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RESEARCH PAPER

Experimental tests of a seasonally changing visual preference for habitat in a long-distance migratory shorebird

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Abstract

Migratory shorebirds show highly organized seasonal cycles in physiological and morphological traits (body mass and composition, plumage, hormone levels, etc.), which in captivity is accompanied by restless behaviour at times when free-living birds would start migration. We introduce the idea that seasonally changing preference for habitat could motivate migrants to embark on migration and that this cognitive process could also guide them to seasonally appropriate places. We explored this by testing whether red knots (*Calidris canutus*), which also in captivity maintain marked circannual phenotypic rhythms, show evidence of seasonal change in preference for pictures of seasonally appropriate habitats. We first developed a method to verify whether red knots are able to memorize and discriminate contrasting pictures projected by LCD projectors. This was followed by two different experiments in which we tested for a seasonally changing preference for breeding or non-breeding habitat. When carried out during the pre-breeding season, the red knots are expected to prefer pictures of mudflats, their non-breeding habitat. At the start of the breeding season, they should prefer pictures of the tundra breeding habitat. We established that knots are able to distinguish and memorize projected images. We failed to demonstrate the predicted change in vision-based habitat preference, but for reasons of test design we do not interpret this as a strong rejection of the hypothesis. Instead, we suggest that experiments with greater numbers of individuals tested once, perhaps in combination with the provision of additional cues such as smells and sounds, will help the development of these ideas further.

KEYWORDS

Calidris canutus, circannual rhythms, cognition, memory, migration, motivation

1 | INTRODUCTION

The ecological opportunities provided by the seasonally changing environmental conditions on Earth have favoured an enormous variety of seasonal migration phenomena (Alerstam, 1990a; Newton, 2007). The animals engaging in such long-distance migrations perform

amazing feats of endurance exercise (Piersma, 2011), and navigation (Åkesson & Hedenström, 2007; Mouritsen, 2018; Muheim, 2006; Muheim, Schmaljohann, & Alerstam, 2018; Ritz, Ahmad, Mouritsen, Wiltschko, & Wiltschko, 2010). What seasonal migrants have in common is the circannual steering of relevant physiological processes in relation to navigation (Pinzon-Rodriguez, Bensch, & Muheim, 2018)

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and the circannual expression of labile physiological and morphological ("physiomorphic") traits that facilitate endurance exercise during migration as well as behaviour for survival and reproduction during the appropriate seasons (Bijleveld, 2015; Gwinner, 1996; Karagicheva, Rakhimberdiev, Saveliev, & Piersma, 2018). Physiological preparation for migration in spring is associated with high corticosterone levels (Eikenaar, Klinner, & Stöwe, 2014; Landys-Ciannelli et al., 2002; Piersma, Reneerkens, & Ramenofsky, 2000), increases in restless behaviour (Gwinner, 1986; Zúñiga et al., 2016) and enhanced cognitive performance (Rattenborg et al., 2004). This prompted the question if migrants, along with the well-studied suite of corporal and cognitive changes, would show corresponding seasonal changes in habitat preferences?

Memory may be an important motivator of goal-oriented movements (Bennett & Tang, 2006; Bracis & Mueller, 2017; Fagan et al., 2013; Rodríguez et al., 2017). Garden warblers (*Sylvia borin*), who were trained to associate temporal and spatial changes in food availability in an experiment where food was available temporarily but predictably in multiple connected rooms, learned to visit a specific foraging site at a given time of the day (Biebach, Gordijn, & Krebs, 1989). Such capacities would be extremely useful for shorebirds such as the subjects of this study, birds depending on a circatidal cycles for the accessibility of its food resources (Bulla, Oudman, Bijleveld, Piersma, & Kyriacou, 2017). Similarly, associating circannual rhythms with spatial changes in habitat characteristics during migration may be adaptive.

Memory-motivated movements are most likely to occur in long-lived species for which the scale of the orientation by individual animals is greater than their perceptual range, for example during long-distance migration (Berbert & Fagan, 2012; Mueller & Fagan, 2008). In a recent review, Winger, Auteri, Pegan, and Weeks (2018) suggested that seasonal migratory routines have evolved as a result of the fitness benefits associated with returning to familiar summer and winter areas rather than previously unvisited, "new," areas. The ability of an individual to return to a previously visited site implies the use of a cognitive "concept of place." The occurrence of a long-lasting spatial memory may be especially adaptive in long-distance migratory birds: they move between sequences of distant habitats for which no up-to-date information is available at the time of departure towards any of them (Berbert & Fagan, 2012; Cristol et al., 2003; Mettke-Hofmann & Gwinner, 2003; Pravosudov, Kitaysky, & Omanska, 2006; Winkler et al., 2014).

Memory could also support motivation. The possibility of mental images of preferred habitats which change with the seasons brings up the notion of "home sickness," a longing for a familiar but distant place. Among other causes for spring migration such as the availability of food and extended day length at northern latitudes, Linnaeus (1757) listed feelings for home. In 1928, Allard published a review on possible directive stimuli that urge and guide migratory birds, between breeding and non-breeding grounds. Possible motivational forces for northward migration include "a longing for light" (previously defined as a driving force by the Finish ornithologist Johan Ludvig Runeberg) and a "drawing force" to go home (contrived by

English, 1923, cited in Allard, 1928). Here, we elaborate on the idea that migratory movements may be motivated (sensu Hogan, 2017) by seasonally changing habitat preferences. The tests for seasonally changing habitat preferences presented here were inspired by a study on dark-eyed juncos (*Junco hyemalis*; Roberts & Weigl, 1984). By their seasonally changing selection for pictures of either breeding or non-breeding habitat, Roberts and Weigl suggested that juncos possess a vision-based concept of habitat. We developed an experimental protocol to test whether red knots (*Calidris canutus*) are able to memorize and distinguish projected pictures of contrasting landscapes. Once this was established, we explored whether red knots showed changing preferences for pictures of seasonally appropriate habitats.

2 | GENERAL METHODS

Red knots, hereafter knots, are sandpipers that migrate many thousands of kilometres between distinct non-breeding (coastal mudflats) and breeding habitats (high arctic tundra) and show strict circannual rhythms in plumage, body mass and other physiomorphic traits, even when held in captivity (e.g. Buehler & Piersma, 2008; Karagicheva et al., 2016; Piersma, 2007).

2.1 | Animal husbandry

The knots studied here were captured with mist nets in September 2012 and between August 2015 and February 2016 at different high-tide roosts in the Dutch Wadden Sea. After capture, the knots were aged on the basis of plumage characteristics either as juvenile, second calendar year or older (i.e. adult). The knots were colour-ringed for individual identification. All knots belonged to the *islandica* subspecies (Piersma, 2007); this subspecies breeds on tundra in north-east Canada and northern Greenland and winters in north-west Europe (Davidson & Wilson, 1992).

On the island of Texel (53°00'N, 04°47'E), in the Experimental Shorebird Facility of the NIOZ Royal Netherlands Institute for Sea Research, the birds were kept in flocks of approximately eight individuals. The facility is located within the natural geographic wintering range of the subspecies. The outdoor aviaries were 4 m long, 1.9 m wide and had a sloping roof at 2.3 m height at one side and 1.9 m at the other. All aviaries contained smoothly coated concrete floors constantly irrigated with running seawater and, at the back of the cage, a mudflat basin (1.9 m × 1.0 m) filled with Wadden Sea sand and running seawater. The knots experienced local ambient temperatures and a seasonally changing photoperiod through a screened window (1.9 m × 0.9 m) in the back wall. When not in the experiments, knots had ad libitum access to Trout food pellets (Produits Trouw, Vervins, France) and freshwater for drinking and bathing in a separate tray.

Every week, while the aviaries were cleaned and disinfected with chlorine, the general health of the knots was checked and their body

mass and body moult scored (Milot et al., 2014). We used plumage score to indicate the extent of physiological preparation for breeding (Karagicheva et al., 2016). Body plumage was scored on a scale from 1 to 7. In winter, knots show white breast plumage and a grey back (indicated with 1). In the weeks before the breeding season, they moult into a rufous-red breast plumage with much darker back feathers (indicated with 7 when in full breeding plumage). This transition takes a few weeks, and the final extent of breeding plumages also depends on the age and the body condition of the bird. When the experiments were finished, the knots were released near the capture site in the Wadden Sea.

2.2 | Experimental room

All experiments were performed in an indoor experimental room measuring 7 m by 7 m, with a height of 2.80 m. The “floor” consisted of two areas of “mudflat” separated by a “gully” (see Figure 1). The two mudflats could be exposed or submerged as the water table could be raised to a depth of 30 cm. The room had no outside-facing windows and was dimly lit during experiments to ensure projection quality. Projections were made on either side of the experimental room on two screens of water-resistant multiplex plywood coated with a thin layer of white epoxy.

2.3 | Experimental rationale

We report on four experiments performed from 2012 to 2015. We first developed an experimental protocol to establish whether knots are able to distinguish projections of natural landscapes (Discrimination Test I). Once this was established, we continued with two experiments to show seasonally appropriate preferences for habitat (Preference Tests I and II). In view of our failure to demonstrate seasonally changing habitat preferences, and indeed the absence of a clear habitat preference in the two tests in general, we again verified that knots can show us that they are able to distinguish

between projected images in the experimental set-up and with the procedures chosen; this was Discrimination Test II.

2.4 | Experimental procedure

Although these experiments served different goals, they were all based on the dichotomous preference test (van der Meer, 1992); the “competing” pictures were semi-randomly distributed between two opposing screens (according to a balanced design but in unpredictable order for each bird).

Every test included the release of a single knot from a blinded wooden cage (1 m by 1 m by 1 m) with a smaller (60 × 40 × 33 cm l × b × h) inset, placed in the middle of the wall at equal distance from the two projection screens (Figures 1-4). The front panel of this cage consisted of a see-through screen. Before the start of a trial, the focal bird was caught from its home aviary and its body mass was taken before it was placed into the release cage. The front screen of the release cage was opened remotely with a pulley system to allow the bird to leave and indicate the image of choice (see below for the exact definition of the images of choice for each test). When a trial ended, the knot was gently herded back to one of the side aviaries and returned to its home aviary (see Figures 1-4).

2.5 | Analyses

For all four experiments, we ran univariate models using the *glmer()* function from the *lme4* package (Bates, Maechler, Bolker, & Walker, 2015) with a logit link (family = “logit”) to model the binomial response variable. To investigate the possibility that individuals differ in their performance, “individual identity” was included as a random intercept in all models. When we found a value of zero for among-individual variance, we confirmed the negligible effect size of bird ID by fitting it as a fixed effect (results not shown). To draw inferences based on simulated posterior distributions, bayesian statistics were used.

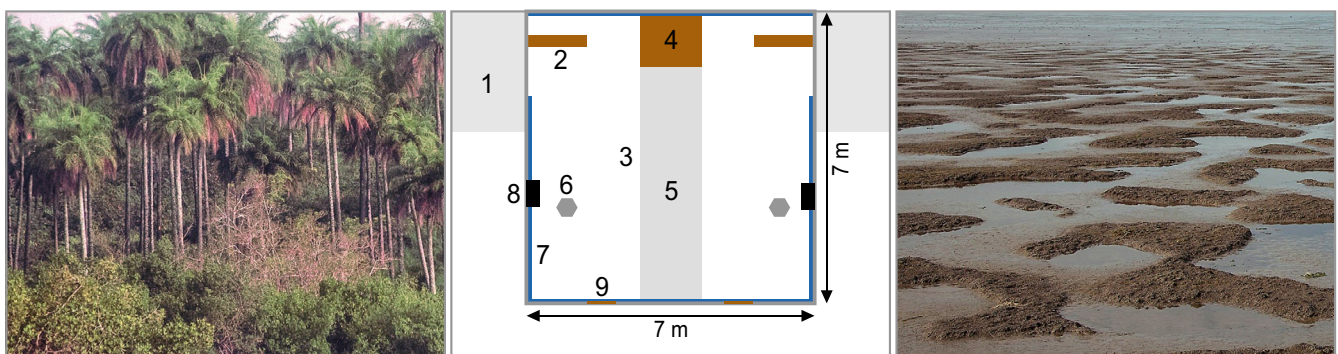


FIGURE 1 Experimental set-up Discrimination Test I. From left to right: picture of a coastal forest in Guinea-Bissau; the experimental shorebird facility: (1) side aviary, (2) access step aviary, (3) mudflat, (4) release cage, (5) concrete lane, (6) feeder, (7) projection screen, (8) projector, (9) entrance door; picture of Dutch Wadden Sea. During the experiments, the side on which either of the projections were made was varied randomly

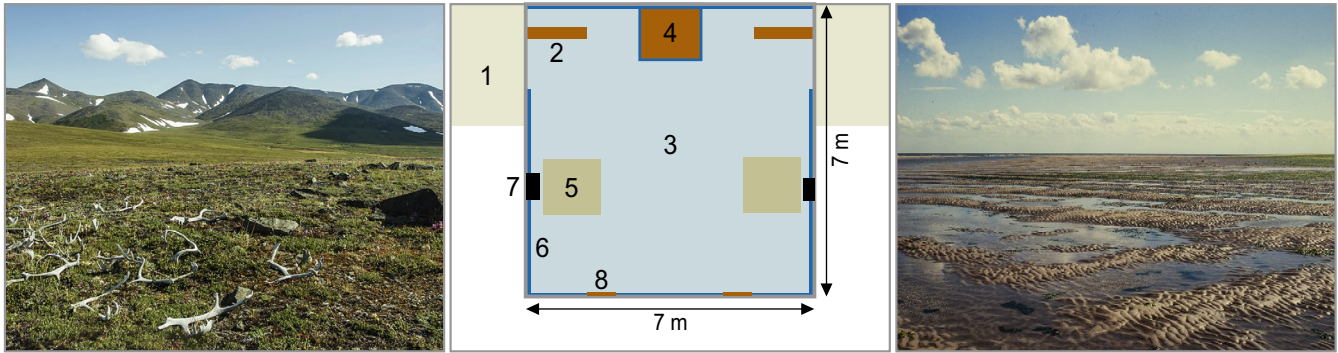


FIGURE 2 Experimental set-up for Preference Test I. From left to right: picture of breeding ground (known knot habitat in the arctic tundra in Chukotka, Anadyr); the experimental shorebird facility: (1) aviary, (2) access step aviary, (3) seawater, (4) release cage, (5) sandy patch, (6) projection screen, (7) projector, (8) entrance doors; picture of wintering ground (Dutch Wadden Sea). During the experiments, the projection side was designed to vary randomly

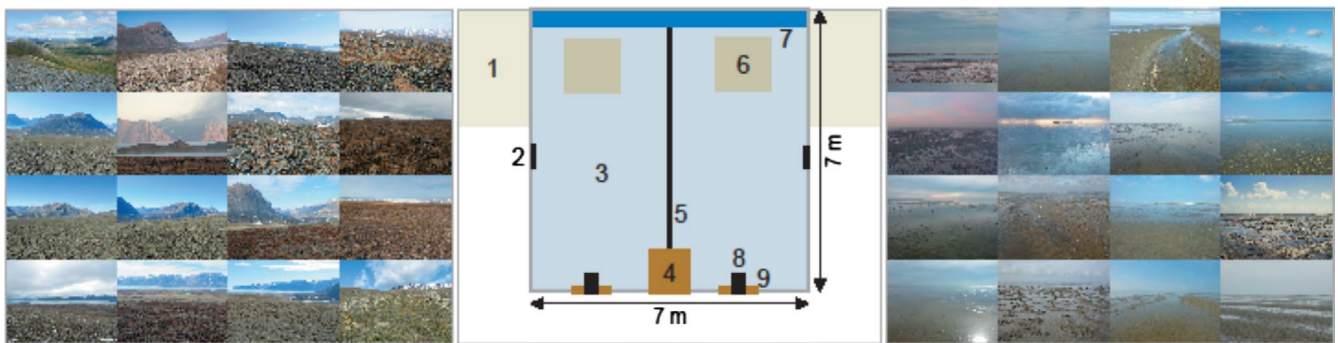


FIGURE 3 Experimental set-up for Preference Test II. From left to right: 16 unique pictures representing breeding ground (known red knot habitat at the high arctic tundra in Greenland), the experimental shorebird facility: upper left: projection screen south, upper right: projection screen north, (1) aviary, (2) camera, (3) submerged mudflat (high tide), (4) release cage, (5) division, (6) sandy patch, (7) projection screen, (8) projector, (9) entrance door, 16 unique pictures representing wintering ground (known red knot habitat in the Dutch Wadden Sea). During the experiments, only one image representing tundra and mudflat was presented and the projection side was designed to vary randomly

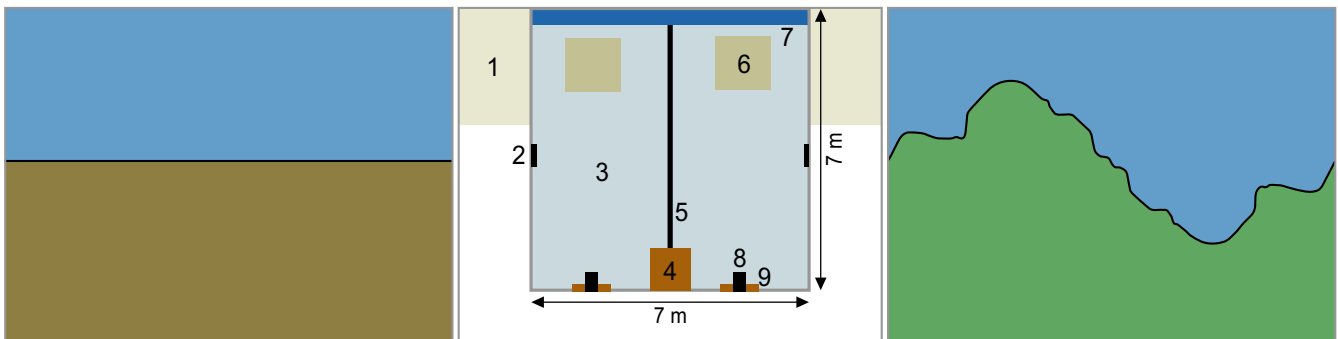


FIGURE 4 Experimental set-up for Discrimination Test II. Left: graphical representation of mudflat, Right: graphical representation of tundra; the experimental shorebird facility: (1) aviary, (2) camera, (3) submerged mudflat (high tide), (4) release cage, (5) division, (6) sandy patch, (7) projection screen, (8) projector, (9) entrance door. During the experiments, the projection side was designed to vary randomly

To simulate values of the posterior distribution of the log-odds of the correct choice given the model parameters (Gelman & Hill, 2007), we used the *sim()* function of the *arm* package (Gelman & Su, 2016). We used 95% credible intervals (CIs) around the mean (β)

fixed effects that were extracted based on 1,000 simulations using the *MCMCglmm* package (Hadfield, 2010). The 95% CI indicates a margin of error in terms of a range of plausible values for β , indicating that we are 95% confident that our CI includes the actual effect size

(Cumming & Finch, 2005). In other words, a 95% CI that does not overlap zero would be considered significantly different from zero ($p < .006$) in a null hypothesis testing framework (Cumming, 2009). For each test, we tested for autocorrelation between subsequent replicates by means of the function *runs.test()* from the *tseries* package (Trapletti & Hornik, 2018). All analyses were done in the R (v3.6.3) statistical environment (R Core Team, 2020).

3 | DISCRIMINATION TEST I

3.1 | Methods

Several bird species have been shown to memorize and distinguish projected images (Bovet & Vauclair, 2000; Brown & Dooling, 1993; Pietrewicz & Kamil, 1977; Watanabe, 2001). However, because no picture-habitat recognition experiments had been done on sandpipers nor on any other shorebirds, we first developed a testing protocol to determine whether knots are able to distinguish between projected images.

During this experiment, the knots were housed in the experimental room and only temporarily removed during testing. In this test, the experimental room was set up such that birds could walk (and optionally fly) to their preferred picture. Pictures were projected on opposite sides of the aviary using two LCD projectors (projector properties—type: BenQ MP615, SVGA: 800×600 , light intensity: 2000 lumen, contrast: 1,000:1, mass: 2.7 kg). The projected areas measured 2.5 m high and 5 m wide (Figure 1).

Two contrasting pictures ($1,024 \times 768$ pixels) of possible non-breeding habitat were selected. One was of an open shore in the Dutch Wadden Sea (mudflat), and the other showed the tropical forest margin of a mudflat in the Archipelago dos Bijagos, Guinea-Bissau (forest) (Figure 1). Feeders were placed in front of the two pictures, but only one of them contained the food reward (Trouvit food pellets). Two knots were trained to find food pellets in a feeder in front of the picture of forest, and the other two birds were trained to find food near the mudflat picture. To avoid the possibility that knots made a choice based on specific colours rather than the scene, the pictures were equalized with respect to reflected colour load using the function *match colour* in Adobe Photoshop (Cs6 Extended).

Tests were preceded by 2 days of training during which either the picture of the mudflat or the forest was projected on both sides with ample pellets in both feeders in front of the projections. During the morning, birds were introduced to the room in pairs. Later, they were individually trained for the release procedure, the reward locations and trial closings. At the start of each test, the focal knot was left in the release box for 1 min to observe both projections. When the front panel was opened, the bird usually left the box immediately. Once the bird approached one of the two feeders up to less than 5 cm, the choice was made. When this was the “correct” feeder (i.e. the feeder containing food), the bird was allowed to take a few pellets from it. The trial ended when the bird lost interest in the feeder (usually after <1 min).

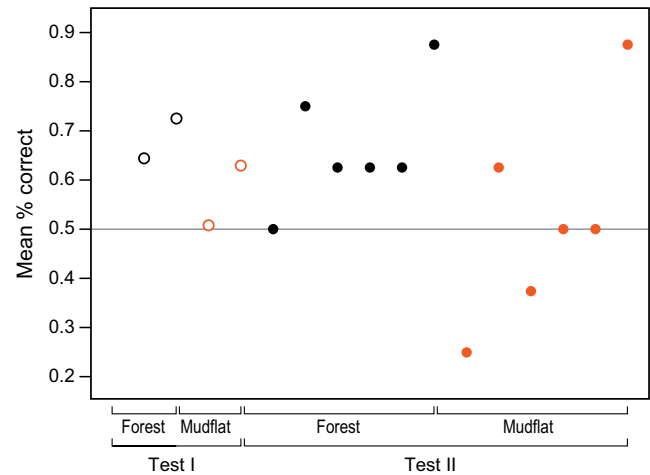


FIGURE 5 Individual performance during Discrimination Tests I and II. Dots represent mean values for correct choices per knot assigned to the forest- or the mudflat group for Discrimination Test I (open circles) and Test II (closed circles). The horizontal line represents 50% correct or random choice [Colour figure can be viewed at wileyonlinelibrary.com]

Birds were tested for 21 days between 9 March and 12 April 2013 with a total of 86 trials for all birds. All birds were tested before the next trial was begun. During the days of experiments, the birds received no other food than what they could eat at the feeder next to the rewarded picture. However, whenever a bird would drop below a critical threshold body mass of 100 g, additional trout pellets were offered between series of experiments. Especially during the first days of testing, the birds were not always motivated to make a choice, probably because they were not hungry enough. These trials were excluded from analyses (see Appendix S1 Table S1).

To test whether birds successfully learned and distinguished projections (i.e. if the proportion of correct choices differed from random choice), we initially ran univariate models without fixed effects and a binomial response variable (0 = false, 1 = correct; indicating if the bird had chosen the image it was trained for). To account for the possibility that the birds might have an initial preference for one side of the room, regardless of the picture presented, we subsequently added a fixed effect for the “side” at which the “correct” image was projected (0 = south side of the room, 1 = north side of the room). Additionally, the fixed effect “group” (forest = 0, mudflat = 1) was included to investigate whether birds assigned to different groups performed differently.

3.2 | Results

Three of the four birds chose the correct side consistently above chance levels. Overall, the knots learned to discriminate between images (after back transformation from the intercept model: $\beta = 65\%$, 95% CI = 56%, 71%, Figure 5). Birds assigned to the forest group performed significantly better than the mudflat group (Table 1, Appendix S1 Table S1). This mainly resulted from the

TABLE 1 Log-odds for the focal bird to choose the rewarded image in the experiments on Discrimination Tests I (left) and II (right)

	Discrimination Test I (n = 4)	Discrimination Test II (n = 12)
Fixed effects	β (95% CI min, max)	β (95% CI min, max)
Intercept ^a	0.95 (0.61, 1.45)	-0.15 (-0.83, 0.64)
Projection side (north)	-0.54 (-0.89, -0.01)	1.69 (0.91, 2.78)
Group (mudflat)	-0.48 (-0.96, -0.01)	-0.61 (-1.76, 0.06)
Random effect	σ (95% CI min, max)	σ (95% CI min, max)
Bird ID	0.03 (0.00, 0.09)	0.04 (0.01, 0.09)

Note: The logit-transformed binary response choice (1 = correct, 0 = false) was based on the first feeder that was visited by the focal knot. Significant effects (i.e. whose 95% CI do not overlap with 0) are indicated in bold.

^aThe intercept represents the choice made by an individual of the group trained on the forest image with the correct picture being projected on the south side of the testing arena.

fact that one individual trained on the picture of a mudflat never learned to discriminate (Table 1, Appendix S1 Table S1). Choices were biased towards a preference for the south side of the room (Table 1). Overall, the performances did not improve with successive trials (one-sided runs test: $Z = -1.05$, $p = .15$, Appendix S1 Table S1).

4 | PREFERENCE TEST I

After establishing that knots are indeed able to distinguish between what must be memorized projections, we continued to test whether knots change their vision-based habitat preference depending on time of the year and physiological state. During testing, the knots were offered the choice between simultaneously projected pictures of a non-breeding habitat (intertidal mudflat) and a breeding habitat (tundra). Tests were carried out in early May (when knots were still preparing for migratory departures) and again in early June (when they are fully ready to take off to the breeding grounds). We predicted that the knots would show a preference for the mudflat picture during the pre-breeding season and for the tundra picture in the breeding season.

4.1 | Methods

Before testing, the 13 birds studied in this experiment were housed in outside aviaries where they were exposed to seasonally appropriate ambient temperature and photoperiod to ensure natural phenotypic circannual rhythms. In March 2014, they were moved to similarly sized indoor aviaries, where the air temperature was held

constant at 12°C and photoperiod followed the outdoor situation. In mid-April, the knots were moved to the indoor experimental room. Here, the photoperiod followed the outdoor situation by means of a "day-light" lamp.

The design of the experimental room was very similar to the design in Discrimination Test I. However, water level in the room was raised so that birds had to fly the 3 m from the release box to a 1-m² sandy patch in front of the projections (Figure 2). During the tests, a single picture of either mudflat or tundra was used repeatedly. Both pictures were taken at a similar angle and had the top one-third taken up by blue sky. During 5 days of training in late April, the knots were first introduced to the room as a group and later individually.

Testing took place from 1 to 10 May 2013 and again from 3 to 12 June 2013. Each bird ($n = 13$) was given one trial per day for ten consecutive days ($n = 10$) in both testing periods. The rest of the flock was confined to one of the two side aviaries during testing (Figure 2). During tests, the focal bird was left in the release box for 1 min before the screened panel was opened. The bird indicated its preference by flying towards its image of choice and landing on the patch in front of it. After 5 min, the trial ended; if the bird had not left the release box by then, the trial was excluded from analyses (see Appendix S1 Table S2). During testing, no food reward was offered, the only reward being the chance to stand on the sandy patches near one of the two projections.

To test whether knots showed seasonally changing preference for habitat, we constructed univariate models with a binomial response variable for habitat (0 = mudflat, 1 = tundra). Besides the inclusion of a fixed effect for the projection side and a random effect bird ID (see the method section for Discrimination Test I for more details), we modelled habitat preference as a response to season (0 = breeding, 1 = pre-breeding season). Weekly obtained plumage scores were interpolated for intermediate experimental days to indicate the extent of physiological preparation for the breeding season. Because not all birds reached full breeding plumage (score = 7, see Appendix S2 Figures S1 and S2), we included a bivariate fixed effect for the presence or absence of breeding plumage (1 = for plumage scores ranging from 1 to 4, and 0 = plumage scores between 5 and 7) to examine the effect of variation in breeding plumage scores on habitat preference.

4.2 | Results

The knots showed a mean preference of 55% for mudflat during both the pre-breeding and breeding season (Appendix S1 Table S2), so no seasonal change in habitat preference was found (Figure 6, Table 2). Individuals did not differ in their seasonal preference for habitat (Table 2; 95% CI for bird ID is centred on 0). Especially during the breeding season, in some trials birds refrained from making any choice at all (missing values during the pre-breeding season $n = 11$, breeding season $n = 25$, see Appendix S1 Table S2); this lowered sample sizes considerably. There was also no association between the extent of breeding plumage and habitat preference,

FIGURE 6 Individual changes in habitat preference. Mean preference values for tundra landscape (dots) are connected for each individual between the pre-breeding and breeding season. The horizontal line indicates 50% preference for tundra, or random choice. A seasonally appropriate change in habitat preference would have resulted in a positive slope between means for each individual [Colour figure can be viewed at wileyonlinelibrary.com]

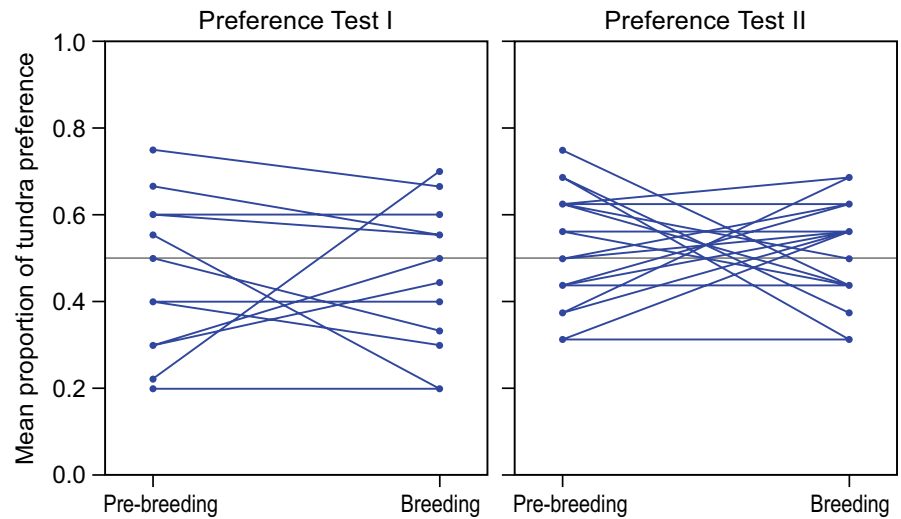


TABLE 2 Log-odds for the focal bird to choose the projection representing tundra landscape during the experiments of Preference Test I (left) and Preference Test II (right)

	Preference Test I (n = 13)	Preference Test II (n = 27)
Fixed effects	β (95% CI min, max)	β (95% CI min, max)
Intercept ^a	-0.13 (-0.72, 0.37)	0.17 (-0.08, 0.46)
Season (pre-breeding-)	-0.02 (-0.51, 0.58)	0.06 (-0.27, 0.48)
Plumage (winter)	0.11 (-0.61, 0.50)	-0.37 (-0.64, 0.23)
Age (immature)	NA	0.03 (-0.27, 0.41)
Projection side (north)	-0.09 (-0.57, 0.51)	-0.04 (-0.35, 0.16)
Random effect	σ (95% CI min, max)	σ (95% CI min, max)
Bird ID	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)

Note: The logit-transformed binary response choice (1 = tundra, 0 = mudflat) was based on the first feeder that was visited by the focal knot.

^aThe intercept represents the choice made by a mature individual in summer plumage, during the breeding season with the correct picture being projected on the south side of the testing arena.

and no bias was found towards one side of the experimental room (95% CIs are centred on 0, Table 2). Also, we found no autocorrelation between successive trials (two-sided runs test: $Z = 1.52$, $p = .13$).

We also considered the possibility that the percentage of time spent near either of the two images may hold additional information on preferences. Therefore, we reran the analyses with a novel binary response variable indicating whether a bird spent more than 50% of the time just in front of the Tundra image (1), or more than 50% of the time immediately in front of the Mudflat image (0). These analyses, based on the percentage of time spent near either image

(rather than the first choice for one of them), yielded similar results (not shown); note that only in a few trials, birds switched between patches ($n = 34/224$).

5 | PREFERENCE TEST II

After having established that knots were able to memorize and distinguish between projected landscape pictures, we were surprised not to find evidence for a preference for the familiar habitats offered visually. We continued with bigger sample sizes and an improved experimental design, and a comparison between adult (>2 years old at the time of testing) and immature knots (<2 years old at testing) was added. Immature birds do not breed in the first summer after their birth, and most do not physiologically prepare for northward migration (e.g. Verhoeven, van Eerbeek, Hassell, & Piersma, 2016). On this basis, we expected adult, but not immature, knots to show a seasonal change in habitat preference.

5.1 | Methods

This experiment included 19 adult and 8 immature knots. This time, to encourage natural circannual phenotypic rhythms to occur, all birds were continuously held in outdoor aviaries where they were exposed to ambient temperature and photoperiod (Karagicheva et al., 2016). Focal birds were only moved to the experimental room immediately prior to testing. In Preference Test I, the pre-breeding testing period took place very close to the known peak departure in the second week of May (Swennen, 1992). In Preference Test II, we therefore advanced the pre-breeding trials in time. The start date for the pre-breeding season remained the same, hence prolonging the time between two test periods. We carried out 16 trials per bird from 9 March to 17 April 2015 (39 days) and again from 19 May to 16 June (27 days). A bird was never tested more than once a day. This resulted in 16 unique choices per bird per

season, 32 choices per bird in total. Further refining Preference Test I, to test for preference for a habitat type (mudflat or tundra), rather than for one specific picture of a habitat, this time a novel combination of pictures was presented each trial. Thus, 16 different pictures of mudflat and tundra landscape were used in random combinations (Figure 3).

In Discrimination Test I and Preference Test I, there was no physical barrier between the screens, so that knots could easily switch position. As knots have a viewing angle in both eyes that is bigger than 140° (Martin & Piersma, 2009), they can assess the two images simultaneously and there is no need for birds to make a dichotomous choice. To force knots to make an unambiguous decision, we redesigned the room, the pictures now being projected side by side on one wall of the indoor room rather than opposite each other (by means of higher-resolution LCD projectors, properties: type: Panasonic-pt-vx600e, SVGA: 800×600 , light intensity: 5,500 lumen, contrast: 10,000:1, mass: 4.8 kg). The two 2.5-m-high and 3.5-m-wide projection screens were separated by a black plastic tarp dividing the room into two halves, with the tarp leading right up to the release cage (Figure 3). Consequently, once a bird had left the release cage, the choice would be irreversible. Note that during training (from 20 February to 7 March 2015), the mid-room tarp ended one meter in front of the release box. This enabled the birds to see both screens and gave enough space for birds to fly around the division after leaving the release box. During the actual tests, the division was pulled up to the release cage to enforce an early unambiguous choice. No food was offered in the experimental room during training and testing. Also, the water level in the aviary was raised so that the birds had to fly 5 m from the release box to reach a sandy patch ($1 \text{ m} \times 2 \text{ m}$) in front of one of the screened images (see Figure 3).

In the first 5 min of testing, the bird was held in the release cage with the screened panel closed. During this time, we recorded the time that the bird was on either side of the release cage, that is facing and possibly looking at either one of the two projected images. The release cage was remotely opened to allow the bird to indicate its preference by landing on one of the patches. In case a bird would not leave the release cage within 10 min, the release cage was slowly lifted (by means of another pulley mechanism) so that the bird was forced out and indicates its picture of choice. Again, 10 min after leaving the release cage a trial ended.

The analyses were identical to the analyses for Preference Test I. However, to examine any difference in preference between adults and immatures, a fixed effect for age was added (0 = adult, 1 = immature). Contrary to Preference Test I, daily plumage scores, recorded before each test, were used rather than interpolated scores.

As birds in the release cage were in the position to observe the images during the 5 min before the front panel was opened, we considered the possibility that the birds already give away their habitat preference by spending more time facing the image of preference. To test for this, we ran a similar model, using a bivariate response variable based on the percentage of time that the bird spent on either side of the release cage in the 5 min before the panel was opened. In this analysis, the same fixed and random effects were included, but

the response variable was replaced by a response variable indicating whether the birds spent $> 50\%$ of its time in the release cage facing the tundra image (1) or the mudflat image (0).

5.2 | Results

Despite what we thought were experimental improvements, the results of Preference Test II were very similar to Preference Test I. The knots showed no preference and no seasonal change (all 95% CI overlap with 0; Table 2, Figure 6). There was no association between habitat preference and the extent of breeding plumage (Table 2). There was no bias towards one side of the experimental room and no variation in preference among individuals (Table 2, Appendix S1 Table S3). Furthermore, there was no autocorrelation between successive trials (two-sided runs test: $Z = 0.80$, $p = .42$, Appendix S1 Table S3). Notably, there was no difference in habitat preference between immature and adult knots (Table 2, Figure 6, Appendix S1 Table S3).

The analyses based on the time facing either of the two images during the 5 min before the front panel was opened revealed that the birds actually spent more time in the half of the release cage exposed to the Tundra image during the breeding season than during the pre-breeding season (95% CI of the intercept does not overlap with 0) (Appendix S1 Table S4). During the pre-breeding season, birds spent less time facing the Tundra image, but this difference was not significantly different from zero (the 95% CI for season overlaps with 0). We found no association between time facing the Tundra image with breeding plumage, projection side or age (all 95% CI broadly overlap with 0, Appendix S1 Table S4).

6 | DISCRIMINATION TEST II

Since we found no distinct preference for habitat in Preference Test II, we once more wanted to confirm that knots are able to distinguish projected images using what we thought was an improved experimental design and protocol.

6.1 | Methods

The experimental layout and procedure were identical to Preference Test II. However, to reduce the stimulus complexity in this experiment natural pictures were replaced by images made in Microsoft Powerpoint and represented a very simplistic graphical visualization of mudflat or tundra. Whereas the mudflat image showed a horizontal edge to a brown surface (mimicking a horizon), the forest image showed a curvy green area. Both images contained equal amounts of blue (sky) (Figure 4). For this experiment, six birds were assigned to the "mudflat" group and trained to find food in the feeder near the mudflat image. The other six knots were assigned to the "forest" group and trained to find food near the forest image (Figure 4).

Having taken part in Preference test II, the knots were already acquainted with the experimental room and general testing procedures. The training on the images took place in two series of training between 17 and 24 September 2015. In the first 4 days of training, each group of six birds was introduced to the room twice a day with the image to be required on one side and a dark (black) screen on the other side. On both sandy patches and in front of the screens, a feeder was placed. Only the feeder in front of the image contained trout food pellets; in front of the black screen, the feeder was empty. During training, the birds received no other food than what they could eat at the feeders. When body mass dropped below 100 g, additional trout pellets were offered to this bird outside the training sessions. After training in groups, training continued with a period of 4 days in which knots were introduced to the room twice a day solely. During the training period, the birds received no other food than what they could eat at the feeders.

Actual testing took place from 25 to 29 September 2015. Knots were individually tested in a random order twice a day ($n = 8$), having to make a choice between the familiar and the non-familiar images. Contrary to Discrimination Test I, no reward was offered during testing. Instead, the knots received food during the rest of the day. When the release cage was opened, the bird indicated its image of choice by flying to the projection, or rather the patch in front. Again, when a bird would not leave the release cage within 10 min, the bird was forced to make a choice. A trial ended 10 min after the choice was made.

6.2 | Results

The knots, which incidentally did not show any seasonal change in preference in this experimental set-up, did actually distinguish between the projected images (after back transformation from the intercept model: $\beta = 61\%$, 95% CI = 50%, 69%, Figure 5). Like in Preference Test I, the birds trained on the forest image again performed better than the birds trained on the mudflat image (Appendix S1 Table S5, Table 1; $p = .03$). And again the knots showed bias to one of the sides of the room, this time preferring the north over the south side (Table 1). Repeated testing did not affect choice (Appendix S1 Table S5; one-sided runs test: $Z = -0.70$, $p = .24$).

7 | GENERAL DISCUSSION

By means of two tests, we were able to show that knots can memorize and distinguish projected images of landscapes. Nonetheless, we were unable to find evidence for a vision-based preference for habitat which changes seasonally. We do not interpret our inability to demonstrate a (changing) visual preference as a strong rejection of the idea that knots may have a seasonally changing preference for habitat. As we will argue, we believe that the testing protocols used may have been an oversimplification of the natural world and the way knots use visual cues.

7.1 | Discrimination I and II

The two experiments on image discrimination revealed that knots can learn to discriminate between projected images (Figure 5). The fact that the mean scores in both tests remained relatively low (64% and 61% correct) may well be due to the inquisitive nature of knots. In previous operant conditioning experiments on the sensory modalities of their bill tip (Piersma, van Aelst, Kurk, Berkhoudt, & Maas, 1998), knots kept exploring the alternatives, even when fully informed. Contrary to expectation, the ability to discriminate was lower in Test II when compared to Test I. In Test II, we attempted to reduce the stimulus complexity in order to emphasize the differences, and potentially simplify discrimination, between contrasting images. However, replacing photographs of natural landscapes with simplistic line drawings did not result in better discriminative abilities in the knots. Stimuli complexity is in the eye of the beholder; while intuitively one may think that abstract line drawings may be easier to discriminate when compared to more complex, stimuli-rich pictures, notably pictures, may be easier to discriminate due to their similarity to the natural scenes they represent (Fetterman, 1996).

In both discrimination tests, but not in the preference tests, the knots favoured one side of the room over the other, albeit in opposite directions. We suggest that this may be due to noise from outside the room, especially during Discrimination Test I when the birds were not only tested, but also housed in the room. Regardless of the side bias, and for reasons that are unclear, the knots trained on the forest images performed better than birds trained on the images of mudflat.

The ability to memorize and discriminate between pictures has been studied in many species including spiders, reptiles, fish and mammals (see Bovet & Vauclair, 2000 for an overview). Most experiments about picture recognition in birds were done with pigeons. The duration of training and the required number of tests in both Discrimination Tests I and II to reach significant results were relatively low compared with other studies on picture recognition in pigeons (Aust & Huber, 2006; Dawkins, Guilford, Braithwaite, & Krebs, 1996; Lechelt & Spetch, 1997; Spetch & Friedman, 2006; Wilkie, Willson, & Kardal, 1989). However, episodic memory ("what-where-when") is also important to achieve homing, and occurs in brood parasitism and food caching behaviour (Emery & Clayton, 2004). Birds have been shown to be able to recover information about flock mates and cached food items years after the initial experience (Emery, 2016).

Although cognitive experiments in shorebirds are scarce, field observations of birds returning yearly to the same locations (Lok, Overdijk, Tinbergen, & Piersma, 2011; Verhoeven et al., 2019) to pair up with the same partner (Kentie, Both, Hooijmeijer, & Piersma, 2014) are clear indications that shorebirds possess long-term memory. In an exceptional experiment with turnstones (*Arenaria interpres*), Whitfield (1986, 1987) showed that individuals are able to remember and recognize conspecifics based on their plumage characteristics. For knots, direct evidence for memory is anecdotal. "Peter" was a knot of the *islandica* subspecies kept as a pet for 20 years (see Piersma, 2002 for details). It remembered

and recognized the barking sound of the pet dog he used to live with even when the barks were played back to him 10 years after the dog died (TP pers. obs.). In this example, a red knot showed evidence of long-term memory for audial information. The length of time over which knots can remember visual cues remains to be established. The testing protocol described here gives us one way to its assessment.

7.2 | Preference Tests I and II

We were not able to demonstrate a preference for either of the two types of landscape pictures (mudflat versus tundra). Indeed, one possibility is that knots do not show seasonally changing preferences for habitat. Instead, seasonal migration may be motivated by means of evolved endogenous phenological mechanisms related to reproduction that are unrelated to habitat.

Alternatively, the knots learned, in successive trials, that the projected landscapes were not “real.” In fact, during the first few trials we observed birds flying into the part of the projection screen taken up by the sky, suggesting that they took this part of the image “seriously.” Having learned the artificial nature of the image, the birds may have lost interest. Interestingly, when we only consider the first trial in which knots were exposed to natural images representing mudflat and tundra in the pre-breeding season, we found a mean preference of 82% for mudflat in Preference Test I. During Preference Test II, knots were already exposed to natural images of mudflat and tundra during training, in the first training session they showed a mean preference for mudflat of 57%. Limiting our data set to only the first trial reduces the possibility to test for individual changes in habitat preference from one season to another. To prevent this potential learning effect, we suggest that for future experiments many birds should be tested once and in different seasons, rather than repeatedly.

Our inability to demonstrate a preference for either of the two types of landscape pictures may also be due to the testing protocol. When we analysed the position of birds in the release cage in Preference Test II, we found that during the breeding season the knots spent more time looking at tundra images than expected under the assumption of random choice. This suggests that a nuanced scoring method, maybe based on time looking at an image, rather than flying to and landing on a patch in front of it, would lead to more explicit results.

Still, the incomplete development of breeding plumages in some individuals (Appendix S2 Figures S1 and S2) could also indicate that some or all knots never reached the physiological threshold at which they would experience the motivation to take off for the tundra breeding grounds (see Piersma & Jukema, 1993; Piersma et al., 2000). Free-ranging knots in the Wadden Sea are known to refrain from spring migration when they are not physiologically fit (TP pers. obs.). However, incomplete physiological preparation does not explain why knots did not show preference for the mudflat images during the non-breeding season.

As for all experiments regarding natural responses in wild animals that are tested in artificial settings, we cannot exclude the possibility that the complete lack of preference followed from a general state of unhappiness related to the captive conditions (Howard, 1955; Wyers, 1994). Note that the results of Discrimination Tests I and II show that the same knots tested under similar conditions were able to acquire a preference for images when a reward was offered. Nevertheless, Discrimination Tests I and II also revealed that individuals vary in their ability to memorize and recognize projected images. Similarly, it is possible that knots vary in their ability to memorize and recognize natural habitats, for example because they differ in experience (Berbert & Fagan, 2012; Pravosudov et al., 2006) or social status (Gibson & Kamil, 2009). Unfortunately, we do not have the power to find among-individual differences in performance on the log-odds ratio of choosing the right images.

We propose that the visual representations of landscapes presented here fell short. This could be due to optical limitations of the projected images, including the angle at which the pictures were taken, the absence of depth (note that the overlap of both fields of vision should enable knots to perceive depth; Martin & Piersma, 2009) and the probable varying reception of colours when compared to humans, most obvious in the ability to see UV-light (Cuthill, 2006). Although several species of birds are found to be capable of object-to-picture transformation in the laboratory (Spetch & Friedman, 2006; Spetch, Friedman, & Vuong, 2006; Watanabe, 1997), results of object-to-picture transformation regarding real-world locations are ambivalent (see Wilkie et al., 1989, for an example of successful picture-to-location transformation and Dawkins et al., 1996, for an example in which pigeons failed to translate pictures to real locations).

If purposive activities such as (breeding) habitat choice would only be provoked if an integration of multiple, specific sensory demands comes together (Lashley, 1938), knots may need more than visual cues to recognize habitats. We suggest that in future experiments on habitat preference, other sensory cues such as smell (Nevitt, 2008; Wallraff, 1990; Wikelski et al., 2015), sound (Hagstrum, 2000) and/or magnetic field (Alerstam, 1990b) should be included. In this study, we were not able to confirm that knots show preference for seasonally appropriate habitats. When taking all above-mentioned limitations (the absence of other natural cues, definition of preference, timing, individual variation, etc.) into account, we consider the absence of a seasonally changing habitat preference in our tests as the result of too much experimental simplification, typical of behavioural experiments in laboratory settings (Wyers, 1994). Consequently, we hope that this detailed account of what we managed to achieve will inspire others, just as we have been inspired by the work of Roberts and Weigl (1984). Whereas scores of studies address questions on “how” birds migrate (in terms of physiology, energy budgets and navigation) and “why” birds migrate (fitness consequences), questions on the causation of migratory behaviour (Hogan, 2017) are sparse (Piersma, 2018). The rarity of studies on cognitive processes in wild birds will indicate fashions in science, but may also reflect

the serious methodological challenges that come with it. With this study, touching upon the role of memory during migration, we hope to have started to scratch the surface on the role of cognitive mechanisms motivating seasonal migration (Hogan, 2017).

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

EMAK, JH and TP conceived and designed of the experiments. EMAK collected and analysed the data. EMAK wrote the manuscript with help from TP and JH. All authors gave final approval for publication.

ETHICAL APPROVAL

This work was carried out under auspices of the Animal Experiment Committee (DEC) of the Dutch Royal Academy of Sciences (KNAW) (permit DEC-NIOZ 10.05).

DATA AVAILABILITY STATEMENT

The full datasets and reproducible code are available from EMAK upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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