

that it is not as broad an explanation for song complexity as originally hoped.

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Pigeons', *Columba livia*, Use of Global and Local Cues for Spatial Memory

The use of more than one source of spatial information should enhance an animal's ability to localize a goal object. For example, the use of spatial information provided by features of the wide environment in conjunction with the use of nearby objects as beacons, could improve the precision of localization (Bossema 1979). The cues that are most useful may also vary at different phases in the search process, or from different vantage points. For example, horizontal beacons may be most conspicuous during approach from the air, whereas vertical objects may be more noticeable when searching from ground level (Bossema 1979).

Attention to several sources of spatial information may also be adaptive because changes in environmental conditions can render certain important sources of spatial information unavailable. As an example, consider the spatial localization problem faced by food-storing birds that appear to rely on memory to recover their caches. Nearby surface objects such as rocks or sticks may provide the most precise spatial landmarks for memory, but may not always be available at recovery time due to snow cover or removal by wind or rain. It would therefore be adaptive to include also some larger, more permanent objects, such as tall trees, in a spatial memory of cache locations (Balda & Turek 1984). Still larger topographical features of the area, such as hills and canyons, may provide the cues used to orient towards cache sites from distant locations, or to prevent the bird from searching at visually similar but incorrect locations (Bossema 1979).

Laboratory studies of spatial memory in food-storing birds have provided some evidence for redundancy of cue use. For example, when objects such as rocks and shrubs are present during caching and retrieval of seeds, Clark's nutcrackers, *Nucifraga columbiana*, appear to rely on these local surface cues: displacing the objects after the caching period caused the birds to adjust their search locations and miss many of the caches (Vander Wall 1982; Balda & Turek 1984). However, Balda & Turek (1984) found that the birds' accuracy in locating their caches was still above the level of chance when the surface objects were removed altogether during caching and recovery, suggesting that the birds had also incorporated information about some of the more global room features into their cache location memory.

Redundancy in cue use also seems to be an adaptive feature of the navigational system of

homing pigeons. The ability to use several sources of information allows place and direction to be determined even when some important sources of information are not available (Keeton 1974). For example, the sun appears to be the primary source of compass information, but is not available under total overcast; at these times homing pigeons apparently rely on a back-up source of compass information (Keeton 1974).

The present experiment provided a laboratory investigation of redundant cue use by pigeons in another type of spatial localization problem, namely learning the location of a baited food site. In previous work (Spetch & Edwards 1986) we found that pigeons displayed accurate working memory (Olton 1978) for which of several food

sites they had recently visited in an open-field setting. Furthermore, they did not rely on cues intrinsic to the food sites, suggesting that they used extrinsic spatial information to remember the visited sites. However, the particular cue or cues that controlled the memory have not been assessed. Furthermore, pigeons' use of spatial information while learning the location of a single baited food site (a reference memory task) has not been analysed. During training and baseline trials of the present experiment, there was a single baited site that could be located on the basis of either of two extrinsic spatial cues: the position relative to two identical but unbaited sites (referred to as local cues), or the location in the room (referred to as global cues). Test trials assessed the degree to which

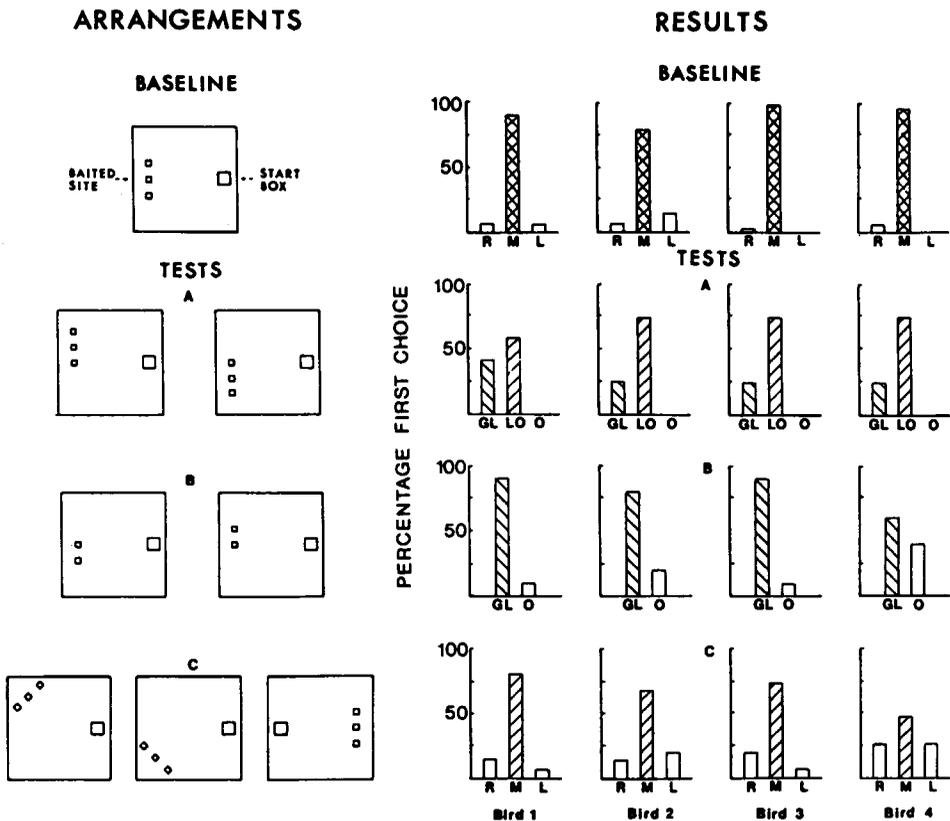


Figure 1. Arrangements: overhead views of the apparatus showing start box and carton arrangements during baseline and test trials (A: tests of global versus local cues; B: tests with global cues only; C: test with local cues only). Results: percentage of trials each carton was chosen first during baseline and tests for each of the four subjects. R: right-hand carton; M: middle carton; L: left-hand carton; GL: carton in the globally correct room location; LO: carton in the locally correct carton position; O: carton in the other position.

pigeons incorporated these redundant but relevant cues into their reference memory for the location of the baited site.

The subjects were four adult white king pigeons, *Columba livia*, maintained at 85% of their free-feeding body weight. Between sessions, the pigeons were housed individually in wire-mesh cages with ad libitum access to water and grit. The experimental space consisted of an open room, 2.4 m long, 2.3 m wide and 2.4 m high. The animals were observed through a one-way window. During all training and baseline trials, the room contained a start box centred against one wall, and three cartons in which food could be hidden (Spetch & Edwards 1986) centred along the opposite wall (see Fig. 1). On each trial, the middle carton was baited with five kernels of corn; the two outside cartons were never baited. To begin a trial, the pigeon was placed in the start box with the room dark. When the light was turned on the pigeon could leave the start box (through an opening that faced the wall) and search among the cartons. The experimenter recorded the first carton chosen on each trial. The pigeon was permitted to continue searching until it located the baited carton. Two min after the pigeon consumed the food, the light was turned out to end the trial.

Each pigeon first received one training trial each day for 50 days. Accuracy (percentage of trials in which the baited carton was chosen first) was near the level of chance (i.e. 33%) during the first block of five trials ($\bar{X} \pm \text{SE} = 35 \pm 15\%$), but increased to a mean of 90% ($\text{SE} = 10\%$) during the last block. In preparation for testing, subjects next received five successive trials each day. They initially displayed lower accuracy on trials two–five, but within 10 days performed accurately on all trials. Adapting the pigeons to five trials per day facilitated subsequent testing because it allowed us to conduct one test trial each day, interspersed among four baseline training trials.

The test phase assessed the degree to which the pigeons' reference memories included the local cues provided by the position of the baited carton relative to the others, and the more global cues afforded by the location of the baited carton in the room. In one type of test (Fig. 1A) these cues were pitted against one another: the cartons were displaced to the left or right so that the local cues would guide the birds to the middle carton whereas global cues would guide the birds to one of the side cartons. Other tests examined control by each cue in isolation. In the global-only tests (Fig. 1B), local, carton-position cues were removed by testing with only two cartons. In the local-only tests (Fig. 1C), the global location cues were negated by moving all three cartons to different places in the room. Each

test session consisted of four reinforced baseline trials, and one test trial. No cartons were baited on test trials. The tests occurred alternately on the third or fourth trial; the corresponding trial of the preceding day served as the baseline for comparison. Each pigeon received 10 global-only test trials, 12 local versus global test trials, and 15 local-only test trials. These tests were presented in a mixed order for each bird, and the order differed between birds. Choice frequencies were analysed with chi-squared tests. All differences reported below were significant at $P < 0.01$.

Fig. 1 (Results) shows the choice behaviour of each of the four pigeons during baseline and test trials in terms of the percentage of trials in which they chose each carton as their first choice. Accuracy in the baseline trials remained high throughout testing: all subjects chose the middle carton first in almost all trials. On the local versus global tests, all pigeons favoured the middle, locally correct carton. However, they also chose the carton in the globally correct room location more often than the remaining carton; in fact, the remaining carton was never chosen on these global versus local test trials. The tests with each cue in isolation also indicated control by both global and local information. During the global-only tests, pigeons chose the carton in the correct room location more often than the other carton. During the local-only tests, the birds chose the middle carton more often than either of the others. Preferences did not change systematically over the repeated test trials, although latency to make a choice on test trials did increase for some birds.

The control exerted by either the local (carton) cues, or the global (room) cues, when tested in isolation, indicates that the pigeons acquired and remembered information about both types of spatial cues. Each cue alone controlled the birds' choice behaviour with a considerable degree of precision. When the two cues were placed in opposition, all pigeons favoured the local cues, but all showed global-cue influence as well. This suggests a hierarchical organization of redundant but relevant spatial information: one source appears to dominate when it is available, but a secondary source can be used for localization with considerable accuracy when the primary one is not available. This appears analogous to the way in which homing pigeons seem to use multiple sources of directional information for compass determination. Thus, in this laboratory task, pigeons displayed the sort of flexible, redundant cue use that should be adaptive in natural spatial localization problems.

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Vocal Recognition of Mates by Breeding Pinyon Jays, *Gymnorhinus cyanocephalus*

The formation and maintenance of groups of cooperating individuals is facilitated by, and may depend upon, an ability of group members to recognize each other (Thorpe 1968; Beer 1970; Axelrod & Hamilton 1981). Recognition of mates and relatives would facilitate cooperation among members of extended families.

The mating system, and the degree to which members of different families intermix, influences the occurrence of mate recognition. Organisms forming long-term, monogamous pair bonds must be able to distinguish their mates from other group members. Mate recognition is especially prevalent

among birds because monogamy is the typical mating system (Lack 1968), and pairs often nest in colonies where coordination of nesting behaviour depends on the ability of individuals to identify signals from their mates out of the array of signals given by other members of the colony (Hutchison et al. 1968; White 1971; Brooke 1978; Miller 1979).

Pinyon jays, *Gymnorhinus cyanocephalus*, are long-lived, permanently monogamous (Marzluff & Balda, unpublished data), colonial nesters (Balda & Bateman 1971, 1972) that live throughout the year in flocks composed of numerous extended families (Marzluff 1987). Therefore, mate recognition should be well developed. Evidence that pinyon jays recognize their mates includes: (1) mates react differently to each other than to other flock members under laboratory conditions (Berger & Ligon 1977; Marzluff & Balda, unpublished data), and (2) mates, separated experimentally for months, reunite the following breeding season (Marzluff & Balda, unpublished data). Here I document vocal recognition of mates by free-ranging jays.

Pinyon jay colonies contain up to 50 pairs nesting in synchrony. The distance between nests averages 40-50 m (Balda & Bateman 1972). Females incubate continuously, especially during the snowy early spring (Balda & Bateman 1972). One of the most striking features of a breeding colony is its sudden transformation from a quiet section of forest to a noisy milieu of calling, flying birds as 20-50 males return synchronously about once per hour to feed their mates. Returning males perch high in trees throughout the colony and give approach calls (McArthur 1979, 1982) before they enter their nest tree. In response, females look up from the nest, utter begging calls, and sometimes fly to their mates. Females appear to respond only to their mates' calls. Unnecessary movement around the nest, or exposure of eggs or nestlings to cold and predators, could reduce success, thus females which are attentive only to the presence of their mates might be expected to have higher reproductive success than indiscriminate females.

Approach calls are a variation of the near-er vocalization described by Balda & Bateman (1972). The near-er apparently encodes a non-aggressive message and is used primarily as a contact call, especially between mates (Berger & Ligon 1977). McArthur (1979) recorded two types of approach near-ers; one with two frequency peaks and one with three frequency peaks. He hypothesized that the increased complexity of the three-peaked calls might function in individual recognition. Individual differences that facilitate recognition by mates and offspring should be especially important in male approach calls because males provide up to