The Auk 122(2):608–617, 2005
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Printed in USA.

HOMING SUCCESS OF MIGRANT VERSUS NONMIGRANT DARK-EYED JUNCOS (*JUNCO HYEMALIS*)

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Abstract.—Within a population, the evolution of migratory behavior is accompanied by a suite of physiological, behavioral, and cognitive adaptations. Spatial memory is associated with the hippocampus in mammals and birds; in some cases, hippocampal neuroanatomy correlates with differences in behavior. In a recent study, a migratory subspecies of sparrow, the Dark-eyed Junco (*Junco hyemalis hyemalis*), performed better on room-scale spatial memory tests than did a nonmigratory conspecific. Migrants collected after migration also possessed greater hippocampal neuron density, which suggests a neurological basis for differences in spatial memory and a link between migratory behavior and enhanced spatial memory. It is likely that homing behavior, like migration, relies to some extent on spatial memory. In some instances, spatial memory performance has generalized across spatial scales, with pronounced differences at larger scales. We tested whether differences in spatial memory between migrants and nonmigrants, previously observed at a room scale, were detectable at a landscape scale; specifically, we investigated whether differences in homing ability could be detected after displacements of 1–40 km. We found no difference in number of returning individuals or in duration of return. Our results suggest that homing in this species may not rely on aspects of spatial memory that differed in aviary tests. *Received 7 November 2003, accepted 15 November 2004.*

Key words: Dark-eyed Junco, homing, *Junco hyemalis*, migration, spatial memory.

Éxito de Retorno al Sitio Natal de Individuos Migratorios y No Migratorios de *Junco hyemalis*

Resumen.—Dentro de una población, la evolución del comportamiento migratorio está acompañada por una serie de adaptaciones fisiológicas, comportamentales y cognitivas. La memoria espacial está asociada con el hipocampo en los mamíferos y las aves; en algunos casos, la anatomía nerviosa del hipocampo se correlaciona con diferencias en el comportamiento. En un estudio reciente, una subespecie migratoria, *Junco hyemalis hyemalis*, se desempeñó mejor en una prueba de memoria espacial a escala de habitación que un coespecífico no migratorio. Las aves migratorias colectadas luego de la migración también presentaron mayor densidad neuronal del hipocampo, lo que sugiere una base neurológica para las diferencias en la memoria espacial y una conexión entre el comportamiento migratorio y una capacidad aumentada de memoria espacial. Es probable que el comportamiento de retorno al sitio natal, como la migración, se base en cierta medida en la memoria espacial. En algunos casos, el desempeño de la memoria espacial se ha generalizado a través de las escalas espaciales, con diferencias pronunciadas a escalas mayores. En este estudio

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evaluamos si las diferencias en memoria espacial entre individuos migratorios y no migratorios, previamente observadas a escala de habitación, eran detectables a escala de paisaje. Específicamente, investigamos si las diferencias en la habilidad de retornar al sitio natal podían ser detectadas luego de desplazamientos de entre 1 y 40 km. No encontramos diferencias en el número de individuos que retornaron o en la duración del retorno. Nuestros resultados sugieren que la habilidad de retornar al sitio natal en esta especie podría no basarse en los aspectos de la memoria espacial que difirieron en las pruebas de aviario.

THE EVOLUTION OF migratory behavior—which usually requires the ability to navigate—has likely resulted in a suite of physiological, behavioral, and cognitive adaptations (Dingle 1996). Navigation requires an animal to assess its spatial position in relation to a goal. Navigating back to a familiar location requires memory and may involve memory of many intermediate spatial landmarks. Thus, for a migratory bird that returns to the same breeding and wintering territories (or both) each year, enhanced spatial processing abilities would be adaptive.

Although the link between spatial memory and migration—or the related behavior, homing—has not been well documented, returning to a familiar location after migration or displacement would be facilitated by accurate memory of spatial locations. Spatial memory is associated with the hippocampus in several mammals and birds. Many studies indicate that hippocampal neuroanatomy correlates with differences in behaviors that may involve spatial memory (Krebs et al. 1989, 1996; Sherry et al. 1989; Jacobs et al. 1990; Jacobs and Spencer 1994; but see Brodin and Lundborg 2003). Because the avian hippocampus is believed to be important in spatial processing, it is reasonable to assume that it also functions in navigation (Bingman et al. 1999, Macphail 2002), migration (Jacobs 1996), and homing.

The relationship between hippocampal size and enhanced spatial memory has been investigated in migratory birds. Migration-experienced (adult) Garden Warblers (*Sylvia borin*) possessed proportionately larger hippocampi than migration-naive (young) birds—a contrast not seen in the congeneric, nonmigratory Sardinian Warbler (*S. melanocephala*; Healy et al. 1996). In a laboratory choice test with the same two warbler species, migrants remembered a location with more food for ≤12 months, whereas nonmigrants remembered the location for only two weeks (Mettke-Hofmann and Gwinner 2003). However, earlier homing studies with the two species suggest that the migratory Garden Warbler is not more likely to home successfully than the nonmigatory Sardinian Warbler (Ioale and Benvenuti 1983, Baillon et al. 1992).

In a recent laboratory experiment using a sparrow that does not store food, the Dark-eyed Junco (*Junco hyemalis*; hereafter "junco"), Cristol et al. (2003) detected a significant difference in spatial memory ability between a migratory (*J. h. hyemalis*; hereafter "migrant") and nonmigratory (*J. h. carolinensis*; hereafter "nonmigrant") subspecies. Migrants captured shortly after migration were better able to remember the locations of hidden food items separated by a few meters than were nonmigrants captured at the same time of year. Migrants also possessed greater hippocampal neuron density than nonmigrants, which suggests a neuroanatomical basis for differences in spatial memory and a link between migration behavior and spatial memory ability.

All birds likely possess some degree of homing ability, yet species vary greatly in the degree to which they exhibit homing behavior (Manwell 1941). Systematic investigations of homing behavior in wild, free-living birds are rare (Baldaccini et al. 2001). Throughout the 20th century, scientists and amateur ornithologists carried out homing studies with wild birds; however, much of that early work consisted of little more than the documentation of the unexpected return of a handful of nuisance birds relocated several kilometers. Some early researchers performed systematic experiments and reported homing feats of hundreds to thousands of kilometers by species such as storks, shearwaters, swallows, and starlings (Matthews 1955). Overall, those and more recent studies indicate that numerous birds readily home during the breeding season (Barber and Robertson 1998, Sokolov and Vysotsky 1999, Bélisle et al. 2001). However, many species are able to home in the winter as well, including migratory juncos (Keiper and Klinger 1977, Ioale and Benvenuti 1983, Baillon et al. 1992).

We designed a field experiment to assess whether differences in spatial abilities demonstrated at the scale of an aviary were detectable at the landscape scale; specifically, we investigated whether differences between migrants and nonmigrants could be detected during homing after displacements of 1–40 km. We simultaneously relocated migratory and nonmigratory juncos and compared homing success and the time required to make the return trip. Juncos—both migrants and nonmigrants—are known to home when experimentally displaced (Keiper and Klinger 1977, Nolan et al. 1986). At the time of year when the present experiment was performed, migratory juncos have more densely packed hippocampal neurons and better performance on a room-scale spatial-memory test than nonmigrants. Therefore, we predicted that the migrants would be more likely than nonmigrants to return successfully and would do so more quickly.

METHODS

Study species and site.—During the breeding season, migrant juncos nest in Canada and the northeastern United States; nonmigrant juncos nest above 900 m in the Appalachian Mountains in the southeastern USA (Nolan et al. 1986). During the nonbreeding season, migrants move hundreds to thousands of kilometers into a winter range that includes most of the eastern United States; nonmigrants either remain on breeding territories or move a few kilometers to new home ranges at lower elevations. In southwestern Virginia, migratory and nonmigratory subspecies of juncos occur in mixed flocks only during the nonbreeding season. To take advantage of this opportunity to control for environmental variation while comparing homing ability in migrant and nonmigrant conspecifics in the wild, we performed our homing experiment during winter. Early winter is also the time of year when spatial memory and hippocampal neuron density differ between the junco subspecies; thus, it is the only season in which one would predict a difference in homing ability.

Sites used to capture birds intended for displacement were within 3 km of a point located at 37°19'47"N, 80°34'19"W in Giles County, Virginia (Fig. 1). Two capture sites, 1.9 km apart, formed a mid-elevation cluster (sites M1 and M2); and three sites formed a low-elevation cluster (sites L1, L2, and L3). The capture sites within the low-elevation cluster were positioned so that ≤0.5 km separated adjacent sites. Two of the sites (L1 and L3) were among those used to examine winter site-fidelity (see below).

All capture sites were positioned below breeding elevation to eliminate the possibility of testing homing in a nonmigrant that was wintering on a potential breeding territory and thus might be unusually motivated to return. In the first of two field seasons, we used an additional capture site located at ~1,150 m elevation—well within the breeding habitat of nonmigrant juncos. A significantly greater proportion of nonmigrants returned to the high-elevation site than to the sites located below 900 m. We believe that the disparity was the result of greater motivation among some birds to return to potential breeding sites; therefore, that site was not used in the following field season. Data from the high-elevation site were used only for the winter site-fidelity calculations carried out prior to the homing experiment.

Release sites were positioned at five distances from each capture-site cluster: 1, 5, 10, 20, and 40 km (Fig. 1). All release sites were in the same valley so that all homing birds faced the same topography. It should be noted that birds returning from the 40-km release sites had to cross a large river. Otherwise, release sites were chosen for similarity of vegetative cover and absence of dense human development.

Capture, relocation, and detection.—Homing experiments were performed during two successive winter field seasons: 19 January through 4 February 2002, and 1–19 January 2003. To capture juncos, we used mist nets (all sites) and Potter traps (site M1 only) baited with corn (*Zea mays*) and millet (*Panicum miliaceum*). Individuals were marked with a single federal metal alloy band and five colored plastic bands (Redbird Products, Sacramento, California) for a total of three bands per tarsus. Identification of subspecies, age, and sex was based on differences in plumage, bill color and shape, eye color, cranial ossification, and length of wing chord (Nolan et al. 2002). One or both of two experienced observers (D.A.C. or C.W.S.Z.) made all subspecies classifications. Individuals

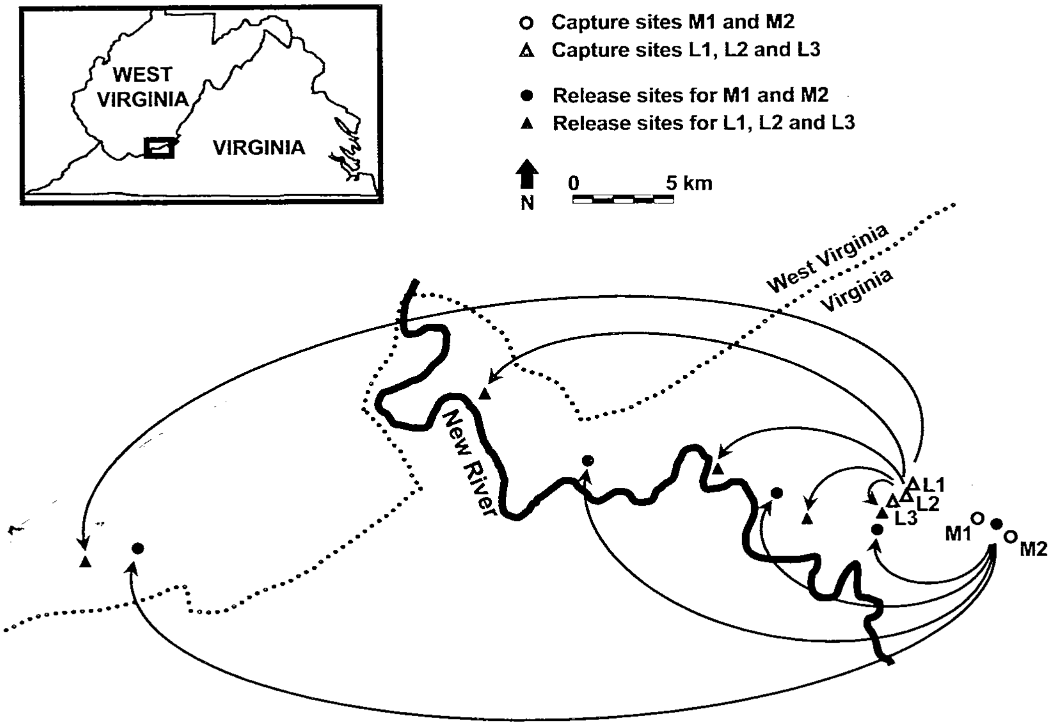

Fig. 1. Schematic map of capture and release sites in southwestern Virginia.

were assigned to one of two age classes: young (<1 year old) or adult. Individuals of uncertain taxonomic status—a total of 10 birds—were not used in the homing experiment.

Banded juncos were placed in holding buckets containing a millet and corn mixture to await transport by automobile to release sites. Birds were transported as individuals or in small groups not exceeding 10 birds per bucket. Birds of differing subspecies, age, or sex were held together during translocation. When multiple birds were simultaneously relocated to the same site, they were released at 60-s intervals to reduce the chance of nonindependent returns. Upon release, juncos always flew to nearby vegetation rather than disappearing over the horizon in the direction of home; in no case did we observe flocking by recently released birds.

We identified successfully homing juncos at all sites by direct observation of color bands and by recapture with mist nets. Because capture sites outnumbered observers on most days, we apportioned our monitoring effort equally among capture sites both within and across days, with one exception. At site M1, we used Potter traps and electronic detection (see below) to identify successfully homing birds; thus, observers spent less time monitoring for returning birds at that site.

Juncos relocated from M1 received a subcutaneously implanted passive integrated transponder (PIT) tag. The PIT tags are one component of a portable transceiver system (PTS; model FS2001; Destron-Fearing, South Saint Paul, Minnesota) that electronically records the date and time when tagged animals come within ~20 cm of the PTS antenna. We constructed wooden bird feeders designed to house the PTS antennas so that homing birds visiting the feeders at their original site of capture could be recorded in our absence. To allow acclimation, the feeder boxes were deployed several weeks before the homing experiment. To assess any negative influence of the PIT tags on homing success, we compared the proportion of successfully homing juncos that received PIT tags with the proportion of successfully homing juncos that did not receive PIT tags. To determine whether use of the PTS biased the detection efficiency at site M1, we compared the detection efficiency at M1 with detection efficiencies at the other sites.

STATISTICAL ANALYSES

Homing success.—We relocated the same number of individuals of each subspecies to each of four distances (5, 10, 20, and 40 km). A previous winter homing study with migratory juncos showed a marked decrease in homing success after displacement beyond ~5 km (Keiper and Klinger 1977). Therefore, to examine potential differences in homing success between subspecies at different distances, we partitioned the displacement distances into two categories: birds displaced to 5 km and birds displaced to ≥10 km. Ideally, in a comparison between subspecies, birds would also have been paired by such traits as age and sex; but, because of the difficulty in capturing subjects with particular characteristics at any given time, that was not possible. Numbers of juncos released at each distance by subspecies, age, and sex are presented in Table 1.

Data from the 2002 and 2003 field seasons were combined for analyses. All analyses were performed on MINITAB statistical software, version 13.32 (Minitab, State College, Pennsylvania). For all tests, we confirmed homogeneity of variances with Levene's test. All tests were two-tailed, with $\alpha = 0.05$. *A priori* estimates of statistical power were obtained from tables in Cohen (1988). All comparisons of homing success between two groups were made with tests of two proportions.

The strength of any conclusions drawn from negative results is dependent on the power of the test. Our experiment was designed to have reasonable power to detect moderate differences in homing success between subspecies. For the 5-km displacement, our *a priori* estimate of statistical power was 0.72 to detect a "medium" effect size ($h = 0.5$); for birds displaced ≥10 km, it was 0.99. To achieve the greatest power, we combined all experimental distances (i.e. 5, 10, 20, and 40 km) and estimated that our planned sample size of 320 juncos would provide extremely high statistical power.

Duration of return.—Juncos typically roost at night outside of the migration season, so it is likely that homing flights occurred during daylight hours (Nolan et al. 2002). We released birds ≥30 min before sunset to allow sufficient time for them to locate roosts. We recorded the time of each release so that we could document the total homing duration of successfully returning birds (i.e. time between release and subsequent detection at original capture site). We assumed there were no nocturnal homing flights; for analysis, total homing duration was converted to daylight minutes. Daily sunrise and sunset times for Pembroke, Virginia (37°19'00"N, 80°38'00"W), were used to calculate the average times of sunrise and sunset and the average number of daylight minutes that had passed during each bird's homing trip. The 2002 field season included a four-day hiatus (30 January through 1 February) during which there were no observers in the field to detect returning juncos. Therefore, in the analyses of duration of return, we excluded any junco detected after 29 January within the 2002 field season ($n = 11$).

We compared the duration of return between subspecies in each of the partitioned experimental groups with a two-sample t-test. For that test, our *a priori* estimate of statistical power was 0.60 and 0.97 to detect a "medium" effect size ($d = 0.5$) in the 5-km and ≥10-km groups,

TABLE 1. Number of juncos relocated to each distance by subspecies, age, and sex.

	Migrants				Nonmigrants				
	Young		Adult		Young		Adult		
Distance	Male	Female	Male	Female	Male	Female	Male	Female	Total
1 km	9	16	11	4	3	5	17	15	80
5 km	10	16	10	4	11	6	18	5	80
10 km	7	16	13	4	13	11	14	2	80
20 km	10	5	15	10	11	11	13	5	80
40 km	5	9	13	13	16	3	15	6	80
Total	41	62	62	35	54	36	77	33	400

respectively. To achieve greatest power, we compared the duration of return between subspecies with all experimental birds combined using a two-sample *t*-test (*a priori* estimate of statistical power >0.99 to detect a "medium" effect size). To assess the effect of distance on duration of return, we used ANOVA with Tukey's method for *post-hoc* multiple comparisons.

Winter site-fidelity.—Homing experiments implicitly assume that birds are motivated to return to a specific location; thus, we had to demonstrate that juncos are site-faithful during the winter. A previous study in the nearby Great Smoky Mountains found that both migratory and nonmigratory juncos exhibit winter site-fidelity within and between years (Rabenold and Rabenold 1985). To determine whether juncos wintering within our study area were at least somewhat site-faithful, we baited capture sites for one month and then, on 2–4 and 11–13 January 2002, we banded and released 360 migrants and 136 nonmigrants at those sites. Birds recaptured at the same location during the second banding period (11–13 January) were classified as site-faithful. Although our methods did not provide overwhelming evidence that each translocated bird was site-faithful and motivated to return to a familiar site with abundant food, we feel confident from our experience at the site over many years that large numbers of those birds, both migrants and nonmigrants, are site-faithful during winter.

Detection efficiency.—To ensure that potential differences in apparent homing success were not attributable to differences in detection efficiency between subspecies, we included a procedural control. Specifically, we compared the proportion of migratory and nonmigratory juncos recaptured after displacement to a distance of 1 km (*a priori* estimate of statistical power = 0.72 to detect a "medium" effect size; $h = 0.5$). Duration of return was compared between subspecies with a two-sample *t*-test (*a priori* estimate of statistical power = 0.60 to detect a "medium" effect size; $d = 0.5$).

The birds that we moved 1 km were probably released near the edges of—or just outside of—their home ranges. Wintering juncos do not defend territories (Nolan et al. 2002), and the winter home-range size of migrants in another study was estimated to be 17–33 ha (Nolan et al. 2002). Those values correspond to hypothetical circular home ranges with radii of <0.5 km. Wintering nonmigrants rarely move between sites located 0.6 km apart (Nolan et al. 2002). Thus, the home ranges of wintering juncos are small as compared with the displacement distances we used.

RESULTS

Homing success.—Tests of the partitioned data indicated that migrants did not show greater homing success than nonmigrants from either 5 km (migrants: 6 of 40, nonmigrants: 13 of 40, $Z = 1.88$, $P = 0.06$) or ≥10 km (migrants: 11 of 120, nonmigrants: 16 of 120, $Z = 1.02$, $P = 0.31$; Fig. 2). Migrant juncos were also not more likely than nonmigrants to home successfully when all experimental distances were combined to achieve the greatest statistical power (migrants: 17 of 160, nonmigrants: 29 of 160, $Z = 1.92$, $P = 0.054$). There was no difference in proportion returning between juncos that received PIT tags and those that did not (tags = 14 of 57, no tags = 48 of 215, $Z = 0.36$, $P = 0.72$).

Only two birds were recaptured at a different capture site than the one from which they had been displaced: one in the 5-km group (migrants: 0 of 6, nonmigrants: 1 of 13), and one in the ≥10-km group (migrants: 0 of 11, nonmigrants: 1 of 16). Each of those nonmigrants was recaptured within the low-elevation cluster from which it had been displaced, but at an adjacent capture site 0.5 km away. If juncos homed only to the general vicinity of the low-elevation cluster—rather than to a specific capture site within the cluster—two-thirds of

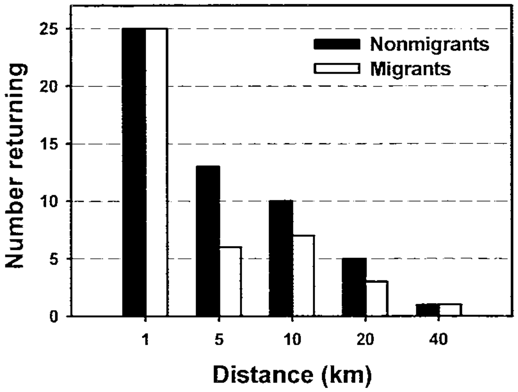

FIG. 2. Numbers of successfully homing Dark-eyed Juncos detected out of 40 individuals of each subspecies relocated to each distance.

the returnees would have been captured at sites other than the one from which they were displaced. That is, only 10 of the 30 birds that successfully returned to the low-elevation cluster would be expected—by chance—to have been detected at the capture site from which they had been displaced. We detected 28 of 30 returning juncos at the capture sites from which they had been displaced ($Z = 6.16$, $P < 0.0005$). Therefore, we demonstrated unambiguously that after experimental displacement juncos home to specific wintering sites.

Duration of return.—There was no difference in duration of return between subspecies when displaced to 5 km (migrants: $\bar{x} \pm SD = 3{,}639 \pm 492$ min, $n = 5$; nonmigrants: $\bar{x} \pm SD = 3{,}069 \pm 1{,}527$ min, $n = 12$; $t = -0.80$, df = 15, $P = 0.43$) or to distances ≥10 km (migrants: $\bar{x} \pm SD = 5{,}186 \pm 2{,}274$ min, $n = 9$; nonmigrants: $\bar{x} \pm SD = 4{,}319 \pm 2{,}243$ min, $n = 15$; $t = -0.91$, df = 22, $P = 0.37$). With all experimental distances combined, there was still no difference in duration of return between subspecies (migrants: $\bar{x} \pm SD = 4{,}634 \pm 1{,}962$ min, $n = 14$; nonmigrants: $\bar{x} \pm SD = 3{,}764 \pm 2{,}024$ min, $n = 27$; $t = -1.32$, df = 39, $P = 0.20$). There was no difference in duration of return between birds that received PIT tags and those that did not (tags: $\bar{x} \pm SD = 3{,}753 \pm 2{,}145$ min, $n = 10$; no tags: $\bar{x} \pm SD = 3{,}228 \pm 2{,}430$ min, $n = 52$; $t = -0.64$, df = 60, $P = 0.53$).

With both subspecies combined—including control birds displaced 1 km—there was a significant effect of distance on duration of return (1 km: $\bar{x} \pm SD = 2{,}204 \pm 1{,}943$ min, $n = 44$; 5 km: $\bar{x} \pm SD = 3{,}236 \pm 1{,}317$ min, $n = 17$; ≥10 km: $\bar{x} \pm SD = 4{,}645 \pm 2{,}246$ min, $n = 24$; $F = 12.44$, df = 2 and 82, $P < 0.0005$). Multiple comparisons between means indicated that duration of return was significantly greater from ≥10 km than from 1 km.

Winter site-fidelity.—Prior to the start of the homing experiment, both subspecies exhibited at least short-term fidelity to wintering sites, because we recaptured 68 (19%) of 360 migrants and 40 (29%) of 136 nonmigrants after initial banding. Only one previously marked bird was recaptured at a different location (<1 km away). In addition, some birds exhibited long-term site fidelity, because we recaptured 13 juncos (5 migrants, 8 nonmigrants) originally banded in 2002 at the same locations in 2003. Only one junco (a nonmigrant) from 2002 was recaptured at a different location in 2003 (~1 km from 2002 site).

Detection efficiency.—There was no difference between subspecies in homing success after displacement to a distance of 1 km (migrants: 25 of 40, nonmigrants: 25 of 40, $Z = 0.0$, $P = 1.0$). Among control birds, there was no difference in duration of return between subspecies (migrants: $\bar{x} \pm SD = 2{,}407 \pm 2{,}351$ min, $n = 21$; nonmigrants: $\bar{x} \pm SD = 2{,}019 \pm 1{,}508$ min, $n = 23$; $t = -0.66$, df = 42, $P = 0.52$). In addition, there was no difference in detection efficiency between M1—the single site at which we used the PTS detection system—and conventional detection at all other sites (PTS detection at M1 = 10 of 57, conventional detection = 48 of 215; $Z = -0.78$, $P = 0.43$).

DISCUSSION

In a landscape-scale homing experiment, we contemporaneously relocated 400 migratory and nonmigratory juncos 1–40 km from their shared wintering ground in southwestern Virginia. Contrary to our predictions, there was no difference in homing success or duration of return between subspecies. In a previous room-scale experiment performed at the same time of year as the present experiment, migratory juncos exhibited better spatial memory than nonmigrants; migrants also possessed greater hippocampal neuron density (Cristol et al. 2003). Avian homing likely shares some of the same navigational mechanisms used during migration—a feat assumed to depend on navigational ability, particularly in species like songbirds that return to the same territories after migration. For those reasons, we predicted that migratory juncos would be more likely to return and would do so in less time than nonmigrants. The lack of any significant difference in homing ability between subspecies suggests that the neural bases and cognitive processes involved in homing are not those important in room-scale tests.

Winter site-fidelity and detection efficiency.—We recaptured only a single bird at a different location (<1 km away) from where it had been banded and released, which suggests that juncos have small winter home ranges and are faithful to them for at least a week and probably much longer. Thus, we have no reason to doubt the validity of our assumption that juncos were motivated to return to the familiar, food-provisioned sites from which we relocated them. The homing challenge imposed by a 1-km relocation is likely minimal, and our high detection rate validates the use of birds displaced to 1 km as a procedural control group.

In a previous winter-homing experiment with migratory juncos, Keiper and Klinger (1977) reported a "recapture baseline" of 80% (i.e. they recaptured 8 of the 10 migratory juncos released at the original site of capture to assess detection efficiency). By comparison, we detected 63% (25 of 40 migrants, 25 of 40 nonmigrants) of juncos displaced to a distance of 1 km. Our recapture baseline is similar to those reported in several other winter homing studies of migratory and nonmigratory passerines (Benvenuti and Ioale 1980, Ioale and Benvenuti 1983). Thus, we are confident that we were able to detect both subspecies with equal success and that during the homing experiment we detected the majority of successfully homing birds.

During our brief preliminary study of winter site-fidelity, we recaptured many site-faithful birds, but only a small percentage of those banded. Our original estimate of site fidelity was based on only three days of detection effort that commenced nine days after the first bird was banded. However, by the close of the field season (three weeks later), the percentage of birds recaptured at their original banding sites had almost doubled: to 29% for migrants and 56% for nonmigrants. Therefore, our reported winter site-fidelity is an underestimate.

Homing ability of Dark-eyed Juncos.—Among experimentally displaced birds randomly dispersing in many directions from a release site—and continuing to move in a fixed direction—some will likely encounter the site from which they were displaced and thereby give the appearance of having successfully homed. This random-search scenario has been invoked to explain decreased homing success with increased distance in several animals. The number of successfully homing birds in our experiment decreased with increased relocation distance, as has been previously reported (Matthews 1955; Fig. 2).

Any homing study with wild birds requires an answer to the question: Did the birds actually home? In homing pigeons (*Columba livia*), a bird is considered to have successfully homed when it returns to its home loft—a highly localized navigational goal. Applying a similar definition, our results indicate that juncos were certainly homing. Out of 46 successfully returning juncos displaced to distances of 5–40 km, only two (nonmigratory) juncos—one each from 5 and 40 km—were recaptured at different capture sites, both within 0.5 km of where they had been displaced.

We had predicted better homing ability in migrants than in nonmigrants because, at the same time of year as the present experiment, migrants have denser hippocampal neurons and perform better at room-scale spatial memory tests. There are several nonmutually exclusive explanations for why this was not found:

(1) Migrant juncos may have been less motivated to return than nonmigrants because capture sites were not located near potential breeding areas and thus the cost of homing may have outweighed the benefits of return. After a pilot study suggested higher return rates of nonmigrants than migrants to sites within the breeding habitat, we designed the present experiment so that all capture sites were below breeding elevation of the nonmigrants, thus reducing the motivation of potential breeders to return to specific sites. Any comparison of homing by migrants and nonmigrants sharing a wintering ground will, by definition, result in differences in proximity to breeding areas. Because capture sites were probably many kilometers from breeding sites, we believe that it is unlikely that greater motivation by nonmigrants masked superior homing performance by migrants, but we cannot rule out that scenario. It is also possible that both subspecies had such low motivation to return that we could not detect superior homing ability of migrants. That explanation seems unlikely, because when we compared only those birds that were motivated enough to return, we did not find that migrants returned more quickly.

(2) A second explanation for why migrants failed to outperform nonmigrants would be that nonmigrants have greater familiarity with local landmarks potentially useful for homing, and that might have masked superior homing by migrants. Any familiarity advantage in nonmigrants would be greatest after short displacements within their year-round familiar area. Nonmigrants were clearly not better at returning after displacements just outside of their home ranges (1 km), and our results do not indicate clear differences at other

distances (though nonsignificant results hint that nonmigrants may have been more likely to return from 5 km). If a familiarity disadvantage was masking better homing performance by migrants, we would have expected the masking effect to be greatest for nonmigrant adults (most experience on site) when compared with migrant young (least experience at site), but a complete analysis (not shown) by age, sex, and displacement distance revealed that young migrants, who had little chance to learn local landmarks, were among the fastest birds to return (Keiser 2003).

(3) Finally, migration and homing may require very different cognitive abilities. Demands of returning from a sudden displacement of tens of kilometers at a time of year when that does not normally occur may be very different from the demands of a routine seasonal migration. The results here suggest that the evolution of migration may have led to changes in cognitive ability and neuroanatomy in migratory juncos without influencing their ability to home; the same appears to be true among Old World warblers (Ioale and Benvenuti 1983, Baillon et al. 1992, Healy et al. 1996, Mettke-Hofmann and Gwinner 2003). Thus, the migrant's denser hippocampus and better spatial memory, though presumably useful during long-distance migration, may play no role in homing behavior.

ACKNOWLEDGMENTS

The research was funded by National Science Foundation IBN-9876108. We thank J. LeClerc and E. Snell-Rood for their assistance in the field. H. Wilbur of Mountain Lake Biological Station and P. Porterfield of Miles C. Horton, Sr., Research Center generously provided logistical support and granted us access to their facilities. We also thank R. Lipcius of the Virginia Institute of Marine Science for providing feedback on data analyses, and T. Meier of the College of William and Mary for logistical support. All procedures for collecting animals were carried out following the Guidelines for Use of Animals in Research, with applicable state and federal permits, and were approved by the College of William and Mary's Research on Animal Subjects Committee (0122) and the Virginia Polytechnic Institute and State University Animal Care Committee (A-3208-01).

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Associate Editor: R. L. Holberton