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Novel Insights into the Map Stage of True Navigation in Nonmigratory Wild Birds (Stone Curlews, *Burhinus oedicephalus*)

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ABSTRACT: In the map-and-compass model of true navigation, animals at unfamiliar sites determine their position relative to a destination site (the map stage) before progressing toward it (the compass stage). A major challenge in animal navigation research is to understand the still cryptic map stage in general and the map stage for free-ranging wild animals in particular. To address this challenge, we experimentally translocated wild, nonmigratory birds (stone curlews [*Burhinus oedicephalus*]) far from their nests and GPS-tracked their subsequent movements at high resolution and for long durations. Homing success was high and cannot be explained by random chance or landmark navigation, implying true navigation. Although highly motivated to return home, the homing trajectories of translocated birds exhibited a distinct, two-phase pattern resembling the map and compass stages: a long, tortuous wandering phase without consistent approach home, followed by a short and direct return phase. Birds retranslocated to the same site initially repeated the original wandering path but switched to the return phase earlier and after covering a smaller area; they returned home via a different path but with similar movement properties. We thus propose the map learning hypothesis, asserting that birds resolve the map by acquiring, potentially through learning, the relevant navigation cues during the wandering phase.

Keywords: true navigation, retranslocation, wandering phase, return phase, resident bird, cue acquisition stage.

Introduction

The navigational capacity that enables animals to reach desired locations is one of the most fundamental components of animal movement (Nathan et al. 2008), yet the question of how animals navigate remains one of the great unanswered scientific challenges (Kennedy and Norman 2005). Birds have long been a major focus of navigation research,

though most concepts and insights stem from a single species, the domestic homing pigeon (*Columba livia* f. *domestica*; Wiltschko and Wiltschko 2003; Wallraff 2005), mainly because these birds were selected for a strong homing drive and are easy to raise and manipulate. Numerous translocation experiments and experimental manipulations have revealed the roles of geomagnetic, celestial, visual landmark, and olfactory sensors in pigeon navigation (Wallraff 2005). However, these sensory mechanisms, and their hierarchy, do not necessarily apply to other bird species (Jacobs and Menzel 2014). Indeed, Wallraff (2005) noted that “some crucial experiments conducted with pigeons should be repeated with other species of various avian orders in the wild” (p. 169). Here we contribute to this call by providing empirical evidence and new insights into the navigational capacity of free-ranging wild birds in complex, real-life systems.

The true navigation concept refers to the most sophisticated navigation capacity, also known as Griffin’s (1952) type III orientation. Kramer’s (1953) canonical map-and-compass model provides a conceptual framework within which true navigation can be evaluated (Able 2001). Although the sensory mechanisms of the map and of the compass must act together throughout the homing process, this model postulates that true navigators at unfamiliar sites first determine their position relative to a destination site (the map stage) and then progress toward it (the compass stage; Gallistel 1990; Wallraff 2005; Jacobs and Menzel 2014). The sensory mechanisms used by birds during the compass stage have been studied extensively, and several generalizations have been broadly accepted (Muheim et al. 2009). The sensory mechanisms and basic characteristics of the map stage have also been studied rather extensively in pigeons but remain debated (Wiltschko and Wiltschko 2009; Gagliardo 2013; Schiffner and Wiltschko 2013). Pigeons established a navigational map by moving around in the home area to acquaint themselves with the local navigational factors (Wallraff 2005).

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An alternative hypothesis postulates that only natal imprinting is needed to enable true navigation, and the map is established later while the animal is farther away from home (Lohmann et al. 2008; Fuxjager et al. 2014; Brothers and Lohmann 2015). Consequently, the most intriguing aspect of true navigation—how animals map an unfamiliar location in relation to their destination—remains one of the biggest mysteries in animal navigation research (Gould 2004; Wiltschko and Wiltschko 2009).

It has been suggested that true navigation is particularly likely to evolve in migratory animals (Bingman and Cheng 2005) and in those with a very large foraging range, where homing to the breeding site is a precondition to successful reproduction (i.e., various procellariiform seabirds; Bonadonna et al. 2003) and the navigational challenges of such long-distance movements are considerably greater than those experienced by nonmigratory species (Mouritsen 2003; Alerstam 2006; Åkesson and Hedenström 2007). Yet translocation experiments found no difference in the homing performance between migratory and nonmigratory birds (Ioalè and Benvenuti 1983; Keiser et al. 2005). Short displacement of 10 migratory and 17 nonmigratory bird species in Mexico resulted in similar (74% and 73%, respectively) return rates (Ramos and Rappole 1994). Furthermore, the paradigmatic true navigator, the homing pigeon, and its immediate precursor, the rock pigeon, are nonmigratory species, though a relative close species, the American wandering pigeon (*Ectopistes migratorius*), was a long-distance migrant. Furthermore, the common occurrence of partially migratory species—with some populations migratory and others resident (Berthold 2001)—suggests that generalizations relating migratory versus resident status to navigation capacity might not hold; alternatively, true navigation might constitute a fundamental capacity of all (or most) birds, including many nonmigratory ones, stemming from high mobility and expressing when the need arises.

Selection for strong homing motivation has been indispensable in making the homing pigeon a leading paradigm in navigation research (Gallistel 1990; Wallraff 2005; Jacobs and Menzel 2014). For other, wild, species, homing motivation is more difficult to control, since it is either unknown, involves multiple motivational elements, or is masked by other factors (Jacobs and Menzel 2014).

Recent progress in wildlife tracking techniques (i.e., GPS-based telemetry) enables accurate quantification of movement patterns and, hence, the ability to hypothesize potential mechanisms (Biro et al. 2004). Lipp et al. (2004), for example, showed that homing pigeons' paths strongly coincide with highways and railways, suggesting a reliance on visual longitudinal landmarks, whereas Dennis et al. (2007) showed homing pigeons' tendency to align parallel and/or perpendicular to the isopleths of the magnetic intensity field. Yet applying this technology to navigation studies of other

species remains limited (Guilford et al. 2011). Moreover, inherent in all translocation experiments of wild free-ranging animals are uncertainties about the animals' movements before capture; hence, the spatial extent of the familiar area beyond which true navigation capacity should be examined is commonly unknown.

In this article, we investigate the true navigation capacity of the Eurasian stone curlew (*Burhinus oedicephalus*), a resident, locally restricted, wild bird species. We translocated birds to four main unfamiliar sites at different distances and tracked homing paths with GPS loggers. Homing motivation was maximized by focusing on breeding birds captured at their nest during active incubation. In the context of Kramer's (1953) biphasic map-and-compass model of true navigation, we aim to address the following research questions and hypotheses:

1. Does a nonmigratory bird species possess a capacity for true navigation? To address this question, we translocated stone curlews to sites well beyond their home range and compared observed tracks of homing stone curlews based on the observed movements of each bird to the null expectation of random return. Our alternative research hypothesis was that stone curlews are capable of true navigation and that the duration and length of their homing tracks cannot be explained by random chance. We also hypothesize that translocated stone curlews will home back without reliance on known landmarks or other familiar cues—including magnetic signposts (Wiltschko and Wiltschko 2005)—that are known to the bird without performing a gradient extrapolation. Such familiar landmarks and cues are likely to be more prevalent at sites in greater proximity to the target (home) area. Therefore, if birds rely on such landmarks and cues (and, hence, cannot be considered true navigators), their consistent movement toward home is expected to start closer to home than the translocation distance. We also expect that a translocated bird will return home the first time it passes through a site with the known landmark.

2. Do translocated nonmigratory birds perform biphasic homing behavior that can be related to map and compass phases? If the evidence for our first question supports true navigation, we hypothesize that translocated birds will exhibit two distinct phases: a map phase, during which a bird explores the unfamiliar environment to acquire or calibrate the map, followed by a compass phase of directed return home. We thus predict that the homing paths of translocated stone curlews will show two phases distinguishable by the less directed, more meandering, slower, and more itinerant (i.e., with many stops) map phase, in contrast to a rapid and directional compass phase with directed movements toward home.

3. Does previous experience improve navigation performance? The null hypothesis asserts that birds experienced

with a navigation task would navigate back home more efficiently in a subsequent trial, with better performance in both map and compass phases (if found, see question [2]). Alternatively, assuming that the map phase involves a more complex learning or cue acquisition process than the compass phase and that spatial memory is sufficient to manifest effects of experience, we hypothesize that there will be more substantial improvement of navigation performance during the map phase in particular. Specifically, we predict that experienced birds retranslocated to the same site will utilize their previous experience in this area to shorten the map acquisition phase compared to the first translocation, with less notable improvement in metrics of navigation performance during the compass phase.

Methods

Species and Study Site

The stone curlew is a nocturnal wader, inhabiting areas of low vegetation. We studied a resident stone curlew population in an agricultural landscape at the Judean Plain in Israel (lat. 31°45'N, long. 34°43'E; figs. A6–A9; figs. A1–A9 available online).

Trapping, Tracking, and Translocating Birds

To control the motivation to home, we trapped incubating stone curlews in three successive years (2010–2012). Birds were fitted with a GPS unit (UVA Birdtracking system with remote download capacity; Bouten et al. 2012) and a VHF transmitter (A2440-80, Advanced Telemetry Systems), altogether carrying 18.5–20.0 g, which constituted $4.6\% \pm 0.4\%$ standard error (SE; range 3.7%–5.3%) of their body mass (for details, see the appendix, available online). The GPS units were set to record location at 300-s intervals during the night and at 1,800-s intervals during the day to allow solar recharge. All birds were subjected to translocation on the night of the day they were captured, and all birds were kept in a closed opaque cardboard box until release (see appendix). Birds were assigned randomly to one of three groups, differing in the translocation distance from the breeding (capture) site: (a) short (32–36 km, $n = 6$), (b) intermediate (68–75 km, $n = 10$), and (c) long (90–93 km, $n = 4$; figs. 1, 2). Ten translocated birds that returned home successfully were recaptured and retranslocated to the same site of their first translocation after 48 ± 720 days. All trapping, tagging, and experimental procedures were approved by the ethics committee of the Hebrew University (permit ns-09-12223-2) and the Israeli Nature and Parks Authority (permit 2010/37711).

Identification, Parameterization, and Comparison of Movement Phases

We classified the GPS data into three distinct movement phases. Data collected before the translocation (for two birds translocated after more than a year of tracking at the home range, one of them tracked since the age of 6 months) or after the bird returned to the breeding site (all translocated birds) were considered home-range movements. Data analysis of translocated birds revealed two distinct movement phases: a wandering phase with no consistent progress toward home, followed by a return phase back home. We identified the switch point between the phases by following the movement track backward from the time the individual bird returned home. We calculated the distance the bird moved toward home, with increasing time intervals from 1 to 72 h, setting a lower bound of 0.5 km/h for the approach rate. The switch point for each bird was specified by using the time interval that maximizes the distance it has approached home (see figs. 3, A1, A3). We then compared the movement track among the three phases, focusing only on the properties that are independent of the defining criteria.

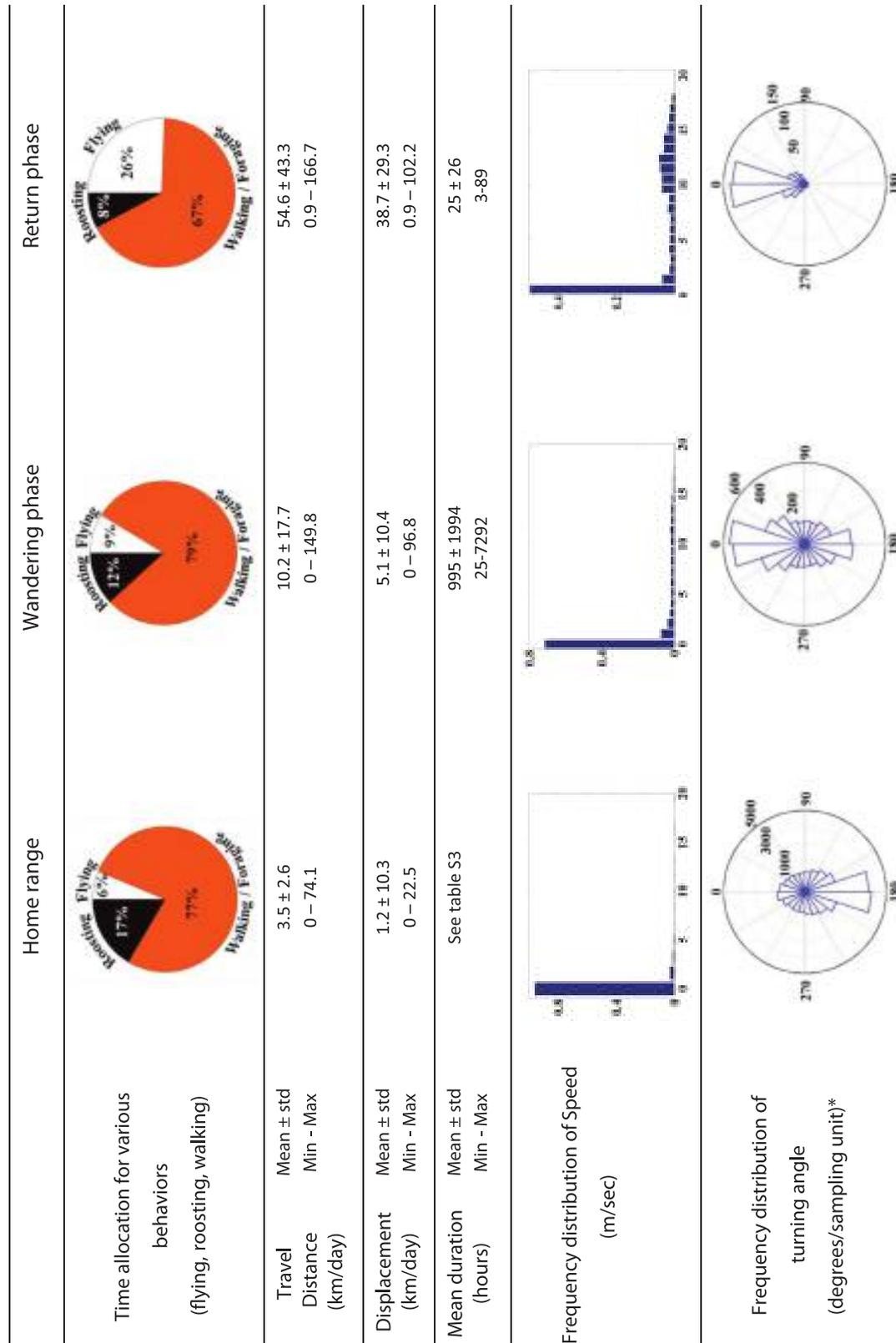
Movement tracks are commonly characterized by the distributions of turning angles and step lengths. We used movement speed rather than step length to account for actual sampling interval inconsistency due to missing data points and GPS localization variance. We subsampled the data set (see appendix) separately for each movement phase for the pooled data set over all birds to assess differences among movement phases. By using the Kolmogorov-Smirnov test and its circular equivalent, the Kuiper two-sample test, we compare the movement speed and turning angle distributions, respectively, of the real data to the simulated data verifying that the distributions are statistically indifferent.

Estimation of Home-Range Size

Home-range size was estimated from all available bird tracks of the focal study site, either before translocation or after return, using the adaptive a-LoCoH method. This method was found to outperform other methods for estimating home ranges and utility distributions and to exhibit high robustness to changes in key parameter values (Getz et al. 2007).

Evaluating True Navigation

Chance return. To examine whether the observed return time distribution could have been obtained by chance, we simulated translocated bird movements using four correlated random walk models, none incorporating navigational capacity. The models were parameterized for each individual bird (see “Identification, Parameterization, and Comparison



* A movement step was defined as the smallest number of 300 s intervals during which the bird displaced > 200 m. If the bird did not move beyond this threshold after 1800 s, step length was set to zero.

Figure 1: Basic statistical descriptors of the movements of free-ranging wild stone curlews during three different behavioral phases. Home-range movements are within the regular area of activity, quantified by GPS data retrieved from 12 birds before translocation and/or after return. The wandering and return phases are two successive stages observed during homing of all 13 translocated GPS-tracked birds (see “Methods” for the definition of the switch between these two phases).

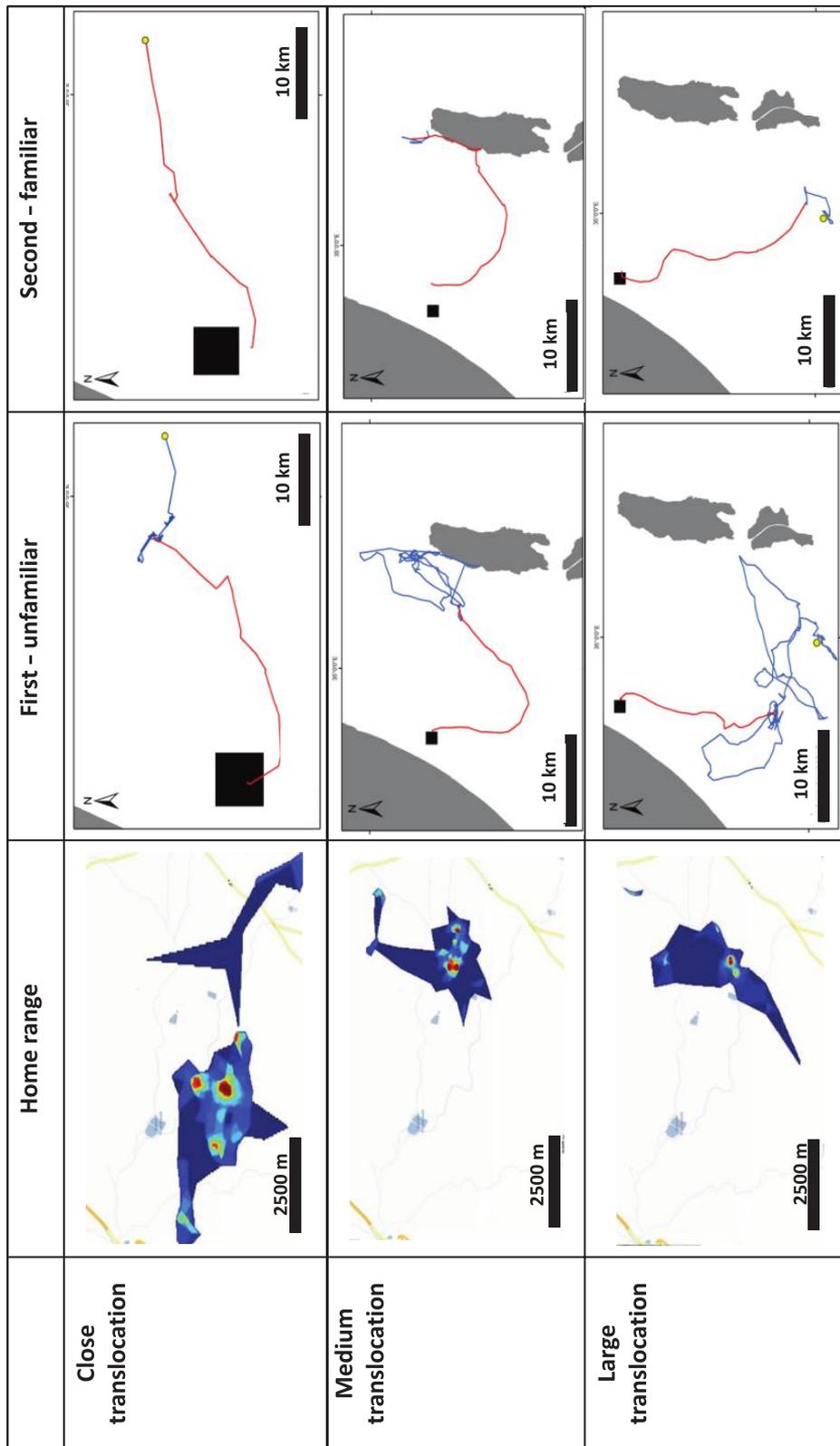


Figure 2: Example of home-range maps, first translocation to unfamiliar areas, and second translocation to familiar areas. Home-range maps, each with >350 tracking days, were calculated using the a-LoCoH method (Getz et al. 2007). Comparison of first and second wandering phases (blue lines) reveals shortening of the spatial extent in the second translocation (see also fig. 8). No difference is visible in the properties of the return phases (red lines). Note that the shift point changes its location, and the second return trajectories are away from the first return trajectories. Also note (as in fig. 2) the directness of trajectories from the north and south as compared to the trajectories from the east, which make a southern loop.

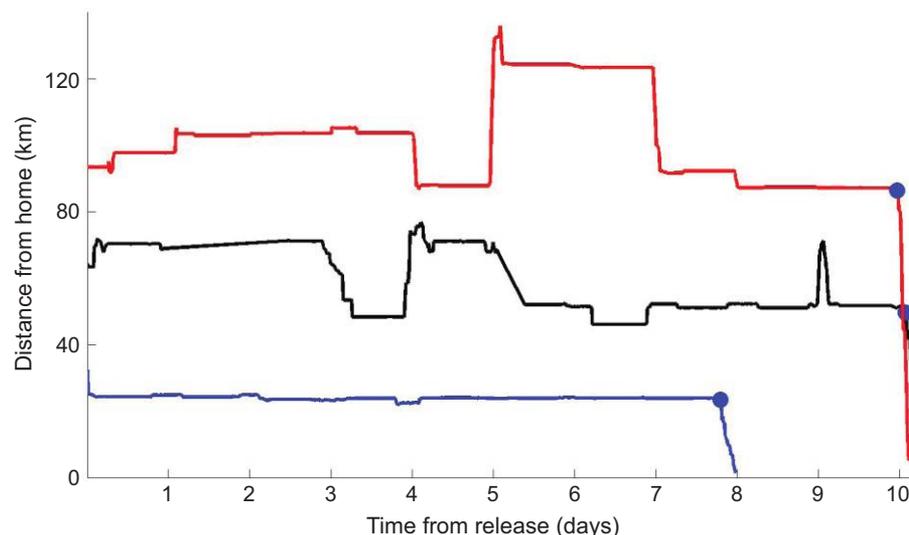


Figure 3: Approach rate to home as a function of time, illustrated for three birds translocated to different distances: close (blue), medium (black), and far (red). Birds tend to stay at a defined distance from home (mean approach rate of -0.12 ± 0.59 km/day, $n = 13$) while wandering and shift to a fast return phase (mean approach rate of 113 ± 38.9 km/day, $n = 8$, medium and far translocations) at a certain temporal point of decision (blue circle). For five birds that were translocated to close areas (32–36 km), the return was a bit slower, with a return mean approach rate of 44.7 ± 18.8 km/day (wandering mean approach rate of -0.03 ± 1.6 km/day).

of Movement Phases”) and accounted for movement speed correlation between consecutive steps and between movement speed and turning angle. The first three models (fig. 4a–4c) were parameterized from a distinct part of the data set: home range, wandering phase, or return phase. The fourth model was set to start with a wandering phase followed by a return phase (fig. 4d). Each simulated bird movement terminated after the observed return time of the real bird. In all models, successful homing was assumed to occur if the simulated track, at any stage, was within 2.5, 5, 10, 20, or 30 km from the centroid of that bird’s home range. A distance of 2.5 km corresponded to the observed home-range radius; longer distances accounted for variation in the (unknown) home-detection distance. The proportion of simulation runs classified as successful homing out of 1,000 replicates was used to estimate the probability of return by chance.

Return by familiar landmarks. According to the hypotheses and predictions above, we calculated the distance of shift point to compare the distance of release and determined whether the bird visited this area (within a 2,000-m radius) before the switch.

Navigation Performance and Previous Experience

To examine whether the area the bird visited during the first translocation is also used during the second translocation, we calculated the percentage of similarity between the first and second tracks and compared this percentage by Z-score test for two population proportions. This second transloca-

tion also enabled control of the homing motivation. Percentage of similarity was defined by the percentage of points in the second track that were less than 1,000 m from one or more points in the first track. We first subsampled the track so points within less than 200 m were filtered out. We tested each track for significance by a Monte Carlo procedure. We performed 1,000 correlated random walk simulations as described in figure 4, with a geographic confinement by the real track minimum convex polygon for the wandering phase, so that every simulated trajectory that exceeded the confinement was discarded and replaced by another simulated trajectory that did not exceed the polygon, to avoid unrealistic trajectories beyond the bird’s physiological capacity. We used the percentage of similarity distributions within the 1,000 trajectories to calculate the significance level.

Results

Overall, we tracked 24 birds and obtained a data set of more than 1 million GPS data points covering 6,788 tracking days for all of the individual birds combined (data deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.t67ng> [Orchan et al. 2016]). Mean home range, estimated for 12 birds with long tracks (median \pm standard deviation 514 ± 143 days; range 350–729 days) was 2.9 ± 1.9 km² using the a-LoCoH method (table A1, available online). A total of 20 birds captured in their nests during active incubation were translocated to 32–93 km from the center of their breeding range. Seventeen birds (85%) returned, of which

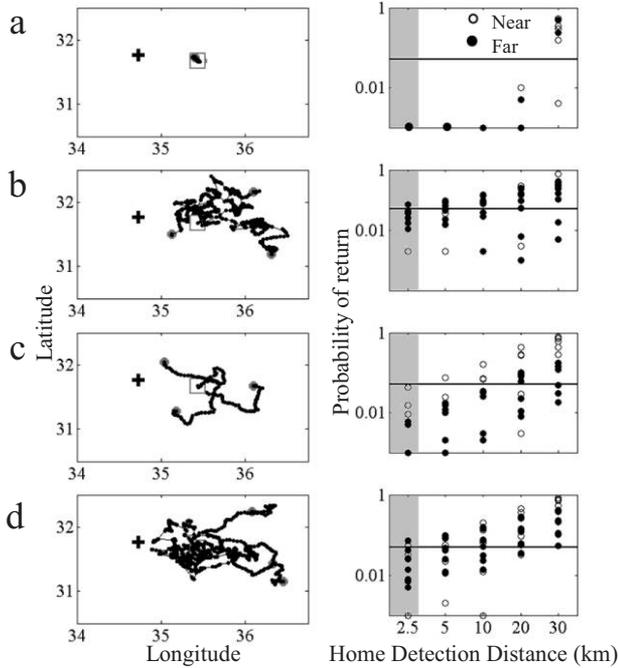


Figure 4: Correlated random walk simulations used to assess the probability of successful homing by random chance. The left column shows examples of the models, illustrated here for bird 13109. The models are based on three different data sets—home-range movements (a), wandering phase (b), return phase (c)—and wandering phase followed by a return phase (d). See “Methods” for details. Each panel shows three trajectories. The open square and the open circle depict the translocation release site and simulation end point, respectively. The cross represents the breeding site. Panels on the right show the probability of a translocated bird to home successfully as a function of the home-detection distance. Home-detection distance varies between 2.5 and 30 km. “Near” and “Far” are translocations to 32–36 km and 68–93 km, respectively. Successful homing occurred when the simulated trajectory intersected the circle of home-detection distance. The solid horizontal line represents the .05 probability.

four were excluded from further analyses due to low data quality (fig. A2). Eight of the 10 retranslocated birds returned home, and all were included in the analyses. Comparisons of the home-range size and the first and second translocations are illustrated in figure 2. Translocated birds showed a typical biphasic profile of the change in distance to home after release (fig. 3); as noted in the “Methods” section, these two phases were denoted as the wandering and return phases.

The Evidence for True Navigation

Testing chance return. Correlated random walk simulations revealed a very low probability of successful homing (<.05) during the observed homing duration for all translocation distances and for all models when home-detection distance was set at the observed home-range size (2.5 km radius; fig. 4). As expected, the probability of successful homing was higher

for larger home-detection distances and for translocation sites closer to the home site. The probability of successful homing was very low for simulations based on home-range movements and was also rather low (<.25) for simulations derived from the wandering- and return-phase distributions for all translocation distances and for home-detection distances of up to 10 km (fig. 4).

Testing landmark navigation. The switch from wandering to return occurred slightly but not significantly farther (0.8 ± 15.8 km) than the translocation distance (fig. 5). Most birds (11/13) reached locations closer to the home site than the switch point during wandering, spent a considerable portion of the wandering phase (median $43.5\% \pm 34.3\%$) closer to home than to the translocation site, and visited the location of the switch point before the actual switch to the return phase, spending 0.4 ± 283 h within a short distance (≤ 2 km) of this location before beginning the return phase (fig. 5). During wandering, the birds changed direction many times and showed no tendency to orient homeward (fig. 6a); after the shift to return, they were consistently oriented toward home (fig. 6b).

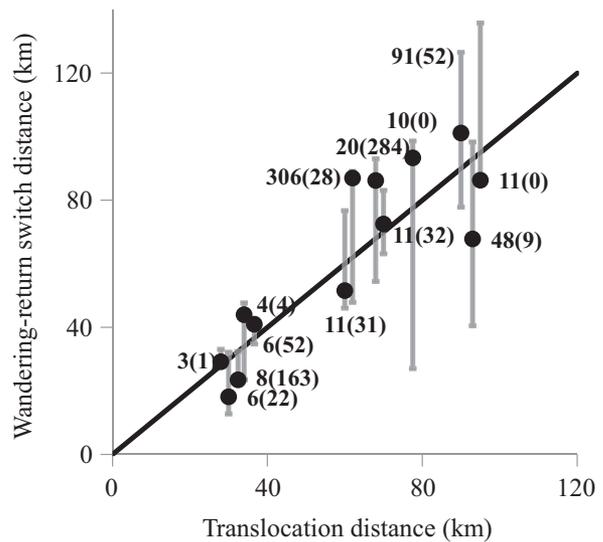


Figure 5: Distance from the breeding site at which translocated GPS-tracked birds switched from the wandering phase to the return phase as a function of the translocation distance (the points were moved manually slightly from the actual translocation distance for visualization of the gray bars). The solid black line indicates the hypothetical reference relationship of switching to the return phase at the translocation distance (i.e., $y = x$). The numbers next to the points indicate the homing (translocation-to-home) period in days and the hours spent near (≤ 2 km) the shift point in parentheses. The gray bars show the wandering space as the closest and farthest points from home. Birds that were translocated close (≤ 40 km) or far (>40 km) showed no tendency to switch farther than the translocation distance (points above the black line) or nearer the home site (points below the black line; Fisher’s exact test, $P = .3$).

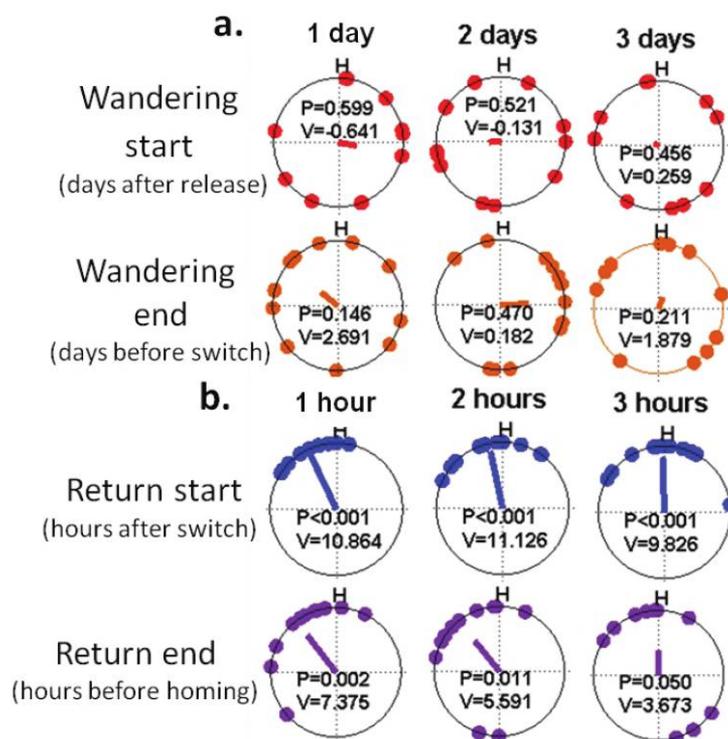


Figure 6: *a*, Vanishing bearings of the translocated birds at daily intervals from the time of release to 3 days after release (wandering start) and then the last 3 days of the wandering phase (wandering end). *b*, Vanishing bearings every hour in the first 3 h after the switch to the return phase (return start) and in the last 3 h before homing (return end). H indicates home direction. The radius lines represent the r vector, and their lengths indicate the significance of the result. V is the V test statistic value, and P is the statistical significance of the test.

Evidence for the Map-and-Compass Model: Biphasic Homing Behavior

A comparison of key movement characteristics among the three movement categories (home range, wandering phase, and return phase) found the most distinct differences between movements in the home range versus in the return phase; movements during the wandering phase represented a mixture of the other two categories (fig. 1). Nevertheless, the wandering and return phases remain highly distinct in some key parameters. Mean daily travel and displacement distances were, respectively, fivefold and eightfold larger in the return phase compared to in the wandering phase, whereas the mean duration of the return phase was 40-fold shorter (fig. 1). Birds flew much more frequently during the return phase, allocating a quarter of their time to flight, a proportion nearly threefold higher than in the wandering phase (fig. 1). Consequently, speed histograms of the return phase showed a pronounced peak of rapid movements (of 10–15 m/sec) that is nearly absent during the wandering phase (fig. 1). Furthermore, the distribution of turning angles during the return phase was highly biased around zero (implying a strong tendency to keep the same direction),

compared to a much more isotropic distribution of turning angles during the wandering phase (fig. 1). More specifically, trajectories during the return phase were very straight for birds returning from south or north, whereas birds released at the eastern translocation sites returned in a directed south-ern loop (fig. A2B).

The Role of Experience: Repeated Translocations

Mean travel distance covered and mean duration of the wandering phase were also significantly smaller in the second translocation (figs. 7*a*, 7*b*, A4). The return phase was initiated from a similar distance from home and extended for the same duration with a route that was neither shorter nor straighter in the second versus the first translocation (figs. 7*a*, A4). Retranslocated birds followed their previous track in the wandering phase but not in the return phase (figs. 7*c*, A4) and switched from wandering to return at a different location, rather distant from the switch point of the first translocation (mean \pm SE: 22.6 \pm 6.03 km, median 20.2 km between switch points of the first and second translocations). The wandering area was significantly smaller in the second

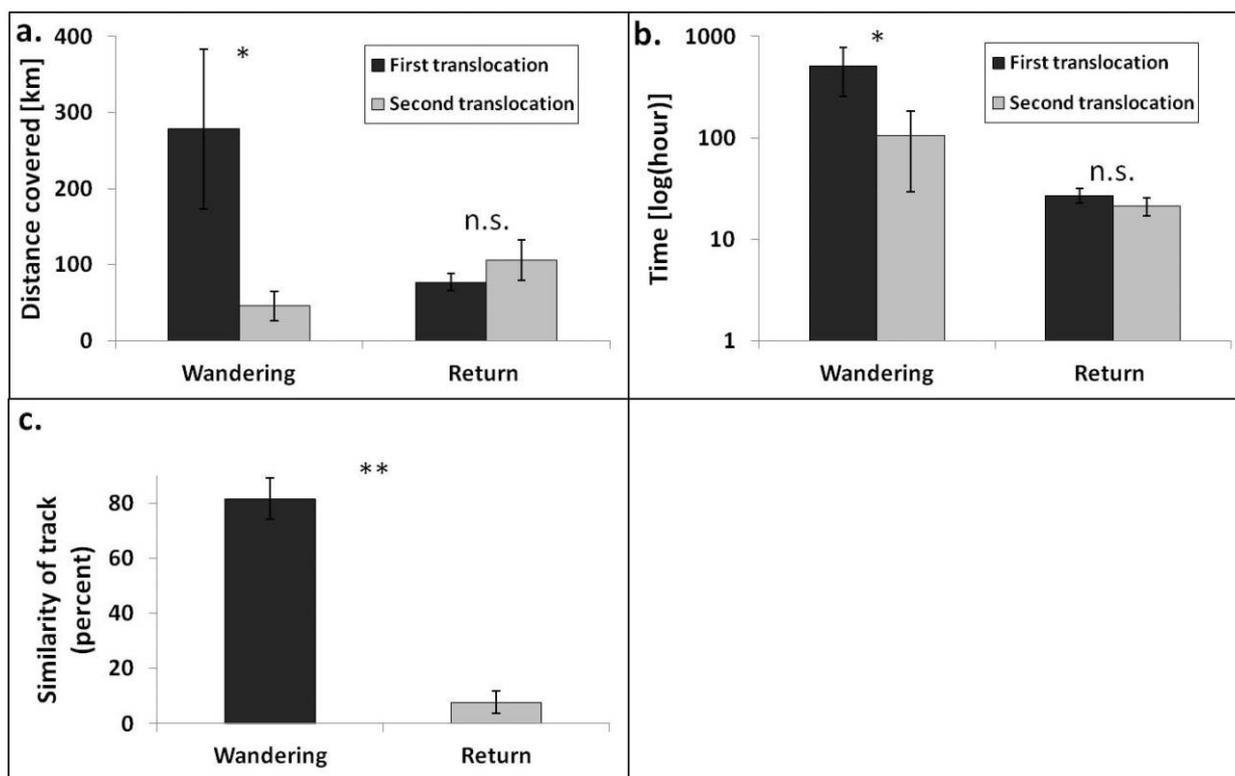


Figure 7: Wandering and return phase patterns during first (unfamiliar) and second (familiar) translocations. *a*, Wandering distance covered during the phase decreases significantly at the second translocation (Wilcoxon test, $n = 7$, sum of positive ranks [SPR] = 28, sum of negative ranks [SNR] = 0, Z -value: -2.36 , $P < .05$), while the return distance is similar at both translocations (Wilcoxon test, $n = 7$, SPR = 18, SNR = 10, Z -value: -0.67 , $P > .05$). *b*, Wandering duration (number of hours) decreases significantly at the second translocation (Wilcoxon test, $n = 9$, SPR = 45, SNR = 0, Z -value: -2.66 , $P < .05$), while the return duration is similar at both translocations (Wilcoxon test, $n = 7$, SPR = 21, SNR = 7, Z -value: -1.18). *c*, Comparison of the similarity between wandering and return trajectories showed a significant difference (higher similarity at wandering phase). This implies that, at their second translocation, the birds followed the known path during wandering and found a new path during return (Z -value: 2.78 , $n = 7$, $P = .008$). One asterisk indicates $P < .05$; two asterisks indicate $P < .01$.

versus first translocation (median, mean \pm SE: 37.9, 83.9 \pm 39.1 vs. 702.8, 1,010.3 \pm 255.5, respectively; t -test, $df = 20$, $t = 2.78$, $P = .01$; fig. 8).

Discussion

High-resolution GPS tracking of wild birds before, during, and after translocation experiments provided insights into the navigation capacity and movement patterns in a resident bird species, the stone curlew. We tracked the birds for long periods (including one full lifetime track, see bird 2797 in figs. A1, A5)—to our knowledge, much longer than any similar study thus far—and found that all birds had highly restricted home ranges. Birds were translocated during active breeding to maintain high motivation to return home, and homing success was indeed high. Homing tracks of individual birds were significantly shorter than those anticipated from calibrated random walk models portraying return by random chance and lacked evidence for landmark-

guided movement. Translocated birds exhibited a clear biphasic movement pattern of a prolonged tortuous wandering phase, followed by an abrupt switch to an oriented return phase that fits well the theoretical map-and-compass model rarely linked to direct empirical findings. Birds retranslocated to the same release site exhibited a much shorter wandering phase, switched to the return phase earlier and at a novel location, and flew back home at a different trajectory but with similar movement properties. Altogether, our findings suggest true navigation capacity for this nonmigratory species, possibly involving learning or acquisition of a navigational map during the wandering phase and preservation of spatial memory for long periods of time.

Birds were translocated to distances that were at least one order of magnitude greater than their regular movements, yet most (85%) of them successfully returned home after their first displacement without prior training. In previous studies of pigeons, in comparison, only about half of the birds translocated to similar distances successfully homed

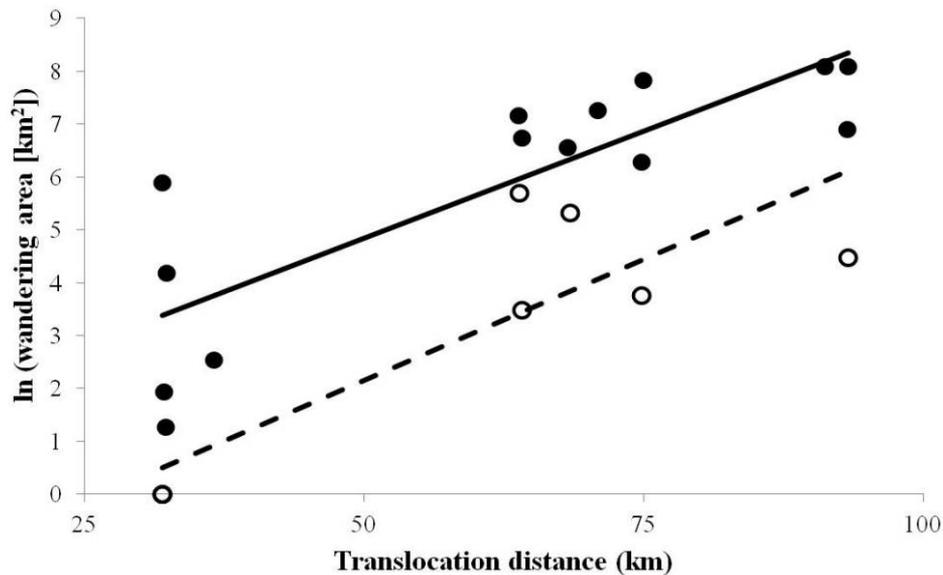


Figure 8: Area covered during the wandering phase (y and Y -axis) for birds retranslocated to familiar (open circles) and unfamiliar (filled circles) sites as a function of translocation distance (x and X -axis). The area covered during the wandering was estimated as the minimum convex polygon given in square kilometers (note the natural log scale). Exponential fits yielded $y = 0.089e^{0.091x}$, $R^2 = 0.691$ (familiar site, solid line) and $y = 2.412e^{0.079x}$, $R^2 = 0.735$ (unfamiliar site, dashed line). The fitted functions are for the original data and have statistically indistinguishable exponents ($F_{1,18} = 0.15$, $P = .71$) but significantly different Y -axis intercepts ($F_{1,19} = 4.46$, $P = .0003$), implying that for similar translocation distances, the wandering area of birds retranslocated to the same (familiar) site is much smaller by an average factor of 27 than that of birds retranslocated to another (unfamiliar) site.

back in their first trial (Wallraff 2005). In previous studies of wild birds (Bonadonna et al. 2005; Thorup et al. 2007; Gagliardo et al. 2013; Reynolds et al. 2015), the home range and movements of individual birds as well as the level of familiarity with the translocation site have been assumed rather than known. Our detailed, long-term tracking provided accurate information about bird movements after release, revealing a clear separation of two phases that can be related to the map and compass phases of true navigation (Guilford et al. 2004; Schiffner et al. 2011). Our study system demonstrates that the map phase can indeed be distinguished, both temporally and spatially, from the subsequent and often indistinguishable compass phase.

High homing success of birds translocated to unfamiliar sites is usually considered evidence for true navigation capacity (Matthews 1953; Wallraff 2005). Although homing success of stone curlews in this study was exceptionally high, even compared to the paradigmatic homing pigeon, we argue that ascribing true navigation still requires rigorous exclusion of return by random chance. We used four different correlated random walk models to estimate the probability of return by random chance for birds moving with the same basic movement properties (e.g., turning angle and speed distributions). We found that if a translocated bird would have moved as it does in its home range, successful return by random chance would be highly unlikely within the time frame

of its actual homing in the first translocation experiment. We have reached similar conclusions from correlated random walk models based on other types of stone curlew movements. Since home-detection radius is unknown for stone curlews (and for nearly all other species), we varied this parameter too and found that chance return is likely in some circumstances if a bird can detect its home from distances much larger than the typical scale of its home movements. Such ability, however, is unlikely and is not supported by our data sets.

Translocated birds spent considerable time in the vicinity of the wandering-to-return switch location long before making the sudden actual switch. This finding suggests that the particular switch site is not necessarily associated with specific familiar landmarks. Furthermore, although (as expected) all translocated birds spent a considerable portion (45%) of the wandering time at areas closer to home—where familiar landmarks are more likely—than to the translocation site, we found no tendency for the wandering-return switch to be placed closer to home than the translocation distance. We thus conclude that stone curlews are not likely to rely on familiar landmarks during the map acquisition phase and, hence, can be considered true navigators.

An animal highly motivated to return to a certain site (e.g., home) from an unfamiliar area first needs to determine its position relative to its destination, that is, to establish the navigational map. The map could be established before or imme-

diately upon release, as proposed for homing pigeons (e.g., Mazzotto et al. 1999). However, the bird might delay its return (thus explaining the wandering phase) not because of unresolved navigational map but due to other factors such as trapping trauma, low motivation, and confusion given the unfamiliar environment. We designed this study to minimize some of these effects by shortening capture time and focusing on incubating birds highly motivated to return to their nests, but we cannot preclude the option of delayed return due to these factors. Alternatively, we propose that the wandering phase reflects a time-consuming establishment of a navigational map through acquisition of navigational cue(s), for example, by learning. Both explanations require a calibration procedure of the home-acquired cue value against the sensed gradient. If this explanation holds for our case, the calibration procedure in stone curlews is much longer than similar processes documented previously in other species. Pigeons tend to circle the release point for an average of 2 min (Schiffner and Wiltschko 2009), and cue-conflict experiments of other bird species showed that compass calibration takes place within 24 h, both in captivity (Muheim et al. 2006, 2009) and in the wild (Cochran et al. 2004). Furthermore, the unique movement patterns observed during the wandering and return phases differ significantly from the typical movements of the same birds in their home range; these patterns neither represent occasional behavior, as they have been observed in all tracked birds without exception, nor inaccurate sampling, given the high-quality GPS tracks we obtained.

We are not aware of any previous report of translocated birds exhibiting a similar prolonged wandering phase followed by an abrupt switch to an oriented return phase. Attempts to link circling behavior to navigation in pigeons has been controversial (Mazzotto et al. 1999; Gagliardo et al. 2001; Schiffner and Wiltschko 2009) and might reflect motivational effects rather than orientation for navigation (Schiffner and Wiltschko 2009). Bank swallows (*Riparia riparia*) orient toward home just after release at distances of up to 75 km from their home range (Sargent 1962). The same holds for wood thrushes (*Hylocichla mustelina*), which showed extended, slower-paced homing over a few consecutive days but began homeward orientation in their first movements following release, thus leading the authors to propose a motivational reason for the delayed arrival to the home range (Able et al. 1984).

The wandering phase was rather variable in duration and spatial extent, with a general tendency of longer and larger wandering at more distant translocation sites (figs. 8, A2). Variation in the wandering-return switch unexplained by the distance effect can be attributed to the interplay of variation among individuals' skills, motivation, and stochastic external effects. On the one hand, for all of our birds, the wandering-return switch occurred after more than 2 days;

for five birds (38%), return started within the first week following release, likely representing birds that were highly motivated, skilled, or encountered sufficient learning rewards. On the other hand, three birds (23%) wandered for more than 1 month; these were presumably less motivated, less skilled birds that failed to gather sufficient rewards during wandering. In this study, we controlled the motivation by translocating breeding birds trapped during active incubation, a methodology adapted from seabird studies (Bonadonna et al. 2003, 2005; Gagliardo et al. 2013). Individual pigeons of different reproductive states and ages differ in their homing motivation (Wallraff 2005; Schiffner and Wiltschko 2013). Wild birds might face higher competition for their breeding territory compared to domesticated pigeons (Jacobs and Menzel 2014), but the length of the breeding season might be shorter in wild birds, hence limiting the period of high motivation. The ground-nesting stone curlews, however, endure high nest destruction (Solís and Lope 1995) and lay up to seven replacement clutches in a single breeding season (February–October), during which they commonly complete two successful breeding cycles. Stone curlews might have suffered from high stress due to trapping and the sudden load of an unfamiliar tracking device, thus causing something similar to wandering, but most translocated birds were observed in their nest after return, and movement trajectories of birds were indifferent in the first days after trapping and tagging compared to subsequent movements recorded for months and up to 3 years after. We thus consider translocated stone curlews to bear strong and consistent homing motivation during all translocation experiments. Another support for high motivation is the order of magnitude reduction in homing times after the second translocation, when the cues (gradients or landmarks) were known, compared to the first translocation (fig. 7). Further research is needed to elucidate the role of potential influential factors such as motivation, trapping, tagging, and navigation skills in determining the length and success of the acquiring process during the wandering phase.

Repeated translocations suggest a good preservation of spatial memory, for more than a year, as the learning process that took place during the first wandering in this region much improved navigation performance in the second trial. The improvement was observed at the wandering stage. The bird followed a similar trajectory (fig. 7c) and decreased the time and distance of the wandering phase. This corresponds well with patterns regularly seen in pigeons (Gagliardo 2013). But stone curlews did not navigate more efficiently during the return phase, which is the case with pigeons. Because of the different characteristics of the wandering and return phases, we propose that these phases not only serve as different stages in the navigation model but that the birds use a different navigation strategy during each phase. When wandering, the birds use a strategy that is based on site recognition and internal cues (if it is an unfamiliar area, the bird may use

large topographic features to guide its way), and during return, the bird navigates by using an external cue or several cues. Contrasting stone curlews with pigeons we observed that, first, the wandering phase of stone curlews is much longer than the circling phase of pigeons (Wallraff 2005). Second, retranslocated pigeons commonly recapitulate the same route for return (Biro et al. 2004, 2005; Meade et al. 2005), whereas retranslocated stone curlews return from different sites and along different routes. This suggests that once the map is resolved for a given site, stone curlews can return from any location within the map's boundaries, further supporting true rather than landmark navigation. This resembles navigation of long-distance migrants such as ospreys (*Pandion haliaetus*; Alerstam et al. 2006) and marsh harriers (*Circus aeruginosus*; Vardanis et al. 2011), both of which exhibit low route repeatability.

We neither manipulated the sensory capacity of experimental birds nor tested the role of potential navigational cues and, hence, cannot strongly argue for one potential navigation mechanism or another. The repeated homing pattern we found might shed light on possible cues used for maplike representation but should be interpreted with caution. During return, birds released in the south or the north consistently flew home along a nearly perfectly straight path, whereas all birds returning from the east first progressed 20–107 km southward, circling the Hebron area, and then approached home in a straight line from south or southeast. These patterns suggest that navigation cue(s) should vary in a different manner along the north-south axis compared to the east-west axis. Translocation experiments with fruit bats (*Rousettus aegyptiacus*) in the same study area provided evidence for the use of visual cues (Tsoar et al. 2011). Bats released from sites with a clear line of sight to familiar visual landmarks homed successfully with no delay, but those released from a site where familiar visual landmarks cannot be seen exhibited a tortuous path at the first stage until the line-of-sight detection and then commenced to a straighter path back home, much resembling the wandering and return phases documented here for stone curlews. The wandering phase of the bats was, however, much shorter (a few hours vs. days or even weeks). The use of magnetic inclination (Phillips 1996; Freake et al. 2006; fig. A8) is in line with the straighter trajectories of the southern and northern translocations compared to eastern translocations. The southern loop, associated with all birds homing from the Dead Sea area could be in line with the use of inclination because the birds need to make a deliberate error in their paths to produce a difference in the magnetic gradient compared with home values (Merkle et al. 2006). This southern loop could at first glance suggest the use of magnetic intensity (fig. A9) cues due to the Hebron magnetic anomaly, which lies between the Dead Sea and the home site of the stone curlews in this study (Shirman 2000). If birds follow a line that reduces the difference of magnetic

values from the release point to the home point, they are predicted to make a southern loop and fly parallel to the magnetic isopleths after reaching an intensity value similar to the one at their home (Dennis et al. 2007). This and other possible navigation mechanisms—such as the use of atmospheric odors (Gagliardo et al. 2013; Reynolds et al. 2015) and gravity vectors (Blaser et al. 2014; fig. A7)—are subject to more detailed research in future evaluation of the mechanisms underlying the distinct patterns of stone curlew navigation.

To conclude, we first join the call for broadscale investigation across wild species and varied study systems aimed at directly testing map stage hypotheses (Jacobs and Menzel 2014) and, in particular, more studies focusing on resident species with a restricted home range. Second, although our long GPS tracking reduces uncertainty about the home range, full information about the lifetime track is required to exclude rare long-range movement events. Translocation experiments with juveniles tagged before fledging (Chernetsov et al. 2004) and experiments over very long distances are promising (Thorup et al. 2007). The impressive return of a Manx shearwater (*Puffinus puffinus*) to Skokholm Island (Wales) from Boston, 5,130 km away, has long been considered compelling evidence for true navigation (Matthews 1953), but this has been questioned given that migration routes, stopover sites, and foraging grounds of this species lie around the Atlantic (Guilford et al. 2009). Therefore, tests of true navigation must consider study species ecology and long tracking prior to the translocation. Third, 3 of our 20 translocated birds (15%) did not return; they might have died, gotten lost, or perhaps found a suitable mate to breed elsewhere. Large-scale data retrieval via satellite or GSM technologies could inform of the fate and the tracks of all birds. Fourth and last, we proposed the map learning hypothesis, asserting the wandering phase as a learning phase for acquiring the cues underlying the map stage of Kramer's model. We emphasize that the term "learning" should be used in the broad sense. At one extreme, it should encompass learning-motivated explorations (as opposed to chance explorations) during which the bird learns the unfamiliar environment while searching for familiar landmarks. At the other, more complex, extreme, the bird might sample the relevant cues in the unfamiliar environment and could even develop sensory skills and neural networks to translate the cues so that the map stage can be resolved. We suggest that establishing a gradient map and extrapolating it as suggested by the magnetic map hypotheses (Phillips 1996) could be established at the release site as well as at the home site. This could be studied by restricting the exposure of birds to their local environmental cues during development. Finally, further research using advanced tracking technologies to record detailed movements of translocated birds should divulge questions about the generality of the biphasic wandering-return pattern reported here across different species and sys-

tems, potentially providing unique new opportunities to elucidate the map stage of true navigation.

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