

Long-term memory for a life on the move

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Evidence is accumulating that cognitive abilities are shaped by the specific ecological conditions to which animals are exposed. Long-distance migratory birds may provide a striking example of this. Field observations have shown that, at least in some species, a substantial proportion of individuals return to the same breeding, wintering, and stopover sites in successive years. This observation suggests that migrants have evolved special cognitive abilities that enable them to accomplish these feats. Here we show that memory of a particular feeding site persisted for at least 12 months in a long-distance migrant, whereas a closely related nonmigrant could remember such a site for only 2 weeks. Thus, it seems that the migratory lifestyle has influenced the learning and memorizing capacities of migratory birds. These results build a bridge between field observations suggesting special memorization feats of migratory birds and previous neuroanatomical results from the same two species indicating an increase in relative hippocampal size from the first to the second year of life in the migrant but not in the nonmigrant.

Many of the estimated 50 billion birds (1) that carry out regular seasonal migrations return to the same breeding and wintering grounds, and even stopover sites, in successive years (2–6). A substantial number of birds have been recovered at exactly the same location a year later, having completed a migratory route of 10,000 km or more (7–9). Yearly journeys often proceed according to rigid seasonal patterns and along well defined species- or population-specific routes (10–12). Many small passerine long-distance migrants travel by night and singly with little evidence of cohesive social units being maintained (13, 14). Therefore, social learning probably plays only a minor role, if any, in determining spatio-temporal migration patterns.

It is known from several in-depth studies that young passerines on their first migration use the sun, the stars, and/or the earth's magnetic field as compasses to guide them into appropriate, presumably innate directions (15–17). The distance, and thus the endpoint of migration, appears to depend, at least in part, on an endogenous circannual program (18). However, there is also evidence that this simple system of "vector navigation" is supplemented or replaced in older birds by more complex navigation systems that are based on learning (19). In addition, it is possible that details of suitable sites like habitat structure and vegetation are also learned and memorized for reference during the next migration season (20–24). Thus, these learned cues must be remembered for a period of 1 year or even more.

That learning during migration is significant is suggested by neuroanatomical differences in the development of the hippocampal formation between migratory and nonmigratory bird species (25), a crucial brain region for processing spatial information (26–28). The relative size of the hippocampal formation of migration-experienced, adult long-distance migratory garden warblers (*Sylvia borin*) is larger than that of migratory-naive, juvenile individuals of the same species. No comparable contrast in relative hippocampal size was found in the closely related nonmigratory Sardinian warbler (*Sylvia melanocephala momus*). These findings are consistent with the hypothesis that migrants acquire spatial information about the route and stopover sites (25) and, more generally, with studies indicating a relatively larger hippocampal size in birds and mammals that are strongly dependent on spatial information (26–28).

So far, little experimental work has been devoted to investigating possible cognitive adaptations to a migratory lifestyle. Therefore, in the present study, we tested whether the garden warbler has a long-term memory for a particular high-quality feeding site and whether its memory retention time is longer than that of the Sardinian warbler, which, as a nonmigrant, does not necessarily have to depend on long-term memory abilities. The two species are closely related members of the same genus (29, 30), inhabit roughly similar habitats, and have a similar food spectrum consisting mainly of insects during the breeding season and a mixture of insects and fruits during the nonbreeding season (30, 31). They do, however, differ in their migratory behavior. Garden warblers are long-distance nocturnal migrants, breeding in Europe and wintering south of the Sahara (31). The subspecies of Sardinian warblers investigated is, in contrast, a year-round resident in Israel (32).

Materials and Methods

Subjects. In 1998 and 2000, a total of 131 nestling garden warblers and Sardinian warblers were collected in Germany and Israel, respectively, and raised by hand. After having become independent, all birds were kept in structured aviaries with their respective natural photoperiodic conditions simulated.

General Experimental Design. The experiment consisted of an exploration phase and a memory test. The experiment started in autumn when the garden warblers showed nocturnal migratory restlessness during their first autumn migration period (33). Autumn was selected for the exploration phase because the free-living migrants encounter many unfamiliar environments on migration during that time. This is the phase of their annual cycle during which these birds are most likely to collect and store information for future journeys. At this time, the nonmigratory species does not go beyond exploring the close vicinity of its home area during territory acquisition. Thus, any differences in memory formation between migrants and nonmigrants would be expected when one is on migration, while the other remains stationary.

During the first migration period of the garden warbler, both species were given access to two unfamiliar rooms (80 × 120 × 100 cm) adjacent to each other, which they could enter from a familiar home cage and explore for 8.5 h (exploration phase). Little is known about the environmental features that are normally learned by migrants and nonmigrants, so we tried to simulate a situation close to the natural one. For this reason, we offered two kinds of artificial vegetation, either silk geranium or silk ivy, to simulate two habitat types rather than more abstract structures. The vegetation was arranged around 13 perches distributed in the rooms. Both rooms were equipped with eight bowls, filled with food (commercially available dried insects and a pollen/sugar mixture) in only one room, so that the rooms represented high- and low-quality habitats (Fig. 1). To prevent the bird from restricting its activity to only one room, it was first allowed access to one room for 1.5 h and then to the other room

This paper was submitted directly (Track II) to the PNAS office.

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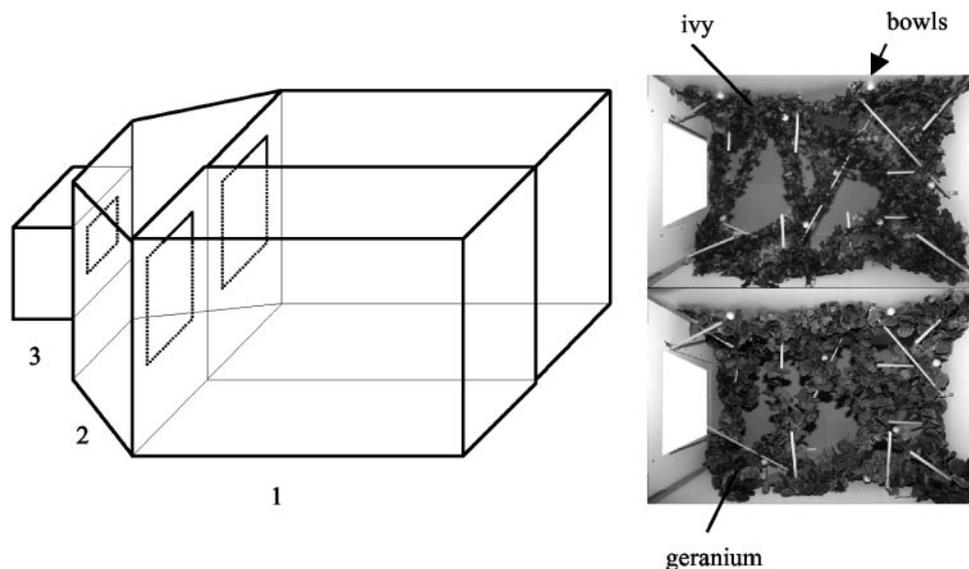


Fig. 1. Experimental design. (Left) Schematic diagram of the experimental design. 1, experimental rooms; 2, neutral room; 3, home cage; dotted lines, openings to the experimental rooms and the cage. (Right) Photograph of the experimental rooms.

for the same period. For the remaining 5.5 h, both rooms were accessible. Food and water were available ad libitum in the home cage. After the exploration phase, the bird was returned to its aviary.

Four birds were run simultaneously in four identical units, each consisting of the two rooms. The first room made accessible to a given bird during the exploration phase provided one of eight combinations of features: ivy with or without food, located left or right, and the same four alternatives for geranium. Before the exploration phase, each bird had been assigned to a specific group for subsequent memory testing at different times in such a way that nest mates were in different groups and sex ratios were relatively uniform; there were six such groups for the garden warbler and five for the Sardinian warbler (Table 1). Within each group, approximately half of the birds received food in the room with ivy, the other half in the room with geranium, and the above-mentioned eight possibilities for the first room accessible were also about equally represented. Finally, the two species, as well as the individuals within each group, were equally distributed among the four units.

The memory test followed after different time intervals (Table 1). The behavior of each bird was video-recorded during both phases.

Specific Experimental Procedure. During the exploration phase, each bird was moved into an individual cage (75 × 40 × 40 cm)

for 1 week to become habituated to it. Passive infrared detectors (Conrad Electronic, Hirschau, Germany) recorded locomotor activity to determine whether the bird exhibited nocturnal migratory activity (33). If this was the case in a garden warbler, the bird was moved to another but identical cage (called “home cage”) in the test chamber, where it remained undisturbed for 2 nights and 1 day. For the resident Sardinian warblers, we did not consider nocturnal activity, but moved each bird after 1 week of habituation to the cage in the test chamber. On the third day, the test day, the bird was allowed to investigate the two rooms adjacent to the home cage for 8.5 h.

Preparation for the memory test, which followed after different time intervals (Table 1), was identical to that for the exploration phase, except that food was removed from the home cage 2 h before the lights were turned off on the pretest day until the end of the test the next day. The test rooms contained neither food nor food bowls. The bird had free access to both rooms simultaneously for 20 min.

Statistical Analyses. During the memory test, we recorded how much time the bird spent in each room. Because there were no differences between years (Kolmogorov–Smirnov test: $P > 0.05$), data were analyzed together. The percentage of time spent in each of the two rooms was compared within each group with Wilcoxon Signed Ranks tests. In addition, differences between species were tested with a two-way ANOVA with species and

Table 1. Test design

| Group | Time since exploration | Species | | | | Corresponding in garden warblers to |
|-------|------------------------|----------------|----------|-------------------|----------|-------------------------------------|
| | | Garden warbler | | Sardinian warbler | | |
| | | Year* | <i>n</i> | Year* | <i>n</i> | |
| 1 | 4 days | 2000 | 8 | 1998/2000 | 12 | First autumn migration period |
| 2 | 2 weeks | 1998/2000 | 13 | 1998/2000 | 12 | First autumn migration period |
| 3 | 1 month | 1998 | 9 | 1998 | 6 | First autumn migration period |
| 4 | 5.5 months | 1998/2000 | 13 | 2000 | 7 | Time in the winter quarter |
| 5 | 8.5 months | 1998 | 7 | — | — | Spring migration period |
| 6 | 12 months | 1998/2000 | 14 | 2000 | 10 | Second autumn migration period |

*Because of time and space limitations, experiments had to be split up into two experimental years.

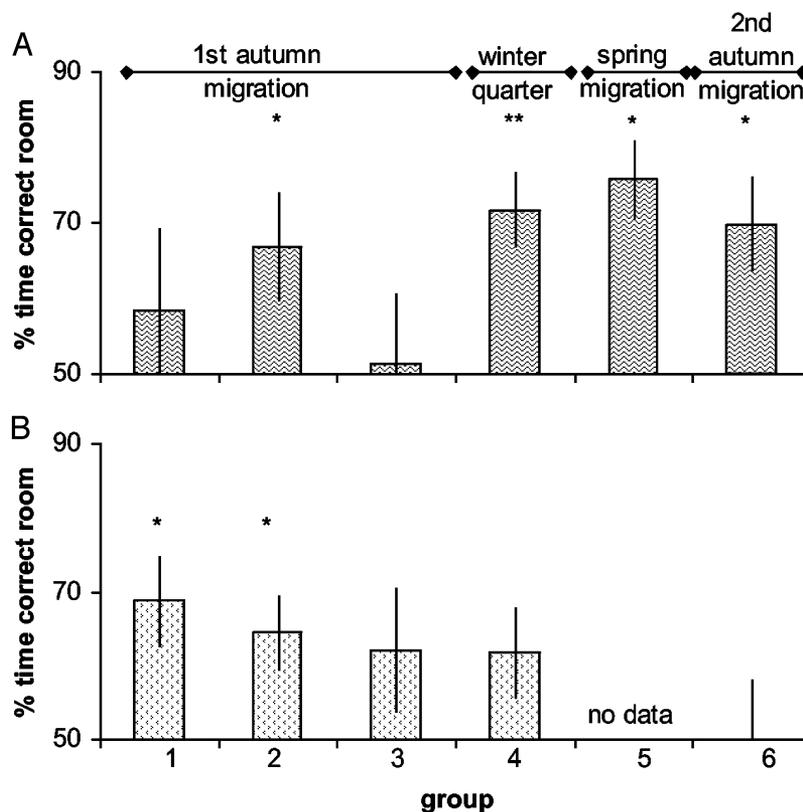


Fig. 2. Percent time (means \pm SEM) spent by the birds of the various groups during the memory-test phase in the room that had contained food during the exploration phase (correct room). (A) Garden warblers. (B) Sardinian warblers. Asterisks indicate significant preferences for the correct room (paired Wilcoxon signed ranks test: *, $P < 0.05$; **, $P < 0.01$). For groups, see Table 1.

group as independent variables and percent time spent in the correct room, expressed as rankings, as the dependent variable. Rankings were used to reach equality of variances (34). We pooled the data of groups 1–3 (tested within the first month after exploration) and 4–6 (tested 5.5–12 months after exploration), respectively.

A total of 9 of 76 garden warblers (maximally two birds per group) and 8 of 55 Sardinian warblers (maximally three birds per group) refused to enter the rooms either during the exploration or the test phase and thus had to be excluded from the analysis. The same was necessary for three garden warblers that showed severe seasonal irregularities in the expression of their migratory restlessness and hence could not be clearly allotted to a particular seasonal state.

Results

In the long-distance migrant, the garden warbler, birds in four of the six groups spent significantly more time in the “correct” room, i.e., the room that had contained food during the exploration phase, than in the “incorrect” room. In particular, the groups tested after 2 weeks (first autumn migration period, Wilcoxon signed ranks test: $z = -2.201$, $P < 0.05$), 5.5 months (winter: $z = -2.824$, $P < 0.01$), 8.5 months (spring migration period: $z = -2.366$, $P < 0.05$), and 12 months (second autumn migration period: $z = -2.449$, $P < 0.05$) showed a clear preference for this room (Fig. 2A).

In the nonmigratory Sardinian warblers, in contrast, only the groups tested after 4 days and 2 weeks preferred the “correct” room (4 days: $z = -2.275$, $P < 0.05$; 2 weeks: $z = -2.353$, $P < 0.05$), whereas the groups tested after 1, 5.5, and 12 months showed no significant preference (Fig. 2B; 1 month: $z = -1.363$,

$P > 0.05$; 5.5 months: $z = -1.690$, $P > 0.05$; 12 months: $z = -0.157$, $P > 0.05$).

A comparison of the percentage of time spent in each room by all birds of groups 1–3 (tested after 4 days to 1 month) with those of groups 4–6 (tested after 5.5 to 12 months) revealed a significant interaction between species and group (ANOVA: $F = 2.909$, $P < 0.05$; species: $F = 3.158$, $P > 0.05$; group: $F = 0.003$, $P > 0.05$; species \times group: $F = 6.179$, $P < 0.02$) indicating species differences with respect to long- and short-term memory. A direct comparison of the performance of garden warblers and Sardinian warblers tested after short intervals (groups 1–3) revealed no significant species difference (t test: $F = 1.133$, $P > 0.05$). On the other hand, the memory of birds tested after long intervals (groups 4–6) was significantly better in the garden warblers than in the Sardinian warblers ($F = 2.923$, $P < 0.005$).

Discussion

The results suggest that the long-lasting memory demonstrated here by a long-distance migrant is an important mechanism guaranteeing a successful journey. We propose that it helps birds remember high-quality stopover sites, thereby optimizing migratory performance during subsequent journeys. At the same time it may allow birds to avoid areas unsuitable for refueling and thus help them save energy and time. Moreover, the long-term memorization of a particular location is probably a major prerequisite for the well known phenomenon of breeding-site fidelity. Familiarity with a particular breeding ground can be advantageous when competing with other birds less familiar with the same location (2). Likewise, a long-lasting memory may increase survival when details of the wintering area are familiar to a bird from previous experience. Nonmigratory birds, in contrast, may not require such a long-lasting memory because

they can continuously update their knowledge of the area in which they live permanently (35). In fact, it may be more beneficial for a nonmigrant to have only a short-term memory because this would reduce interference between old and newly memorized information (36). Our results suggest that the migratory lifestyle has shaped the evolution of particular cognitive abilities.

Although it is clear from many observations and experiments that learning and memory are involved in the navigational performance of migratory birds, many details of the underlying mechanisms are not yet known. Presumably, the overall navigation system is composed of a number of different submechanisms. Wallraff (37) has suggested the following scenario: the most basic mechanism used for orientation is a circannual time and direction program; it is already in use when inexperienced birds perform their first migration. This innate program can hardly be the result of prior learning, but is capable of guiding birds to the gross vicinity of their wintering quarters and breeding grounds (33). Navigational mechanisms *sensu strictu* come into play only after the first migratory journey. On a larger scale, navigation based on gradient maps that have been acquired through individual experience allows birds to get closer to their goal areas, even from unfamiliar sites. On a smaller scale, the birds use a topographical map, built up during previous exploration of site-specific features. Like the gradient map, the topographical map is entirely based on learning and memory; it allows birds to eventually pinpoint last years' breeding site and wintering quarters, as well as previously used resting and staging areas along the route that were favorable. It is likely that the long-term memory for a particular site demonstrated in the present experiment, as characterized by its position and vegetation, is related to the latter kind of short-distance orientation mechanism rather than to the establishment of a gradient map used for orientation over longer distances.

The long-lasting memory of Garden warblers is exceptional and, to our knowledge, provides the first evidence that memory duration may be related to migration. A comparable long-term memory has been documented in Clark's nutcrackers (*Nucifraga columbiana*). During winter and spring, this species depends heavily on food caches created during autumn. Under experimental conditions, birds are capable of remembering food caches for up to 285 days (38). As another example of long-term memory Kendrick *et al.* (39) showed that sheep (*Ovis aries*) can remember each other faces in a social context for up to 2 years, after having received considerable training, i.e., 400–500 trials.

Our behavioral data bridge the gap between field observations indicating a long-term memory for particular sites during breeding, migration and wintering (site fidelity) and the neuroanatomical evidence of hippocampal changes mentioned above. Long-distance migratory garden warblers have the cognitive ability to remember high-quality feeding sites for at least 1 year, and we propose that this capacity helps them to return to suitable places widely separated in space and time. The hippocampal formation is a plausible neuroanatomical substrate for this type of memory process (25).

The results and conclusions presented here are based on the comparison of only two related species, one being strongly migratory, the other resident. Although these two species are similar in many aspects, we cannot, of course, exclude the possibility that their different memorizing abilities are associated with differences unrelated to migration. More comparative work employing experimental approaches similar to those used in the present study is required to elucidate whether a long-term memory is a general characteristic of migratory birds.

Future work should also address the question as to whether migratory birds differ from nonmigratory ones with regard to cognitive abilities other than just memory duration. For instance: (i) do migrants assess environmental information more rapidly than nonmigrants? A more rapid evaluation of cues regarding the special features of the environment might help migrants that have only recently arrived at a stopover site to become familiar with it more quickly and reduce predation risk. (ii) Are there differences between migrants and nonmigrants in the kind of information memorized? For instance, are habitat characteristics or spatial cues more important? A related question is (iii) do migratory birds differ from nonmigrants only in specific memory tasks, or are differences consistently found across a variety of tasks? And (iv), what precisely is the relationship between spatial learning by migratory birds and their hippocampal development?

In showing that questions of this kind can, in principle, be experimentally investigated in caged birds, our present study suggests a possible route for future work on the special cognitive mechanisms that migratory behavior may require.

We thank P. Bartell, R. Brandstaetter, H. Fugger, B. Helm, H. Schwabl, and H.-G. Wallraff for helpful comments. C.M.-H. was partly funded by the Herbert-Quandt-Stiftung of the Varta AG and partly by postdoctoral grants from the Max Planck Society. Logistic support was provided by Ferrero OHG mbH.

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