

CACHING AND RECOVERY IN SCRUB JAYS:
TRANSFER OF SUN-COMPASS DIRECTIONS FROM
SHADED TO SUNNY AREAS¹

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Current models of navigation and homing (e.g., Wallraff 1974, Wiltschko and Wiltschko 1987) assume that compass orientation not only guides the birds on their homeward flight but is also used to build a navigational "map." This "map" is taken to be directionally oriented mental picture of the spatial distribution of navigational factors. Recent findings of Wiltschko and Balda (1989) indicate that compass orientation is also of major importance in foraging. For example, Scrub Jays, *Aphelocoma coerulescens*, were observed in an octagonal outdoor aviary when caching and recovering their seeds. When their internal clock was shifted 6 hr between caching and recovery, they altered the sectors of their search by the predicted 90° thus showing that they used the sun compass. This suggests that birds might generally have a directionally oriented view of space that is used for a wide variety of tasks.

In our earlier experiments (Wiltschko and Balda 1989), caching as well as recovering took place in sunshine. Although the Scrub Jays live in a relatively dry, open environment, they may have opportunities to cache in the shade and recover in the sun or vice versa—the distribution of shaded and sunny areas could be quite different at the times of revisiting cache sites. This raises the question whether a jay can remember a cache site relative to a sun compass direction when it was unable to see the sun directly while caching. Is it possible that a bird includes a site in its sun compass oriented spatial map that it has never seen in sunshine? Here we report the first results of an attempt to answer this question.

MATERIAL AND METHODS

The study was performed at Flagstaff, Arizona, from 10 September–1 November, 1989. Test birds were three Scrub Jays that had been captured six months earlier in the pinyon-juniper woodland near Flagstaff, Arizona. One of them refused to cache after the first con-

trol test. The birds were kept indoors in individual cages under a photoperiod simulating the natural one and transferred to the aviary in paper bags. Aviary and test procedure are described in detail in Wiltschko and Balda (1989), so here we summarize only the most important points:

Aviary and surroundings. We used an octagonal outdoor aviary which stood in a courtyard on the campus of Northern Arizona University. The surroundings were not homogeneous, consisting of buildings of different heights and shapes, each with a different configuration of windows and doors. In the early morning and in late afternoon, the aviary itself was shaded by these buildings. There was a period of direct sunshine during 4 hr around local noon each day. Different parts of the courtyard floor were in the sun during all parts of the day.

The wooden aviary floor was divided into eight pie-shaped segments, each containing six identically arranged holes which could either hold cups filled with sand to allow caching and probing or could be closed with a tap (see Kamil and Balda 1985). The floor of the aviary was void of all other objects. For caching, only the 12 cups of two adjacent segments were available, and the jay was allowed to make two to four caches. The position of the "caching sector" varied between tests and between birds. For recovery four to six days later, all 48 holes were open. We counted all probes until the bird had successfully recovered its caches. Repeated probing in the same hole was counted only once.

Procedure. Before the experiment began the birds were placed into the test aviary for six, one hour habituation sessions. During these sessions the aviary was always in the shade of the buildings, but sunshine was present in different parts of the courtyard. Thus, the progression of the sun could have been perceived by the birds.

The experimental paradigm was the same as in our earlier experiments, namely control I, followed by a 6 hr slow clock shift, a 6 hr re-shift back to normal time and control II (see Wiltschko and Balda 1989). In control I, however, the birds cached and recovered in the shade. For the shift tests and the re-shift tests, the birds cached while the aviary was shaded; after this, the birds were held for at least five days in a light-tight room

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TABLE 1. Caching sector indicates the original caching sector; r, o and l are the sectors to the right, opposite and left of it, respectively. SH marks the sector that is expected to be preferred if the birds use the sun compass. The sum line gives the number of probes and the number of seeds recovered. For the shift tests "Set" indicates which set of seeds—the originally cached ones or the "shifted" ones (SH, see method section)—was completely recovered when the test was terminated. The numbers in parentheses are number of seeds recovered from the other set. The last line gives the number of false probes (i.e., probes that did not recover a seed).

Bird	Control I: Caching and recovery in shade Number of probes (caches)					6 hr slow clock-shift: Caching in shade, recovery in sun Number of probes (caches)					Set	
	Caching sector	r	o	l	Probes/cache	Caching sector	r = SH	o	l	Probes/caches		
89-1	6 (3)	2	0	5	13/3	2 (1)	6 (2)	0	2	10/2 (1)	SH	
89-2	4 (2)	0	0	0	4/2	5 (1)	10 (2)	2	0	17/2 (1)	SH	
89-3	3 (2)	0	0	0	3/2							
Sum	13 (7)	2	0	5	20/7	7 (2)	16 (4)	2	2	27/4 (2)		
False probes:		13 = 186%						21 = 350%				

Bird	Re-shift to normal: Caching in shade, recovery in sun Number of probes (caches)					Set	Control II: Caching in shade, recovery in sun Number of probes (caches)					
	Caching sector	r	o	l = SH	Probes/cache		Caching sector	r	o	l	Probes/cache	
89-1	4 (1)	2	1	10 (4)	17/4	SH	9 (4)	2	3	6	20/4	
89-2	2 (1)	0	0	5 (2)	7/2	SH	8 (3)	1	2	4	15/3	
Sum	6 (2)	2	1	15 (6)	24/6 (2)		17 (7)	3	5	10	35/7	
False probes:		16 = 200%						28 = 400%				

shifting their internal clock (see Schmidt-Koenig 1958) and then were allowed to recover their caches while the aviary was in full sun. In these recovery sessions, not only the cups where the birds had originally cached contained seeds, but also the cups 90° clockwise of them in the position where the birds were expected to search if they used the sun compass (see Fig. 1). We counted all probes until one set—either the original (Or) or the "shifted" seeds (SH)—was completely recovered. For control II, the birds cached in the shade and recovered in the sun.

Data analysis. We are aware that probes by a single bird are not strictly independent, but the non-parametric Chi-square test appears to be the most adequate statistical test, especially when comparing the distribution of probes by the experimental birds to those of the control birds. The data were analyzed on the basis of a summary distribution of probes in the four 90° sectors which was tested for deviation from random using the Chi-square test (H_0 : homogeneous distribution). The Chi-square test was also used to compare the various experimental conditions (H_0 : distribution similar to controls).

RESULTS

The data of the individual birds are given in Table 1. Figure 1 gives the distribution of probes in the four experimental conditions, which is different from random in all four conditions. In the two control tests, most of the probes are concentrated in the segment where the birds had originally cached. In the 6 hr clock-shift tests and in the re-shift tests, the maximum numbers of probes were in the segment right and left of it, respectively (i.e., the birds searched where predicted

under the assumption that the sun compass was used). Both distributions are different from the ones found in the control tests. The two birds recovered all of the "shifted" seeds completely; one original cache was recovered in each of the four experimental tests.

There was an increase in the proportion of false probing from control I to control II, indicating that the birds might lose some accuracy in the course of testing. In the shift tests, the jays recovered one original cache each; however, in control II, the birds also did a relatively high amount of probing in a neighboring sector so that the distribution of probes appears asymmetrical. This corresponds to similar observations in our earlier tests where caching and recovery had both taken place under sun (Wiltshko and Balda 1989).

DISCUSSION

Comparing the birds' behavior in the present study to that of the Scrub Jays in our previous tests, it is striking that, in general, shade does not seem to affect the accuracy of recovery. In control I, when caching and recovery were done while the sun was not directly visible, the percentage of false probes was 186%, compared to 229% when both took place under direct sun (data from Wiltshko and Balda 1989). A comparison of the other data yields a similar picture. Thus, although they use sun information when available, Scrub Jays do not seem to mind whether a cache site is shaded or hidden from the sun, a finding which appears ecologically meaningful. In their normal environment in the pinyon-juniper woodland, a given location might be in the shade and in the sun at different times of the day, so that they must be able to cope with these changes while caching and later recovering their seeds.

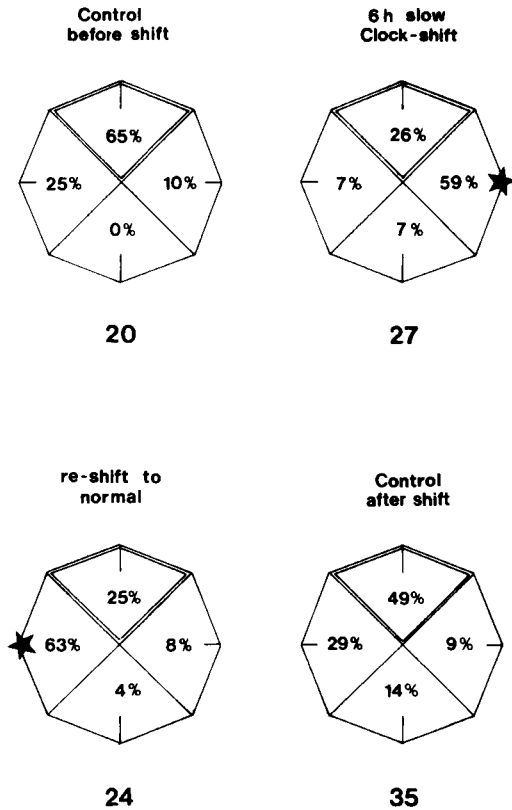


FIGURE 1. Distribution of holes probed, in percent of the total number of probes, which is given below. The original caching sector is double framed. In the clock-shift and re-shift tests, the sector expected to be preferred if the birds follow sun compass information is marked by a star. For more information, see Table 1.

Our results again indicate that the sun is not utilized as a kind of "sky mark," comparable to a prominent landmark, but that it is used as a compass to remember the locations of previously stored seeds. These findings are in good agreement with the assumption that compass orientation structures the spatial distribution of orientational cues (e.g., visual landmarks) also in the home range of birds. For example, pigeons are assumed to have a directionally oriented mental picture of the "lay of the land" around their loft, a "mosaic map," of which compass orientation is an integral part (Wiltschko and Wiltschko 1982). This is demonstrated by the finding that shifting the internal clock results in a predictable deviation of the flight directions even when pigeons are released in the vicinity of their home loft. Birds may know the courses from a given landmark to their home and probably also to other sites of special interest such as shelter, cache sites, water supply, etc. This allows them to move on straight paths fast and efficiently throughout their home range.

By not providing any objects in the aviary which could be used as nearby marks, our tests put emphasis

on mechanisms such as compass orientation. In earlier tests in closed rooms where the sun was invisible, but marks were provided, Scrub Jays could recover their caches at above chance levels (Balda and Kamil 1989). This clearly shows that the spatial orientation system is robust.

It was unexpected that the sun compass is also used in recovering caches when the birds could not directly observe the sun while caching and mentally store the information of the cache location. We can only speculate how this is achieved. One possibility is that the sun compass is still functioning even when the sun is not directly visible. During habituation and caching sessions the birds had ample opportunities to form a cognitive map of their environment. The birds might use information from the distribution and movement of sunny and shady spots in parts of the courtyard outside the aviary. A more remote possibility is that the jays derived the position of the sun from the pattern of polarized light as the sky was clear during all habituation and caching sessions. Such a system has been described for insects (Wehner 1976, Brines and Gould 1982). Migratory birds have been shown to use polarized light for orientation, at least around sunset (Able 1982, 1989; Moore and Phillips 1988; Helbig and Wiltschko 1989). Another possibility is that a magnetic compass was used during habituation and caching and that the same direction was localized with the sun compass during recovery. This would mean that directional information from the two compass systems is comparable, suggesting that the directional sense of birds is flexible, i.e., they are able to substitute one source of directional information for another, depending on the availability of cues. Further experiments with over-cast skies and magnetic manipulation are needed to clarify this point.

The pattern of probing when searching for caches was of interest. For example, bird 89-1 made no errors to find its first cache during both experimental conditions. In the clock-shift condition the first cache located was an original one, whereas in the normalization trial it was a shifted cache. The next cache recovered in this trial was an original one. Bird 89-2 made 8 errors before finding its first cache in the clock-shift condition, and this was an original. During the normalization trial this bird made one error to find its first cache and this was also an original cache. During both trials the second cache to be located was a shifted one! Neither bird showed any evidence of using random searching to find the first cache and then switching to an area restricted search pattern to locate the remaining caches.

The fact that both birds did recover one original cache in each experimental condition may indicate that these birds were experiencing a "cue conflict" situation. The original environmental landmarks in the cognitive map were all in proper locations, but the directional information provided by the sun was now different.

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A PROBLEM IN STATISTICAL ANALYSIS: SIMULTANEOUS INFERENCE¹

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An analysis of variance (ANOVA) problem is often used as a general example of simultaneous inference since decisions about main and interaction effects are made concurrently. Furthermore, the various multiple-comparison techniques (e.g., Fisher's LSD Procedure, Duncan's New Multiple Range Method) are well-known methods of simultaneous inference. We wish to bring to the attention of ornithologists a common statistical error involving simultaneous inferences or conclusions based on two or more tests of hypotheses. Simultaneous inferences are drawn from a family of concep-

tually related hypotheses. These related hypotheses usually emanate from groups of observations that are collected by an individual researcher or research team (Miller 1981).

As an example, consider a researcher who quantifies several response variables in a single study. Finch (1991) used a number of reproductive measures (e.g., mean laying date, rates of nest failure, initial clutch size, fledgling rates) in a study of the effect of three levels of flooding on timing of reproduction and productivity of House Wrens (*Troglodytes aedon*). Because Finch reaches a set of simultaneous conclusions about the relationships among reproductive measures and flooding, they constitute a family of hypotheses.

We set α , the probability of a type I error (rejection of the null hypothesis when it is true), at a conventional value such as 0.05. Therefore, the probability of accepting the null hypothesis when true, $(1 - \alpha)$, is quite high for a single test of hypotheses (see, for example,

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