter to its presence, and *vice versa*.

Overall, the results of these tests support some species difference. The rock pigeons searched for a location defined by the interpolation of relative and absolute metric information (i.e. using an intermediate of both metrics) more so than the pinyon jays. Furthermore, the rock pigeons that searched in the cluttered environment used absolute metrics from one or more preferred landmarks more than those that searched in the open environment. This group difference was not found for the pinyon jays.

When the unique color of each landmark was removed and replaced with a color that was consistent across all four landmarks, the rock pigeons in both groups made more errors when searching for the goal. However, pinyon jays were not affected by the removal of the landmarks' distinctive color information.

Finally, when the birds were presented with the Reversal Test, in which the birds trained in the open condition were tested in the cluttered condition and *vice versa*. Both rock pigeons and pinyon jays made greater errors when environmental clutter was added, and made lesser errors when clutter was removed. Together, these results suggest that rock pigeons and pinyon jays differ in how they use metric information from landmarks, as well as their sensitivity to changes in landmark color information. Moreover, abrupt addition and removal of environmental clutter affects the accuracy of both species in searching for a goal using a landmark array. Findings of the present study addressing each of the five hypotheses are summarized in Table 1.

Table 1: Summary of findings addressing each hypothesis of the study.

Hypothesis	**Findings**	**Hypothesis supported?**
Environmental clutter increases error in estimating goal using landmarks.	Both species in both groups searched with similar accuracy at the end of training.	No
Pigeons encode absolute distance from individual landmarks in an array.	Pigeons interpolated absolute and relative distance metrics in both environments. Pigeons searching in the cluttered environment also used absolute distance from single landmarks independently.	Partially supported
Pinyon jays encode both absolute and relative distance metrics from the landmark array.	Pinyon jays used absolute distance from individual landmarks to search in both environments.	No
Pigeons are more affected than pinyon jays by the removal of landmark color information.	Removing color information decreased the search accuracy of pigeons, but not pinyon jays.	Yes
Pigeons are more affected than pinyon jays by a change in environmental clutter.	Adding environmental clutter induced greater search error in both species. Removing environmental clutter decreased search error in both species.	No

Table 1. Summary of findings addressing each hypothesis of the study.

Metric encoding

Both rock pigeons and pinyon jays are clearly capable of learning the location of a hidden goal using multiple landmarks. The results of the Expansion Test show that rock pigeons and pinyon jays differ in their use of a configuration of landmarks. Neither species, regardless of training condition, showed a tendency to search in the center when the training array was expanded. This aligns with previous findings by studies that used similar spatial tasks (Kelly *et al.* 2008; Spetch *et al.* 1996, 1997) with rock pigeons and another food-storing bird (Clark's nutcracker). All four rock pigeons searched mainly by interpolating absolute and relative metrics. Interpolation of the two metrics in the Expansion Test was demonstrated by rock pigeons searching in between the locations as predicted by using either absolute distance from single landmarks or relative distance from the configuration of the array. This distribution of searching is similar to the findings of Cheng (1988; 1989), in which the rock pigeons also searched between the location as predicted by a shifted landmark and the original position as predicted by one or more unshifted landmarks. However, this search pattern contrasts somewhat to the findings from Spetch *et al.* (1997), which reported that rock pigeons estimated the distance to the goal only by using the absolute metrics from individual landmarks to the goal. The present results show that, in addition to using absolute metrics, the rock pigeons were able to encode relative metrics. Whereas Spetch and colleagues (1996; 1997) concluded that rock pigeons do not learn the abstract concept of "middle", the tendency of the rock pigeons in the current study to search at a place intermediate of two adjacent landmarks and the array center suggests that a "middle" or "center" concept was used. A possible reason for this discrepancy is the distinctive colors of the individual landmarks used in the present study, in contrast with the identically colored landmarks used during previous studies. When landmarks have distinctive colors, the birds may identify and rely on a subset of the array to establish goal distance. With color information available to distinguish between individual landmarks, it may have been easier for the rock pigeons to incorporate the relative distance metric when two landmarks were used instead of four. A previous touchscreen experiment (Spetch and Mondloch 1993) reported similar findings using landmarks with distinctive colors and shapes. The authors trained rock pigeons to consistently peck at a place on a vertical computer screen, with the goal-landmark array presented in various locations across trials. Among the four landmarks in the array, one landmark was positioned further from the goal than the rest. When presented with landmark-manipulation tests that involved shifting one of the four landmarks out of its configural position or presenting a single landmark in isolation, the rock pigeons searched more accurately when one or two landmarks were present and less accurately when the same landmark(s) were absent. While individuals differed in the landmark that they gave the most weight to, based on the landmark's color, none of the rock pigeons depended on the furthest landmark to search accurately. This result suggested that rock pigeons prefer landmarks that are closest to the goal and use one landmark or a subset of landmarks over others in the array based on its distinctive color. Furthermore, the individuals differed in their preferred landmark color. This conclusion is further supported by the results from the Geometry Test of the present study. When the distinctive colors of each landmark in the training array were replaced by a novel color for all the landmarks, the rock pigeons searched with greater error. These findings concur with the conclusions from Kelly (2010) that landmark features such as color can improve the use of geometry in a spatial memory task. However, in contrast to Kelly's study using Clark's nutcrackers, the heavy reliance on landmark color information was not seen with the pinyon jays. In the current study, pinyon jays did not search with significantly more error when the distinctive landmark colors were removed.

Taken together with the Kelly study, the current findings suggest that species vary in their use of color information in goal estimation, even within the same taxonomic family.

In contrast to rock pigeons, the pinyon jays in the present study did not search extensively at locations that suggest the interpolation of absolute and relative metrics. Instead, the jays searched mainly by using only the absolute metrics from single landmarks. This search pattern suggests that pinyon jays strictly encoded the distance to the goal from individual landmarks and encoded the direction to the goal from the configuration of multiple landmarks. This is similar to the findings in a study of another corvid (Kelly *et al.* 2008), in which the Clark's nutcracker also searched by using absolute rather than relative distance on array expansion tests. Although both species of Corvids seems to exclusively use individual landmarks to judge distance in the four-landmark array searching task, the studies using two-landmark arrays (Kamil and Jones 1997) shows that corvids are nevertheless capable of encoding relative distance to find a goal, when absolute distance cannot be used. Kamil and Jones (1997) trained Clark's nutcrackers with the goal positioned halfway between the hypothetical line connecting the landmarks. Across the training trials, the inter-landmark distance changed, but the goal could always be found at the halfway point between the two landmarks. As the absolute distance vector from one trial could not inform the goal location in the next trial, the nutcrackers could not depend on the absolute metrics to encode the goal. When presented with tests using new inter-landmark distances, the nutcrackers searched mainly at the halfway point between the two landmarks. In addition to the ability to learn a relative halfway rule, Kamil and Jones (2000) further showed that Clark's nutcracker can learn the relative concept of "quarter". These studies demonstrated that at least one corvid species is capable of judging distance by a configuration of the landmarks. The experimental paradigm used in the present study did not vary the inter-landmark distances during training. By preserving both the absolute and relative distance metrics from the landmarks to the goal, the birds could find the goal with either or both strategies. If a future experiment used a similar four-landmark square array design but varied the inter-landmark distances, I predict that both rock pigeons and pinyon jays would search at the center of the landmark array when the landmarks are manipulated in a way that put absolute metrics in conflict with relative metrics. In terms of species differences in search error, the between-species comparison in the Expansion Test supports my hypothesis that rock pigeons search with more error than the pinyon jays. Within the region associated with the use of absolute distance from each landmark, the rock pigeons searching in the open environment made greater errors than both groups of pinyon jays. The superior search accuracy by corvids was also reported in Jones *et al.* (2002), which found that Clark's nutcracker outperformed rock pigeons in search accuracy on a landmark-based spatial task in an open arena. The present study extends our knowledge of whether this species difference in search accuracy translates to a different environment and experimental condition, and suggest that in both open and cluttered environments, corvids search more accurately than rock pigeons in a landmark-based spatial task. This species difference in search accuracy may be associated with differences in natural history. Pinyon jays find their thousands of caches of food by searching for each one within a few centimeters of error. Rock pigeons do not make caches, and the location of their food source is often visually salient (e.g. seeds, crops, insects above ground). Rock pigeons learn spatial relationships to return to a single loft site, which is several times larger than each of the pinyon jays' caches. Therefore, it is possible that spatial tasks performed by rock pigeons in the real world do not require as much precision as the cache-recovery tasks performed by pinyon jays.

Effect of environmental clutter

The results from the current study also suggest that environmental clutter has both a species-specific effect on landmark-based searching strategy and an overall effect on search accuracy. During the Expansion Tests, the rock pigeons searched extensively in locations associated with absolute distances from individual landmarks in the cluttered environment but not in the open environment. This suggests that when clutter is present in the search space, rock pigeons may prefer to rely on a distinctively colored landmark and estimate its absolute distance to the goal. In a cluttered environment, additional vectors from uninformative cues to each other and to landmarks may increase the cognitive load and distract from the animals' use of goal-landmark vectors. Identifying a single distinctive landmark and using its goal-landmark vector to search may be easier than identifying multiple landmarks among the uninformative cues. Future research should investigate whether this difference in rock pigeons' search pattern between open and cluttered environments extends to real world search spaces. For example, a similar landmark array can be established on the flat roof of a building and an operating junkyard. On one hand, an open, relatively unoccupied building roof can represent the open arena in the current study. On the other hand, the junkyard, with the constant addition and removal of objects, can represent the conditions of the cluttered arena. Replicating the present study paradigm at a larger scale outside of the laboratory can provide the opportunity to study how environmental clutter can interact with other stimuli (e.g. acoustic noise) to affect landmark metric encoding. Rock pigeons can be reinforced with food rewards to search at a particular location informed by only the landmark array. A subsequent array expansion test can compare the birds' landmark-based search strategies to the findings of the current study.

Unlike the rock pigeons in the present study, the pinyon jays did not use an additional strategy to search in the cluttered environment. Instead, they maintained the use of absolute distance from single landmark whether clutter in present or absent in their search space. This result reflects the food-storing corvids' transfer of landmark-based searching strategies to different environments. The pinyon jay's natural habitat can vary in the degree of environmental clutter across time. For example, the rocks and branches that can be seen across the forest floor when pinyon jays make their caches during autumn are often covered by a uniform layer of snow when the caches are recovered during winter and early spring. The pinyon jays could have adopted a spatial strategy that efficiently solves the task regardless of any uninformative cues within the search space. Specifically, pinyon jays may prefer to learn a single distinctive landmark to estimate the distance to the goal because it is faster to make a distance estimate from a single landmark than from multiple landmarks. Pinyon jays live in large flocks of hundreds (Balda and Bateman 1971). As a flock moves together throughout the forest when making and recovering caches, each member has a limited amount of time to complete the spatial task before rejoining the flock and moving to the next location. The pinyon jays may cope with the short windows of time allotted for each spatial task by establishing the general direction of the goal from multiple landmarks and establishing the distance to the goal by absolute metrics from one landmark. Keeping track of multiple landmarks to apply a relative distance rule may take more time than allotted to complete the task. Thus, the robust control by absolute distance metrics in both experimental conditions is not unexpected. Pinyon jays can be further examined in their landmark use across a larger spatial scale by using the previously described experimental design for rock pigeons, except the experiment would be set up in open and dense forest spaces, for example.

The comparison of search error in the Reversal Test demonstrates that both rock pigeons and pinyon jays searched with greater error in the cluttered condition than in the open condition. This difference in search accuracy was detected regardless of whether the birds were trained in the open environment or the cluttered environment. When using metric information from landmarks, both species may have experienced some difficulty in ignoring the uninformative objects in the search space. Thus, the results support the hypothesis that the presence of uninformative environmental information increases search error. The presence of clutter in the searching environment has a species-specific effect on the landmark-based metrics that animals use to compute a goal.

The present study is among the first to examine the landmark use in pinyon jays, which provided more insight into how spatial learning is generalized across food-storing corvids, as well as the ways in which related species differ in spatial processing. Comparing the food-storing pinyon jays and the non-storing pigeons in the same experimental setting helped to separate the differential spatial performance due to ecological differences from those that are due to experimental differences. By controlling for non-landmark navigational cues in the laboratory, the present study conducted a rigorous investigation of environmental clutter as an independent variable on the encoding of landmark-based spatial information. These findings provide evidence that suggest rapid landscape modifications may require species to shift in their processing of spatial information when needing to relocate to important positons, such as food stores, nest sites or areas of nourishment. The information gained through the experiments conducted in this thesis, combined with our current understanding of landmark spatial cognition both in the laboratory and in the field, further our understanding how storing and non-storing birds respond to environmental changes, supporting future evidence-based policies for landscape management and wildlife conservation.

Limitations and future directions

Statistical power was limited by the small sample number of each species and group. However, the apparent distinctions in landmark use and search accuracy between rock pigeons and pinyon jays, and between open and cluttered environments, suggests a species effect and an effect of environmental clutter on landmark-based spatial learning. Moreover, this study used a uniform set of objects to simulate environmental clutter and it is unclear whether these items completely reflect the cluttered environments of the real world, which are often comprised of uninformative objects that vary vastly in featural and geometric properties. Future studies can explore the use of more naturalistic objects, such as tree trunk sections, at larger spatial scales. Nevertheless, the clutter stimuli used in the current experiment significantly impacted the search accuracy of rock pigeons and pinyon jays and the search strategy of rock pigeons. Based on the results from this study, subsequent studies of the role of environmental clutter on spatial performance can assess if a set of distinctive clutter objects has a larger impact on spatial searching than a set of uniform clutter objects.

Conclusion

This thesis has shown that rock pigeons and pinyon jays differ in how they use landmarks to estimate the distance of a goal location. When a spatial task can be solved by using both absolute and relative distance, rock pigeons learned to interpolate the two metrics whereas the pinyon jays relied on the absolute metrics from individual landmarks as their exclusive strategy. The presence of environmental clutter reduces the search accuracy of both species, suggesting that the varied visual nature of natural habitats impact animals' learning of spatial relationships. Findings from the present study support the previous research on the landmark use of rock pigeons and provide one of the first reports on the use of landmarks by pinyon jays. Future studies should examine whether the variance in the properties of uninformative objects impacts the landmark-use and search accuracy of animals in a cluttered environment.

References

Balda, R. P., & Bateman, G. C. (1971). Flocking and Annual Cycle of the Piñon Jay, Gymnorhinus cyanocephalus. *The Condor*, *73*(3), 287–302.

Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery by three corvid species. *Animal Behaviour*, *38*(3), 486–495.

Biegler, R., & Morris, R. G. M. (1993). Landmark stability is a prerequisite for spatial but not discrimination learning. *Nature*, *361*(6413), 631–633.

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, *23*(2), 149–178.

Cheng, K. (1988). Some psychophysics of the pigeon's use of landmarks. *Journal of Comparative Physiology A*, *162*(6), 815–826.

Cheng, K. (1989). The vector sum model of pigeon landmark use. *Journal of Experimental Psychology: Animal Behavior Processes*, *15*(4), 366–375.

Cheng, K., Spetch, M. L., Kelly, D. M., & Bingman, V. P. (2006). Small-scale spatial cognition in pigeons. *Behavioural Processes*, *72*(2), 115–127.

Collet, J., Sasaki, T., & Biro, D. (2021). Pigeons retain partial memories of homing paths years after learning them individually, collectively or culturally. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1963), 20212110.

Collett, T. S., Cartwright, B. A., & Smith, B. A. (1986). Landmark learning and visuo-spatial memories in gerbils. *Journal of Comparative Physiology A*, *158*(6), 835–851.

Jones, J. E., Antoniadis, E., Shettleworth, S. J., & Kamil, A. C. (2002). A comparative study of geometric rule learning by nutcrackers (*Nucifraga columbiana*), pigeons (*Columba livia*) and jackdaws (*Corvus monedula*). *Journal of Comparative Psychology*, *116*(4), 350.

Kamil, A. C., & Cheng, K. (2001). *Way-Finding and Landmarks: The Multiple Bearings Hypothesis*. *204*(1), 103–113.

Kamil, A. C., & Jones, J. E. (1997). The seed-storing corvid Clark's nutcracker learns geometric relationships among landmarks. *Nature*, *390*(6657), 276–279.

Kamil, A. C., & Jones, J. E. (2000). Geometric rule learning by Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes*, *26*(4), 439–453.

Keeton, W. T. (1974). The Mystery of Pigeon Homing. *Scientific American*, *231*(6), 96–107.

Kelly, D. M. (2010). Features enhance the encoding of geometry. *Animal Cognition*, *13*(3), 453–462.

Kelly, D. M., Cheng, K., Balda, R., & Kamil, A. C. (2019). Effects of sun compass error on spatial search by Clark's nutcrackers. *Integrative Zoology*, *14*(2), 172–181.

Kelly, D. M., Kippenbrock, S., Templeton, J., & Kamil, A. C. (2008). Use of a geometric rule or absolute vectors: Landmark use by Clark's nutcrackers (Nucifraga columbiana). *Brain Research Bulletin*, *76*(3), 293–299.

Ligon, J. D. (1978). Reproductive Interdependence of Pinon Jays and Pinon Pines. *Ecological Monographs*, *48*(2), 111–126.

Murton, R. K., Thearle, R. J. P., & Thompson, J. (1972). Ecological Studies of the Feral Pigeon Columba livia var. I. Population, Breeding Biology and Methods of Control. *The Journal of Applied Ecology*, *9*(3), 835.

Sasaki, T., & Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications*, *8*(1), Article 1.

Spetch, M. L., Cheng, K., & MacDonald, S. E. (1996). Learning the configuration of a landmark array: I. Touch-screen studies with pigeons and humans. *Journal of Comparative Psychology*, *110*(1), 55–68.

Spetch, M. L., Cheng, K., MacDonald, S. E., Linkenhoker, B. A., Kelly, D. M., & Doerkson, S. R. (1997). Use of landmark configuration in pigeons and humans: II. Generality across search tasks. *Journal of Comparative Psychology*, *111*(1), 14–24.

Spetch, M. L., & Mondloch, M. V. (1993). Control of pigeons' spatial search by graphic landmarks in a touch-screen task. *Journal of Experimental Psychology: Animal Behavior Processes*, *19*(4), 353–372.

Tomback, D. F. (1980). How Nutcrackers Find Their Seed Stores. *The Condor*, *82*(1), 10–19.

Tommasi, L., Chiandetti, C., Pecchia, T., Sovrano, V. A., & Vallortigara, G. (2012). From natural geometry to spatial cognition. *Neuroscience and Biobehavioral Reviews*, *36*(2), 799–824.

Vander Wall, S. B. (1982). An experimental analysis of cache recovery in Clark's nutcracker. *Animal Behaviour*, *30*(1), 84–94.

Vander Wall, S. B., & Balda, R. P. (1977). Coadaptations of the Clark's Nutcracker and the Pinon Pine for Efficient Seed Harvest and Dispersal. *Ecological Monographs*, *47*(1), 89–111.

Wall, S. B. V., & Balda, R. P. (1981). Ecology and Evolution of Food-storage Behavior in Conifer-seed-caching Corvids. *Zeitschrift Für Tierpsychologie*, *56*(3), 217–242.

Wiltschko, W., & Balda, R. P. (1989). Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*). *Journal of Comparative Physiology A*, *164*(6), 717–721.