## ORIGINAL ARTICLE

# Effects of sun compass error on spatial search by Clark's nutcrackers

Debbie M. KELLY,[1] Ken CHENG,[2] Russell BALDA[3] and Alan C. KAMIL[4]

[1]Department of Psychology, University of Manitoba, Winnipeg, Canada, [2]Department of Biological Sciences, Macquarie University, Sydney, Australia [3]Department of Biological Sciences, Northern Arizona University, Flagstaff, USA and [4]Department of Biological Sciences, University of Nebraska-Lincoln, Lincoln, USA

## Abstract

Animals employ compasses during navigation, but little attention has been paid to how accuracy is maintained in the face of compass error, which is inevitable in biological systems. The use of multiple landmarks may minimize the effect of compass error. We allowed Clark's nutcrackers to cache seeds in an outdoor aviary with either one or four landmarks present, and subsequently subjected them to small clock-shifts mimicking the effects of compass error. As predicted, the results showed a significant decrease in search accuracy following the clock-shift when one landmark was present but not when four landmarks were present. These results support that nutcrackers encode information from the sun as well as terrestrial landmarks, and these spatial cues are used in a flexible manner. Overall, our results are important as they support the hypothesis that multiple landmarks may be used during situations where the sun compass has even a small amount of error.

**Key words:** Clark's nutcracker, clock-shift, error, landmarks, sun compass

## INTRODUCTION

Many animals are faced with the task of navigation. For some species, these navigational feats seem truly remarkable. For instance, some loggerhead turtles [(*Caretta caretta* (Linnaeus, 1758)] have migratory routes that extend over substantial distances (Lohmann & Lohmann

*Correspondence*: Debbie M. Kelly, 190 Dysart Road, Department of Psychology, University of Manitoba, Winnipeg MB R3T 2N3, Canada.
Email: Debbie.Kelly@umanitoba.ca

1996). Common pigeons [(*Columba livia* Gmelin, 1789)] relocate their home lofts even when released from locations never previously experienced and outside of familiar visual cues (see Walcott 1996). Invertebrates also show remarkable navigational feats, such as the path-integration and landmark-use abilities of several ant species (see Collett & Collett 2000; Wystrach *et al*. 2011) or the long distance migratory routes of monarch butterflies [(*Danaus plexippus* (Linnaeus, 1758)]; Calvert 2001). Investigations into the navigational abilities of such long-distance navigators, as well as feats on shorter scales, have revealed many discoveries about the mechanisms underlying animals' spatial navigation abilities (for reviews see Bingman & Cheng 2005; Cheng &

Jeffery 2017; Pritchard & Healy 2017).

Spatial navigation is also important for food-storing animals, and particularly so in scatter-hoarding species. Clark's nutcrackers [(*Nucifraga columbiana* (Wilson, 1811)], for example, store seeds in thousands of different locations every fall, often traveling 20 or 30 km between harvesting areas and storage sites. They scatterhoard their seeds in many different locations, subsequently recovering these stored seeds throughout the winter and spring, using a well-developed spatial memory system (Tomback 1977, 1980; Vander Wall & Balda 1981; Kamil & Balda 1990). Early research on the food-storing abilities of nutcrackers show that they use objects within their environment as landmarks to encode the locations of their hidden caches (Balda 1980; Vander Wall 1982), and subsequent laboratory studies have ruled out other non-spatial explanations for these remarkable abilities (Kamil & Balda 1985, 1990). During the retrieval stage of the food-caching process, a nutcracker is digging for a target approximately 1 cm in diameter, buried in the ground, often with no immediate local cues, sometimes under snow cover, all this with a very small beak for a shovel. To examine the content of the nutcrackers' spatial memory during this cache-retrieval process, carefully controlled laboratory studies have been adopted. These studies have supported the hypothesis that nutcrackers tend to encode information from multiple, typically distant, landmarks when caching, or when required to retrieve a cache made by an experimenter (such as during spatial search tasks; see Kamil & Balda 1990; Kamil & Jones 1997; Kamil *et al.* 1999; Kelly *et al.* 2010).

Kamil and Cheng (2001) propose the multiple bearings hypothesis to account for why nutcrackers use multiple landmarks when encoding a cache location rather than a single landmark to beacon towards. Based on previous research, the authors proposed that nutcrackers encode a set of bearings from each cache site to a set of landmarks. These bearings include distance and directional information. Although this formal hypothesis contained several specific predictions, including how the spatial arrangement of the landmarks affects encoding, for the purposes of our study, two central aspects of the multiple bearings hypothesis are most important. First, the authors proposed that nutcrackers should be more accurate with a multiple landmark array compared to a single landmark. This is not a novel prediction in itself, and the authors discuss their model in relation to others also supporting the encoding of multiple landmarks. However, a key aspect is the use of multiple landmarks

in conjunction with other sources of spatial cues, in particular the sun compass. Thus, the second aspect of the multiple bearings hypothesis we were interested in examining is the interaction between landmarks and a sun compass when an animal needs to relocate to a precise position, as a nutcracker would when searching in the snow for a small cache site. In particular, we examined the prediction that multiple landmarks may aid a bird in correcting for small amounts of error in its sun compass, compared to a single landmark. It is these two ideas combined which we proposed to examine in this study.

A general compass heading such as that produced by the sun compass may be sufficient for movement over large distances, such as when navigating or orienting (Wehner 2003; Wiltschko & Wiltschko 2003; Bingman & Cheng 2005), but it alone may not be sufficient for the precise navigation required by food-storing species which need to return to an exact cache location (see Duff *et al.* 1998; Kamil & Cheng 2001). The multiple bearings hypothesis suggests that the use of multiple landmarks may be used to minimize the effects of any compass error for such precise cache relocation (Kamil & Cheng 2001). Therefore, we used the well-studied clock-shifting paradigm to induce error in the sun compass of our subject, while manipulating the number of landmarks available to the subject.

Clock-shifting manipulates the internal circadian rhythm of the subject through altering the apparent time of day by adjusting the time at which the lights in the housing room are turned on or off. As the sun compass is time-compensated, this manipulation allows us to create a conflict between the spatial information provided by the position of the sky and the landmarks provided to the subjects, as to where a cache site was previously made. As an example, if a bird is clock-shifted 4 h backward, its circadian clock reads 1200 hours when it is actually 0800 hours. If it is released into an outdoor aviary on an autumn day in the Northern Hemisphere, the sun will be in the east, but will appear to the bird to be in the south. Many experiments, studying a variety of taxa, have found that clock-shifting results in displacements of guided movement in the direction predicted by the sun compass hypothesis (Wiltschko & Wiltschko 2003; Bingman & Cheng 2005). Indeed, food-storing birds have been shown to use a sun compass during the cache-retrieval process, as clock-shifting the birds between caching and subsequent retrieval caused the birds to shift their searching in alignment with the position indicated by a sun compass (Wiltschko & Balda 1989; Balda & Wiltschko 1991; Duff *et al.* 1998; Wiltschko *et*

*al.* 1999). These previous studies examined the use of a sun compass when external landmark cues were available from the landscape external to the cache-retrieval arena, by clock-shifting the subjects after a caching event but before retrieval. We adopted a similar approach, but rather than exposing the birds to large clock-shifts (which make the sun compass conflict noticeably with other compass cues), we wanted to mimic small errors in the sun compass, and determine whether the ability to use multiple landmarks would allow birds to continue searching accurately despite such compass error.

During this experiment, we allowed nutcrackers to cache seeds in an outdoor aviary and then subjected them to small clock-shifts to mimic the effects of a compass error of approximately 30° with either one or four landmarks present. Each nutcracker received four experimental cache-recover cycles intermixed among baseline cycles (see Methods for details). During two of these cycles there was a single, centrally-located landmark present; during the other two, there were 4 landmarks present, located on the periphery of the test area. We deliberately placed the single landmark centrally in a circular arena to maximize the difference in usefulness of landmarks between the 1-landmark setup and the 4-landmark setup. A landmark at the periphery provides better directional information than one located exactly at the center of a circular arena. During one of the 1-landmark and one of the 4-landmark test cycles for each bird, apparent time of day was shifted forward 2 h by changing the timing of the lights coming on and going off in the colony room where the birds were housed. With a single landmark, the only available coding of the cache location would be in terms of the distance and direction from the cache to that single landmark, and a clock-shift should affect the directional information, as has previously been shown (Wiltschko et al. 1999). With multiple landmarks, however, there would be many more ways of coding the cache location, including relative bearings (angular information between multiple landmarks) and using a combination of absolute distance and direction information, many of which would be resistant to compass error. We predicted that there would be a significant decrease in search accuracy following a small clock-shift when only one landmark was present but not when four landmarks were present.

## MATERIALS AND METHODS

Nine wild-caught adult Clark's nutcrackers (*N. columbiana*) cached and recovered seeds in a round met-al tub (184 × 22.5 cm, diameter × height) located at the center of an enclosed circular outdoor arena (550 × 150 cm, diameter × height) on the campus of the Northern Arizona University in Flagstaff. The arena had a wire mesh ceiling which allowed the sun to be visible, but tall walls to limit the view of the surrounding trees or possible panorama cues. The walls of the arena were covered in opaque plastic-coated canvas, effectively blocking the terrestrial surround except for any experimentally provided landmarks. To ensure the birds could see the sun, all sessions were conducted on clear days, between 0900 and 1400 hours Mountain Standard Time. Birds entered and exited the arena through one of two randomly chosen doors operated using a pulley system.

Following a familiarization session, during which birds were allowed to explore within the arena, each bird received several cache-recovery cycles. Each cycle consisted of a caching session followed by either a baseline retrieval or test retrieval session. During the caching session, birds were provided with a bowl of 100 pinyon pine seeds to cache or eat. During half of the caching-recovery cycles, one landmark was situated at the center point of the metal tub. During the remaining cycles, four visually distinct landmarks were placed at the perimeter of the tub, with one at each of the four cardinal directions. Each landmark was a distinctly colored plastic PVC cylinder (3.8 × 140 cm, diameter × height). Each caching session continued until the bird either made at least three caches or 20 min had elapsed, whichever occurred latest. The position of each cache was identified from video recordings, obtained from a centrally located camera, and confirmed through visual inspection. Four to six days after a caching session, each bird received either a baseline retrieval session or a test retrieval session. During all retrieval sessions, the same landmark arrangement was present as during the previous caching session. During baseline retrieval sessions, caches were replaced using the *x* and *y* coordinates of the caches recorded from the caching session (including the same number of seeds per cache) and sessions ended when all caches were recovered or 20 min had elapsed. During test retrieval sessions, the caches were not replaced from the caching session (no seeds were present) and the session continued until the bird probed at each cache location, 50 probes were made or 20 min had elapsed.

Four cache-recovery cycles were presented with the test retrieval sessions: two cycles with one landmark and two cycles with four landmarks present. During the four days preceding one of the single-landmark and

one of the 4-landmark test retrieval sessions, birds were clock-shifted 2 h forward (after the associated caching session). To clock-shift the birds, a bird was held in one of two colony rooms. The regular colony room maintained a 10:14 h light : dark cycle with lights on at 08:00 hours, whereas to induce a clock-shift the birds were held in a separate colony room maintained at 10:00 light onset. Test retrieval sessions were embedded among baseline retrieval cycles. These test retrieval sessions were intermixed among baseline retrieval cycles to minimize the effects of recovery sessions, which were conducted without caches present.

The location of the first 10 probes of each test retrieval session and the location of each cache site was determined from the video recordings. The mean distance between the location of each of the first 10 probes and the location of the cache site nearest to that probe was calculated. For the analysis of search error, only one cache site was considered, the cache to which the majority of the probes were most proximal. Each bird experienced each of the four combinations of landmark (LM) arrangement and clock-shift (HR) condition once (i.e. 1LM-0HR condition, 1LM-2HR condition, 4LM-0HR condition and 4LM-2HR condition). Each condition was separated by one cache-recovery cycle with a baseline retrieval session. Conditions were presented in four different orders of presentation across subjects.

Principles of Laboratory Animal Care (NIH Publication Vol 25, No. 28 revised 1996; http://grants.nih.gov/grants/guide/noticefiles/not96-208.html) were followed, and the experimental procedures used were approved by the Northern Arizona University animal care committee. The research conforms to the provisions of the Declaration of Helsinki (as revised in Edinburgh 2000).

## RESULTS

Total search error was measured (cm) between the cache site and the retrieval probe, for the four conditions (1LM-0HR condition, 1LM-2HR condition, 4LM-0HR condition and 4LM-2HR condition). The total error stood out as being the greatest in the combination of one landmark and a clock-shift (the 1LM-2HR condition; see Fig. 1). A repeated-measures analysis of variance (ANOVA) showed that the main effects both of the number of landmarks and of the clock-shift condition were not significant ($F_{1,8} = 0.42$ and 2.93, respectively, ps > 0.1). However, there was a significant interaction between number of landmarks and clock-shift con-

dition on overall search accuracy ($F_{1,8} = 17.95$, $P < 0.01$). Newman–Keuls post-hoc comparisons revealed that the birds' search error was significantly greater during the 1LM-2HR condition (M = 45.83 cm) compared to the 1LM-0HR condition (M = 18.35 cm), and the search error did not differ significantly as a function of clock-shift condition when the birds were provided with an array of four landmarks (M = 32.85 and 23.46 cm, for the 4LM-0HR and 4LM-2HR conditions, respectively).

When we calculated the mean search position for each bird for each test session, the increased variability of search during the 1LM-2HR condition was clear on visual inspection (see Fig. 2). For the plots of Figure 2, all cache locations were transformed to a single point in polar coordinates, with direction = 0°, distance = 100 cm and the center of the arena as the origin. This characterization allowed us to partition search error into distance and direction components (Kamil & Jones 1997) and to conduct separate ANOVAs on each measure. The distance component was defined as the absolute difference from 100, whereas the direction component was defined as the absolute difference from 0°.

To analyze these data obtained by partitioning search error into distance (measured in cm) and direction (measured in absolute degrees) components, we conducted separate ANOVAs on each measure. For each bird, only one cache site per condition was considered, the cache to which the majority of the probes were most proximal. The spatial position of the average location of up to the
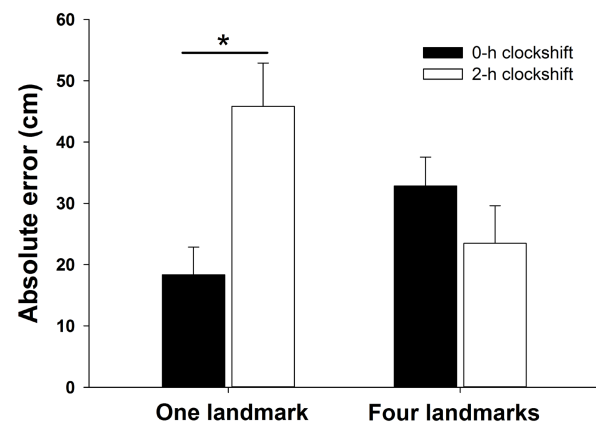


**Figure 1** Total search error (±SE), measured as the distance between the cache site and the retrieval probe, when presented with either one landmark or four landmarks after no clock-shift (filled bars) or a 2-h clock-shift (empty bars).

first 10 probes was examined. We found no significant main effects of either clock-shift ($F_{1,8} = 1.75$, $P = 0.22$ and $F_{1,8} = 1.75$, $P = 0.22$) or number of landmarks ($F_{1,8}$ = 0.81, $P = 0.39$ and $F_{1,8} = 0.57$, $P = 0.47$), in both the distance and direction components, respectively. On the distance component, we found a significant interaction
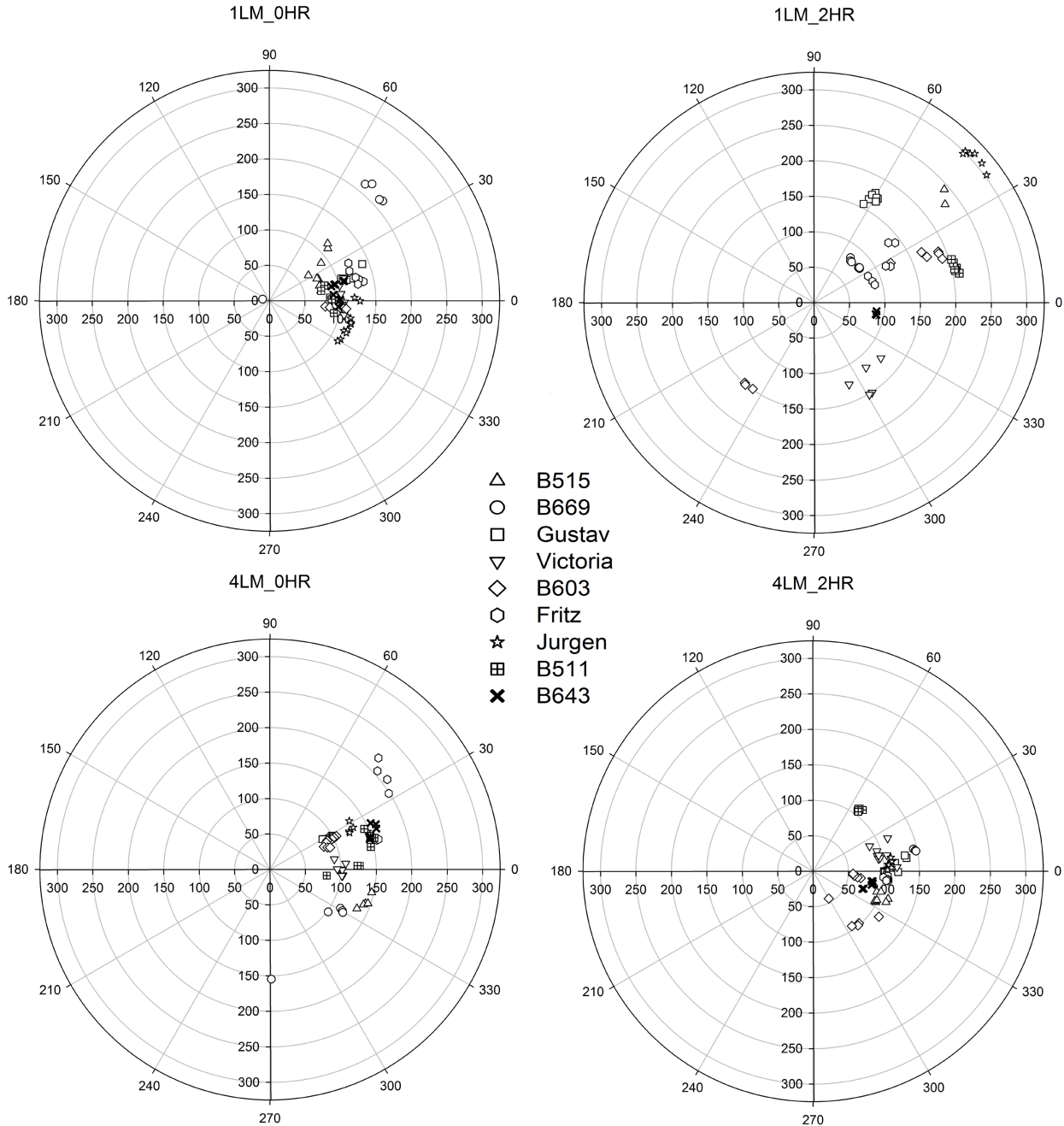


**Figure 2** Each panel shows a polar plot indicating the position of each bird's probe position using a standardized cache (coordinate 100, 0) during the 4 testing conditions.
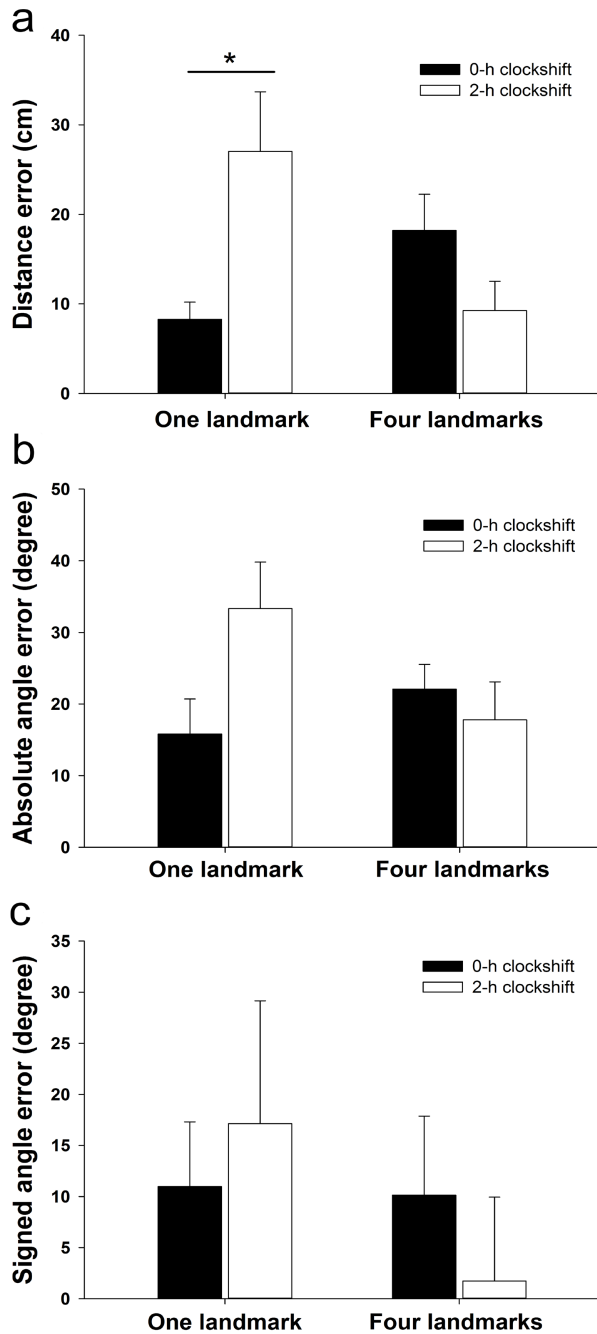
**Figure 3** Search error was partitioned into: (a) distance error (measured in cm), (b) directional error (measured in absolute degrees) components and (c) directional error (measured in signed degrees) to evaluate directionality of search shift, with positive values indicating a counter-clockwise rotation. Graphs show means (±SE), measured between the cache site and the retrieval probe, when presented with either one landmark or four landmarks after 0-h clock-shift (filled bars) or a 2-h clock-shift (empty bars).

of the hours of clock-shift by number of landmarks ($F_{1,8}$ = 8.70, $P$ = 0.018), but the interaction failed to reach significance for the direction component ($F_{1,8}$ = 4.68, $P$ = 0.06), presumably because of the relatively small magnitude of the clock-shift, and a lack of sensitivity to clock-shift when four landmarks were present. Post-hoc analyses of the distance component revealed that there was an increase in distance error during the 1LM-2HR condition compared to the other three conditions (Ms = 8.26, 27.03, 18.21 and 9.25 cm and for 1LM-0HR, 1LM-2HR, 4LM-0HR and 4LM-2HR; see Fig. 3a). Although the interaction did not reach significance (and, therefore, a post-hoc analysis was not performed), the absolute direction component also showed similar differences among the conditions (Ms = 15.81, 33.34, 22.06 and 17.78 cm and for 1LM-0HR, 1LM-2HR, 4LM-0HR and 4LM-2HR; see Fig. 3b). To evaluate the directionality of the search error, further analysis of the signed directional component showed that although the search tended to be shifted in the counter-clockwise direction (which would be expected from the clock-shift), the interaction of the clock-shift by landmark number was not statistically significant ($F_{1,8}$ = 0.67, $P$ = 0.44); the main effects of clock-shift and number of landmarks were also not significant ($F_{1,8}$ = 0.02, $P$ = 0.88, and $F_{1,8}$ = 0.58, $P$ = 0.58, respectively). Although the interaction did not reach significance (and, therefore, a post-hoc analysis was not performed), the signed directional component also showed similar differences among the conditions (Ms = 10.98, 17.14, 10.13 and 1.71° for 1LM-0HR, 1LM-2HR, 4LM-0HR and 4LM-2HR; see Fig. 3c).

Thus, when four landmarks were available, the compass error induced by the clock-shift had little effect. When information was available from multiple landmarks at the periphery of the arena, this information allowed the birds to maintain accuracy despite error in the estimation of absolute direction. When only a single landmark was present at the center of the arena, in contrast, the 2-h clock-shift resulted in a substantial increase in search error. The total search error following the clock-shift was more than double that following no clock-shift in the single-landmark condition. These results clearly show when multiple landmarks are available, nutcrackers are better able to correctly orient when a small clock-shift has induced error in their compass. In contrast, when only a single landmark is available the birds' ability to accurately locate their caches is severely disrupted by the clock-shift.

## DISCUSSION

As predicted, we found a significant increase in search error following a small clock-shift when one landmark was present but not when four landmarks were present. This supports a functional explanation for the use of multiple landmarks when nutcrackers need to precisely relocate a small cache location, and also shows an important interaction between the use of compasses and of landmarks. The clock-shift effect with a single landmark demonstrates use of a sun-based compass; the increase in error following a 2-h clock-shift with a single landmark demonstrates the effects of error in this compass. The absence of an effect of the clock-shift when multiple landmarks were present shows either that the sun compass was not used to encode cache locations or the sun compass information was ignored when the clock-shift resulted in conflicting information from a multitude of landmarks (Kamil & Cheng 2001). In either case, there is clearly an interaction between the nature of landmark arrays and the use of sun-based compass information. The number of available landmarks determines the extent to which the birds rely on the sun compass.

One point concerning the errors in cache relocation worth remarking on is that statistically it was the total error and the distance component that differed significantly between groups, but the direction component just failed to reach significance. We are not inclined to try to find some mechanistic explanation for these statistical differences. For practical reasons of working with wild-caught animals, our sample size was limited. The trends in all three kinds of errors are in the same direction, and we take the fact that two of three components reached statistical significance to provide confidence that relocation errors in the clock-shifted birds using only one landmark were, indeed, larger.

Although one might expect clock-shifting to induce a bigger effect on directional errors than on distance errors in the 1-landmark condition, in retrospect, the mismatches created by clock-shifting in this situation might lead to more distance error as well. Clock-shifting creates differences in the retrieval context for the birds, compared with their caching context. For instance, the sun would be at the wrong height compared with its expected height at a similar circadian time on the caching day. The intensity of sunlight might also mismatch. Memory retrieval depends on context (Bouton 2007), and mismatches between caching and retrieval context, which we take to be especially salient during the 1-landmark condition, could cause memory problems on all components, distance and directional information.

Clark's nutcrackers travel hundreds to thousands of kilometers in seasonal eruptions when the pine cone crop has failed, returning to their original home ranges weeks or months later (Vander Wall *et al.* 1981). They regularly traverse a large home range, with their nests located in different areas than their caches, and they must also engage in specific, highly precise search for cached food. From our study, their sensitivity to clock-shifts when only a single landmark is present, show nutcrackers are able to use a sun compass when navigating within their environment. Furthermore, the success of the non-shifted condition with only 1-landmark (this condition resulted in total error as low as during the 4-landmark condition, and perhaps even less error, but not significantly so) suggests the birds were determining the direction from the landmark by using celestial cues; terrestrial visual sources of directional information were not available. However, our finding that a clock-shift had no effect on search when multiple landmarks are present shows that the birds are able to switch between using a sun compass to local landmarks when engaged in relocating specific seed caches, or when the sun compass is erroneous. Indeed, the use of local landmarks might be common as most cache locations would have multiple surrounding landmarks.

It must be noted that in the design of our study, not only was the number of landmarks changed between the 4-landmark condition and the 1-landmark condition, but the spatial location of the landmark(s) within the arena was also modified. As our testing conditions were necessarily conducted in extinction (all caches were removed), and nutcrackers very quickly learn to cease searching under extinction, our study could only include a few testing sessions as we anticipated that the testing sessions would be quickly differentiated from baseline sessions by the birds. Therefore, rather than place the single landmark at each of the positions of the four landmarks (substantially increasing the number of testing sessions needed and resulting in an unbalanced experimental design) we chose to balance the number of 4-landmark and 1-landmark sessions. Furthermore, having a centrally located landmark roughly equated the distance from the single landmark to the arena edge compared to the distance from each landmark during the 4-landmark condition to the center of the arena. A single landmark at the center is also less useful for directional information than one at the edge, and for an initial study of this theme, we wanted to maximize the manipulation.

Controlling for not only the number of landmarks present but also their spatial position within an arena is certainly an issue worthy of future research.

The interaction between the nature of the landmark arrays and use of the sun compass may be of general importance to the field of navigation. The sun and the pattern of polarized light it creates, the sky compass is an important cue for many animals from homing pigeons (Chappell & Guilford 1995) to desert ants (Wehner 2003). The nature of the relationship between visual landmarks and other cues has not, however, been clear (for reviews see Holland 2003; Guilford & Biro 2014). Desert ants do use the terrestrial panorama as well as celestial cues for compass information (Wehner 2003; Cheng *et al*. 2009; Graham & Cheng 2009; Legge *et al*. 2014). In cases in which celestial and terrestrial cues conflict, as a result of experimental manipulations, desert ants often combine the two types of cues, heading in a direction intermediate between the directions according to celestial and terrestrial cues (Collett 2012; Legge *et al*. 2014; Wehner *et al*. 2016). It is possible that the clock-shifted Clark's nutcrackers in this study might have averaged sun and landmark cues as well, but our sample size is too small to detect such an effect, especially with such a small conflict of 30°.

Desert ants inhabiting a habitat poor in panoramic cues, the North African *Cataglyphis fortis* (Forel, 1902) living on salt pans of Tunisia, have been shown to do something similar. They learned to search near one corner of a square array of identical cylindrical landmarks for their nest (Åkesson & Wehner 2002). The ants did this even when the array of landmarks was at a distant location from their nest, a finding that rules out the possible use of some unspecified distant terrestrial panorama. Under natural, as opposed to experimentally contrived, conditions, this integration might be especially important for locations at which the distal panorama is poor in defining direction, for example, a tree surrounded by a confusing clutter of other trees of similar height. This scenario may be similar to the conditions of our current study, as we constructed the arena such that the walls would occlude a substantial amount of the surrounding arena. Research has shown that desert ants [(*Melophorus bagoti* Lubbock, 1882)] can, indeed, use visual information from a stable panorama for navigation (Cheng 2012; Pritchard & Healy 2017). Thus, a future approach to examining spatial cue use by nutcrackers when engaged in cache-retrieval would be to determine if, and to what extent, a stable visual panorama might be useful, as under controlled laboratory experiments non-storing avian species have been suggested to use view-based spatial information (Pecchia & Vallortigara 2010).

Our study focused on understanding how two types of visual information are used by Clark's nutcrackers when searching for previously hidden food caches. We used two predictions from the multiple bearings hypothesis to guide our investigation of whether the ability to encode multiple landmarks influences spatial search error when birds experience slight error in a sun compass. The first prediction proposed that nutcrackers should be more accurate with a multiple landmark array as compared to with a single landmark. The second predication was that the error of the sun compass would have less of an effect on search accuracy if nutcrackers were encoding their cache locations using multiple landmarks rather than a single landmark. Our results showed that the birds had similar search accuracy when presented with a single-landmark condition or a 4-landmark array, when the sun compass was not manipulated (when the birds were not clock-shifted). Thus, the first prediction was not fully supported. However, the availability of multiple landmarks, as opposed to a single landmark, when error was induced in the sun compass (when the birds were clock-shifted), did allow the birds to continue searching accurately. Nevertheless, this does not rule out the use of other potential cues, such as a magnetic compass or other directional information from the sun that does not require time-compensation (see Guilford & Taylor 2014). Examining the interactions among these many available sources of spatial information is again an exciting topic for future study.

In summary, many animals use multiple cues for successful navigation. The results from our study show that when Clark's nutcrackers are engaged in the important task of food-storing, not only do they encode information from a sun compass, but also terrestrial landmarks. However, how they rely on these cues is flexible, and when presented with a situation where the sun compass information is at odds with multiple stable landmarks, the nutcrackers use these landmarks to guide their search. Our results support the hypothesis that multiple landmarks may be used during situations where the sun compass has even a small amount of error, error which would be typical of a biological system.

## ACKNOWLEDGMENTS

## REFERENCES

Åkesson S, Wehner R (2002). Visual navigation in desert ants *Cataglyphis fortis*: Are snapshots coupled to a celestial system of reference? *Journal of Experimental Biology* **205**, 1971–8.

Balda RP (1980). Recovery of cached seeds by a captive *Nucifraga caryocatactes. Zeitschrift für Tierpsychologie* **52**, 331–46.

Balda RP, Wiltschko W (1991). Caching and recovery in scrub jays: Transfer of direction from shaded to sunny areas. *Condor* **93**, 1020–3.

Bingman VP, Cheng K (2005). Mechanisms of animal global navigation: Comparative perspectives and enduring challenges. *Ethology, Ecology & Evolution* **17**, 295–318.

Bouton ME (2007). *Learning and Behavior: A Contemporary Synthesis*. Sinauer Associates, Sunderland, MA.

Calvert WH (2001). Monarch butterfly (*Danaus plexippus L., Nymphalidae*) fall migration: Flight behavior and direction in relation to celestial and physiographic cues. *Journal of the Lepidopterists' Society* **55**, 162–8.

Chappell J, Guilford T (1995). Homing pigeons primarily use the sun compass rather than fixed directional visual cues in an open-field arena food searching task. *Proceedings of the Royal Society B*: *Biological Sciences* **260**, 59–63.

Cheng K (2012). How to navigate without maps: The power of taxon-like navigation in ants. *Comparative Cognition & Behavior Reviews* **7**, 1–22.

Cheng K, Jeffery KJ (2017). Spatial cognition. In: Call J, ed. *APA Handbook of Comparative Psychology* (Vol. 2: Perception, Learning, and Cognition). APA, Washington, DC, pp. 463–83.

Cheng K, Narendra A, Sommer S, Wehner R (2009). Traveling in clutter: Navigation in the Central Australian desert ant Melophorus bagoti. *Behavioural Processes* **80**, 261–8.

Collett M (2012). How navigational guidance systems are combined in a desert ant. *Current Biology* **22**, 927–32.

Collett TS, Collett M (2000). Path integration in insects. *Current Opinion in Neurobiology* **10**, 757–62.

Duff SJ, Brownlie LA, Sherry DF, Sangster M (1998). Sun compass orientation and landmark orientation by black-capped chickadees (*Parus atricapillus*). *Journal of Experimental Psychology: Animal Behavior Processes* **24**, 243–53.

Graham P, Cheng K (2009). Ants use the panoramic skyline as a visual cue during navigation. *Current Biology* **19**, R935–7.

Guilford T, Biro D (2014). Route following and the pigeon's familiar area map. *Journal of Experimental Biology* **217**, 169–99.

Guilford T, Taylor G (2014). The sun compass revisted. *Animal Behaviour* **97**, 135–43.

Holland RA (2003). The role of visual landmarks in the avian familiar area map. *Journal of Experimental Biology* **206**, 1773–8.

Kamil AC, Balda RP (1985). Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columiana*). *Journal of Experimental Psychology: Animal Behavior Processes* **11**, 95–111.

Kamil AC, Balda RP (1990). Spatial memory in seed-caching corvids. In: Bower GH, ed. *The Psychology of Learning and Motivation*, Vol 25. Academic Press, New York, pp. 1–25.

Kamil AC, Balda RP, Good S (1999). Patterns of movement and orientation during caching and recovery by Clark's nutcrackers (*Nucifraga columbiana*). *Animal Behaviour* **34**, 1289–98.

Kamil AC, Cheng K (2001). Way-finding and landmarks: The multiple-bearings hypothesis. *Journal of Experimental Biology* **2043**, 103–13.

Kamil AC, Jones JE (1997). The seed-storing corvid Clark's nutcracker learns geometric relationships among landmarks. *Nature* **390**, 276–9.

Kelly DM, Kamil AC, Cheng K (2010). Landmark use by Clark's nutcrackers (*Nucifraga columbiana*): Influence of disorientation and cue rotation on distance and direction estimates. *Animal Cognition* **13**, 175–88.

Legge ELG, Wystrach A, Spetch ML, Cheng K (2014). Combining sky and earth: Desert ants (*Melophorus bagoti*) show weighted integration of celestial and terrestrial cues. *Journal of Experimental Biology* **217**, 4159–66.

Lohmann KJ, Lohmann CF (1996). Orientation and

open-sea navigation in sea turtles. *Journal of Experimental Biology* **199**, 73–81.

Pecchia T, Vallortigara G (2010). View-based strategy for reorientation by geometry. *Journal of Experimental Biology* **213**, 2987–96.

Pritchard DJ, Healy SD (2017). Homing and navigation. In: Call J, ed. *APA Handbook of Comparative Psychology* (Vol. 2: Perception, Learning, and Cognition). APA, Washington, DC, pp. 485–508.

Tomback DF (1977). Foraging strategies of Clark's nutcrackers. *Living Bird* **16**, 123–61.

Tomback DF (1980). How nutcrackers find their seed stores. *Codor* **82**, 10–9.

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

Vander Wall SB, Balda RP (1981). Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. *Zeitschrift für Tierpsychologie* **56**, 217–42.

Vander Wall SB, Hoffman SW, Potts WK (1981). Emigration behavior of Clark's nutcrackers. *Condor* **83**, 162–70.

Walcott C (1996). Pigeon homing: Observations, experiments and confusions. *Journal of Experimental Biology* **199**, 21–7.

Wehner R (2003). Desert ant navigation: How miniature brains solve complex tasks. *Journal of Comparative Physiology A* **189**, 579–88.

Wehner R, Hoinville T, Cruse H, Cheng K (2016). Steering intermediate courses: Desert ants combine information from various navigational routines. *Journal of Comparative Physiology A* **202**, 459–72.

Wiltschko W, Balda RP (1989). Sun compass orientation in seed-caching scrub jays. *Journal of Comparative Physiology A* **164**, 717–21.

Wiltschko W, Balda RP, Jahnel M, Wiltschko R (1999). Sun compass orientation in seed-caching corvids: Its role in spatial memory. *Animal Cognition* **2**, 215–21.

Wiltschko R, Wiltschko W (2003). Avian navigation: From historical to modern concepts. *Animal Behaviour* **65**, 257–72.

Wystrach A, Beugnon G, Cheng K (2011). Landmarks or panoramas: What do navigating ants attend to for guidance? *Frontiers in Zoology* **8**, 21.

**Cite this article as:**