Received: 21 January 2021 | Revised: 10 February 2022 | Accepted: 18 February 2022

DOI: 10.1111/ddi.13510

RESEARCH ARTICLE

Diversity and Distributions WILEY

Translocation experiment gives new insights into the navigation capacity of an African duck

Graeme S. Cumming[1,2] | Dominic A. W. Henry[2,3,4] | Chevonne Reynolds[2,5]

[1]ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia

[2]DST/NRF Centre of Excellence at the FitzPatrick Institute, University of Cape Town, Cape Town, South Africa

[3]Statistics in Ecology, Environment and Conservation, Department of Statistical Sciences, University of Cape Town, Cape Town, South Africa

[4]Endangered Wildlife Trust, Johannesburg, South Africa

[5]Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

Correspondence

Graeme S. Cumming, ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville 4811, Qld, Australia.

Email: graeme.cumming@jcu.edu.au

Funding information

DST/NRF Centre of Excellence at the FitzPatrick Institute

Editor: Christine Howard

Abstract

Aim: Movement is integral to the distribution and abundance of wildlife. We undertook an experimental test of the navigation capacity of Egyptian Geese *Alopochen aegyptiacus* to better understand the movements of moult-migratory waterfowl and the implications of navigation capacity for their ecology.

Location: Southern Africa. In June 2015, we translocated six post-flightless moult Egyptian Geese 1250 km south, from north-west South Africa (Barberspan) to the south-west coast (Strandfontein). We compared their movements to those of 29 previously tracked resident Egyptian Geese from the source and translocation sites, and three additional sites (Voelvlei; Jozini Dam; Lake Manyame, north-central Zimbabwe).

Methods: We used solar-powered satellite GPS to track movement patterns and compared the movement paths of different birds using net-squared displacement analysis and multiple regression analysis of different measures of movement paths.

Results: Over time periods up to 658 days, none of the translocated Egyptian Geese returned to Barberspan and only one appeared to fly towards it. Translocated birds showed some novel and risky behaviours. Longer, searching-type movements were evident with the onset of both the breeding and moulting seasons. Quantitative comparisons suggested that translocated birds retained elements of learned behaviours.

Main conclusions: Navigation by Egyptian Geese appears to have a strong learned (internal) element, with long-distance movement triggered by internal states such as the need to moult. Translocated animals modified their movement patterns in ways that mostly allowed them to survive. Our results have interesting implications for understanding the dynamics of individual populations; a strong reliance on learned behaviours may explain the unresolved conundrum of why no African duck species has colonized Europe without human assistance. Our analysis demonstrates the complexity of influences on animal movement and highlights the importance of navigation capacity for conservation biogeography.

KEYWORDS

behavioural ecology, dispersal, movement, waterfowl, wetland

1 | INTRODUCTION

The study of movement has long been recognized as fundamental to our understanding of ecological pattern-process dynamics and biogeography (Elton, 1927; MacArthur & Wilson, 1967). As anthropogenic climate change reorganizes the world's ecosystems, movement ecology has an important role to play in connecting ideas about environmental change, individual responses to change and population persistence (Hebblewhite & Haydon, 2010). At present, the foundations for understanding movement lie primarily in individual-based models (Dodge et al., 2016). The widely accepted Movement Ecology Framework (MEF; Nathan et al. (2008)) describes animal movement paths as an outcome of the interactions between external factors (e.g. environmental conditions, predation or social influences) and an individual's internal states, motion capacity and navigation capacity. Movement paths in turn influence internal states, which may change in response to changes in the surrounding environment. Internal states relevant to movement include such elements as an animal's body condition, its level of hunger, its breeding status, its fear of predators and its learned behaviours. Motion capacity describes how easily and how far an animal can move in a particular landscape. Lastly, navigation capacity describes an animal's ability to find its way through a landscape—whether between particular locations or resources, or back to a specific location.

The MEF clarifies how understanding navigation capacity contributes to a more general understanding of movement ecology. In practice, however, field studies of vertebrate movements have focused more on the link between external factors and motion capacity (Holyoak et al., 2008). A 2020 evaluation of 8000 papers in movement ecology published between 2009 and 2018 found that most (77%) studies tackled movement in relation to external factors and only 9% of papers considered navigation capacity (Joo et al., 2020). In vertebrates, navigation capacity ranges from a simple ability to undertake directed movement (i.e. retracing a route or using path integration to go in a straight line), through to a highly advanced ability to travel directly to a chosen location from a previously unknown location, independently of direction and without having to use a familiar route (i.e. using a map-like spatial representation of the landscape) (Toledo et al., 2020; Tsoar et al., 2011).

Navigation capacity is particularly important for latitudinal migrants (Able, 2001; Kishkinev et al., 2015, 2020). These intercontinental movements are a focus of many studies of animal movement (Guilford et al., 2011), and the conservation needs of latitudinal migrants have been formalized in the Convention on Migratory Species, but conservation strategies for species that adopt other movement strategies are poorly articulated (Runge et al., 2014). Avian movement strategies are influenced by seasonality and environmental predictability (Dean & Siegfried, 1997). Hence, they can be viewed on a continuum, with strategies ranging from sedentary to migratory where resources vary predictably and becoming increasingly nomadic with increasing environmental variability (Figure 1) (e.g., see also Roshier et al., 2006; Roshier & Reid, 2003). We would expect to find predictable differences in navigation capacity within this continuum, with latitudinal migrants being more capable but possibly less flexible navigators.

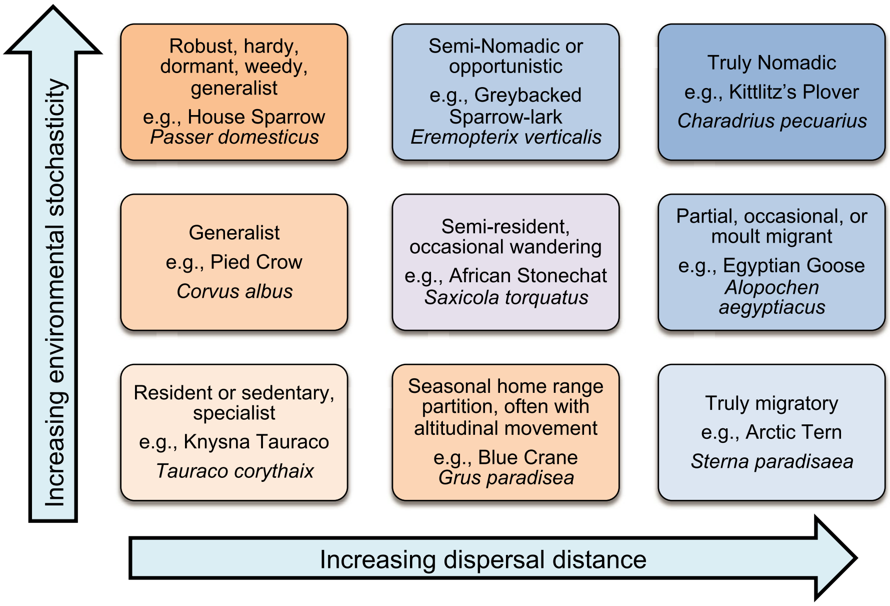

FIGURE 1 The continuum of avian movement strategies. Movements can be viewed along two different axes relating, respectively, to the predictability of the environment (at different scales, ranging from home areas through to both departing and receiving environments for long-distance migrants) and the distance that birds move. A prerequisite for the success of true migration as a movement strategy is that the receiving environment is predictable—for example, that birds leaving snowy weather in the northern hemisphere do not find it snowing when they arrive in the south. Birds that inhabit more variable environments have different but potentially strong motivations to remain in, or return to, familiar environments. Examples based on information from Hockey et al. (2005)

Waterfowl in arid and semi-arid areas are generally considered to be well adapted to coping with environments that exhibit high variance and relatively low predictability in both space and time (Kingsford et al., 2010). However, their navigation capacity and its relationship to external and internal factors are poorly understood and have never been experimentally tested. Able (2001) distinguishes between homing and nonhoming forms of navigation; of particular relevance to this paper is his distinction in the homing category between route-based navigation (homing navigation performed on the basis of information perceived during the outward journey) and map-based navigation (an animal returns home solely on the basis of information available at the distant release point). Following Able (2001), repeated use of the same route to and from sites used for flightless moult (Cumming et al., 2012) suggests a reliance by African waterfowl on a sun compass (i.e. using the sun to determine a bearing on which to fly) and route-based navigation using landmarks, but their ability to find and return to suitable patches of habitat implies a potential for map-based navigation capability. In this paper, we address this gap in existing knowledge.

To better understand how navigation capacity affects the movements of African waterfowl, we undertook a controlled long-distance translocation experiment on Egyptian Geese. By removing the cues obtained during the outward journey, and thus the potential for route-based navigation, we tested whether Egyptian Geese are capable of map-based navigation. This was the first translocation experiment for any African duck, and more generally the first for any species that undertakes moult migration rather than seasonal latitudinal migration. Previous translocation experiments on birds have tended to focus on either local homing behaviour and habitat permeability for species that move relatively short distances (Bélisle et al., 2001; Gobeil & Villard, 2002; Kemink & Kesler, 2013), or on latitudinal migrants (Kishkinev et al., 2020; Slager et al., 2015; van Toor et al., 2013). The only directly relevant previous study that we are aware of is that of van Toor et al. (2013), who moved Mallard ducks (*Anas platyrhnchos*) from Sweden to Germany prior to migration. They found that (1) most Mallards remained over winter in the new location; and (2) Mallards returned to Sweden in the spring. However, van Toor et al. (2013) could not correct for the social influence of other returning migrants passing through the overwintering location in the spring, so the navigation capacity of their birds could not be determined independently.

We captured adult individuals in the late stages of wing feather moult at a large wetland (Barberspan) in the North West Province of South Africa, and moved them 1250 km south to Strandfontein, in the Western Cape Province near Cape Town. The subsequent movements of these birds were contrasted both qualitatively and quantitatively with a control group composed of another 29 adult individuals from five moulting locations (including the locations for the translocation experiment, Strandfontein and Barberspan) in South Africa and Zimbabwe.

After releasing the six translocated birds at Strandfontein, we expected to see one of three outcomes: (Outcome 1) translocated birds might return to Barberspan for their next moult migration, or to their breeding sites (which are usually near their home areas, not their moult sites), providing strong evidence for map-based navigation capacity together with compass or vector navigation; (Outcome 2) translocated birds might remain at Strandfontein and gradually start to exhibit movement patterns like those of Strandfontein residents, slowly building up an internal map of the landscape by increasing movement frequency and social learning (providing strong evidence for route-based local navigation capability, the influence of the surrounding landscape and flexibility in movement behaviours; see also Mueller et al. (2013)); or (Outcome 3) translocated birds might try to move around the Western Cape in the ways that they do in the North West Province, but not return to Barberspan. Outcome 3 would suggest a strong role for internal states, and particularly for memory and past experience, in movement by waterfowl. Our primary aims in this study were thus to determine whether Egyptian Geese are capable of map-based navigation, and if not, to offer insights into their navigation capacity; to more deeply explore the relevance of location for movement patterns; and to contextualize previous information on Egyptian Geese movements in the light of our new information, including providing a more complete picture of the biology of the species and demonstrating the range of variation in movement patterns across southern Africa.

2 | METHODS

2.1 | Background on study species

Despite their common name, Egyptian Geese (*Alopochen aegyptiacus*) are a species of shelduck. Egyptian Geese are primarily grazing ducks that forage on the edges of wetlands, on lawns and on young shoots in agricultural fields. They lay their eggs in scruffy nests up tall trees and on buildings within walking distance to water. They can be considered residents for much of the year, tracking emerging grasses and their seeds by moving between wetlands and foraging habitats. They undertake an annual directed movement from their resident wetlands (which are often shallow, ephemeral, or flowing; golf courses also appear to provide ideal habitat) to and from a permanent, predator-secure wetland for the purpose of moulting their flight feathers, which entails a 3–4-week flightless period. Birds appear to have home areas (i.e. site fidelity at broader scales than a classical home range, with some areas not being used regularly) to which they return after moult. Flightless moult is a particularly vulnerable time in their annual cycle (Appendix S1). Fidelity to individual moulting sites is high (>60% for a particular lake or pond, and >80% if waterbodies within 5 km on the same river system are considered the same "site"). During roaming periods, when they typically move across the landscape in small flocks after either aggregating to moult or pairing off to breed, Egyptian Geese are capable of anticipating variability in food resources and tracking patches of high food abundance in the local landscape and so seem to have high navigation capacity at a local (up to ~50 km) scale (Cumming et al., 2012;

TABLE 1 Summary of movement data for Egyptian Geese used in this analysis

Site	Number of birds	First active day	Last active day	Range of tracking period	Mean tracking period	Median tracking period	PTTs
BAR	7	07/06/08	31/01/12	234–1333	778	727	7712202, 7712701, 7712801, 7712901, 7713001, 7713101, 7713201
BARSTR	6	18/06/15	07/04/17	64–658	321	225	7711603, 7711703, 7711803, 7711903, 7712103, 7713303
JOZ	4	04/05/12	30/12/14	183–970	416	257	7711702, 7712002, 7712102, 7713302
MAN	3	07/05/08	30/08/11	42–1210	495	233	7712401, 7712501, 7712601
STR	11	04/12/08	21/09/12	70–1387	473	364	7709401, 7709501, 7711601, 7711801, 7711802, 7711901, 7712101, 7712302, 7713301, 7713401, 7713501
VOE	4	18/04/13	03/05/14	102–380	216	192	7711602, 7711902, 7712402, 7712602

Note: Gaps in tracking data are summarized in Appendix S3.

Abbreviations: BAR, Barberspan; BARSTR, birds captured at Barberspan and released at Strandfontein; JOZ, Jozini Dam; MAN, Lake Manyame; STR, Strandfontein; VOE, Voelvlei.

Henry et al., 2016; Ndlovu et al., 2013, 2014). It remains unclear which movements are undertaken as individuals and which are in family groups or larger flocks.

Egyptian Geese offer an intriguing case study for understanding map-based long-distance navigation in species that are not true migrants, because they appear to be range-constrained by internal factors (e.g. physiological and behavioural need to moult in a predator-safe wetland; see account by Milstein (1993) of responses of birds to delaying moult) rather than geographic constraints or movement capacity (Cumming et al., 2012). Their historic distribution is pan-African, excluding the Sahara and Namib deserts and the rainforest of central Africa (Cumming et al., 2012). Many duck species (e.g., Garganey *Anas querquedula*, Northern Pintail *Anas acuta*, White-headed duck *Oxyura leucocephala*) move regularly between Africa and Europe, and individual Egyptian Geese have been recorded moving between moult sites as far as ~850 km in a single day; but populations of Egyptian Geese only colonized Europe once they had been introduced by people. Thus, while Egyptian Geese have high movement capacity and considerable within-population variance in movement trajectories, and have been demonstrably able to colonize new landscapes after their gradual introduction by people (Lensink, 1998), it is unclear how flexible their long-distance movement behaviours are.

2.2 | Study system and choice of field sites

This research forms part of a longer term study of the ecology of African waterfowl. Prior to undertaking the translocation experiment in 2015, we collected detailed information on Egyptian Goose movements from flightless moult locations in South Africa (Barberspan, Strandfontein, Voelvlei and Jozini) and Lake Manyame in Zimbabwe. Detailed information about each of these sites and their waterfowl populations is published elsewhere (Cumming et al., 2011, 2012; Henry, 2016; Henry et al., 2016; Milstein, 1975, 1993; Ndlovu, 2012).

We selected Barberspan and Strandfontein as focal sites for this experiment for several reasons. They are extensive wetland areas that are heavily used by hundreds to thousands of moulting ducks; they are situated far apart, but not too far for a duck to move in several steps (1250 km; birds can fly up to at least 850 km/day); and they lie on a natural latitudinal gradient, meaning that birds with the capacity to orientate along a north–south gradient would be able to use the sun, stars or other cues (Mouritsen, 2018) to orientate. Our prior research had indicated that these two populations had distinctly different movement patterns and did not typically overlap. There are two older records in the SAFRING (South African Bird Ringing) database of birds ringed (banded) at one site and recovered at the other. These records show that it is possible but extremely uncommon for an Egyptian Goose to move from Barberspan to Strandfontein (Underhill et al., 1999); genetic data for Yellow-billed Duck *Anas undulata* provide similar evidence (Brown et al., 2019; Stephens et al., 2020), although neither our previous telemetry research nor a 2-year colour-ringing field study (Ndlovu et al., 2013) documented any movement of Egyptian Geese between the two sites. We included data from additional sites where we have worked in order to provide a reference point and offer a more general synthesis and overview of all available telemetry data for this species.

2.3 | Field methods

We translocated six individual adult Egyptian Geese. Our sample size was limited by financial and ethical considerations, with five birds being considered a minimum number (from preliminary assessment of previously tracked birds; see Table 1 and Appendix S2 for details) to obtain a consistent movement pattern and a definitive answer to the question of whether birds could return to their moulting grounds or home areas. Birds were captured using walk-in traps at Barberspan during the later stages of flightless moult or just after completion, as evidenced by their wing feathers. All birds were banded, colour-ringed, and driven in cardboard boxes to Cape Town in a blackened cab, so that they would not be able to obtain any environmental or landmark cues about their direction of travel. They were then kept outdoors in a cage for two weeks to habituate to local photoperiod and sun angles. In June, mid-winter, Strandfontein receives about 50 min less daylight than Barberspan. Although resident birds were not held in captivity for longer than one to two days prior to release, all tracked birds were regrowing their wing feathers; thus, in both treatment and control, all birds had been in a single location and unable to fly for a period of at least two weeks before being put through the same handling and transmitter attachment process, by the same person (GSC), with release either the same day or one day later. Resident and translocated birds were not housed together. Subjectively, field observations of tracked birds and a subset of colour-ringed birds that were held in captivity for longer periods during a study of muscle growth (Ndlovu et al., 2010) suggest that Egyptian Geese adopt normal movement patterns, including longer flights, within 1–2 days of release. In our experience, it is, therefore, extremely unlikely that the small differences in prerelease conditions between treatment and control could explain differences in the subsequent behaviour of the translocated animals at a time frame of months or years.

A 32 g solar-powered satellite GPS PTT (manufactured by Microwave Telemetry) recording GPS fixes every 2 h was attached to each bird using a Teflon backpack harness, as described by Cumming and Ndlovu (2011). All six translocated birds were released at Strandfontein, at one of the southernmost ponds, in the middle of the day on the 18 June 2015. Subsequent data downloads were obtained via the Argos satellite.

2.4 | Telemetry data analysis

We first explored the net-squared displacement of the translocated birds and then compared them to our controls, which were resident (nontranslocated) birds. We extracted information on key movement parameters and then contrasted these summary data between locations for individual birds using linear models.

2.5 | Classification of movement paths of Barberspan birds

We analysed movement paths using a model-driven net squared displacement (NSD) framework to quantitively classify patterns over an annual cycle. The analysis of NSD (square of the straight-line distance between a starting point and each successive location) has become a popular method for classifying individual coarse-scale movements as either resident, nomadic, dispersal, migratory or mixed migratory (Bastille-Rousseau et al., 2016; Bunnefeld et al., 2011; Cagnacci et al., 2016). The mixed migration model allows for the distance travelled between seasonal ranges to vary and includes cases where the individual comes close but does not return exactly to its original starting point. The process works by fitting a series of nonlinear models (each representing a different movement strategy) to the NSD data and then evaluating the relative support for each model using Akaike's Information Criterion (AIC; Burnham & Anderson, 2002). We applied this modelling approach to birds that were tracked for at least 340 days (i.e. end of one moult cycle to the beginning of another), resulting in the inclusion of six resident birds previously captured and released at Barberspan (PTT IDs: 7712202, 7712701, 7712801, 7712901, 7713001 and 7713201) and two of the translocated birds that were captured at Barberspan and released at Strandfontein (PTT IDs: 7711603 and 7711703; see Table 1 and Appendix S2 for track details). For each bird, the NSD data were split into single calendar years starting on 15 June 2008 for resident Barberspan birds (one week after the birds were fitted with PTTs) and 19 June 2015 for translocated birds. This allowed for inclusion of unique year-long NSD time series data sets ("bursts"), which were modelled using functions in the *migrateR* R package (Spitz et al., 2017). Following the recommendation of Bunnefeld et al. (2011), we thinned the movement data for the NSD model selection to include only one relocation point per day (performed by randomly selecting a point within each day). By comparing the AIC values, the top model for each burst was identified, which in turn indicated the movement strategy that had the highest support. We used the plotting functions from the *migrateR* package to visualize the fit of each model to the NSD data, as well as to evaluate the relative strength of each model (using the ΔAIC measure). There were three instances where models failed to converge, and these were omitted from the final set of results (7712201 year 1 resident model, 7713201 years 1 and 3 mixed-migration models).

2.6 | Comparison of tracked birds to controls

We next compared the movement paths of translocated birds to those from 29 previously tracked but not translocated birds (Table 1). All birds for which data were analysed were tracked for at least six weeks, with some tracked for over two years. The comparison of greatest interest was that of translocated birds to the movements of resident birds tracked from the sites of origin (Barberspan) and release (Strandfontein), but we have included data from the other sites because they help to frame the range of possible movement patterns and provide a broader context. Data from birds captured at Voelvlei were particularly relevant given their close proximity to Strandfontein. All ducks were tagged during or soon after flightless moult, during which ducks synchronously shed and regrow all of their primary and secondary wing feathers. Flightless moult occurs over a four-week period once a year, at the same time of year in a given location but at different times in different bioclimatic regions (Ndlovu et al., 2017). It usually causes a significant shift in movement patterns as birds undertake moult migration to a permanent waterbody. Moult site fidelity appears to be high, and moult cannot be delayed for long (Milstein, 1993; Ndlovu et al., 2013). Breeding periods also involve changes in movement patterns, but are less predictable (Cumming et al., 2016).

All analyses were undertaken in *R* 4.0.3 (R Core Team, 2013). Data were reprojected from a Lat-Long coordinate system into a southern African Albers equal-area projection prior to analysis. To quantitatively describe the properties of different movement trajectories we focused on the seven movement measures identified as fundamental to more advanced analysis by Calenge (2015) (see also Calenge et al., 2009). These measures include changes in location and time; distances between locations; absolute and relative angles between the lines connecting locations; and the squared distance between the first relocation of the trajectory and the current relocation (squared displacement). They are all calculated automatically using the *ltraj* function in the *adehabitatLT* package (Calenge, 2015) when creating an animal movement trajectory from telemetry data. We selected five summary measures as particularly suitable for our analysis: mean daily distance moved; mean absolute angle; standard deviation of daily distance moved; the standard deviation of squared displacement; and the standard deviation of the relative turning angle (see rationale in Table 2). These measures include, either explicitly or implicitly, information about how far, how fast, how directionally and how variably animals move. The use of solar-powered PTTs meant that on a few occasions, transmitters stopped for several weeks and then resumed transmission when they received sufficient sunlight to charge. Some data sets, therefore, have internal gaps of days to weeks between observations (Appendix S3). However, the manner in which we calculated the movement measures negated the effect of gaps in telemetry data because they were small relative to the size of the data set. For the distance measure components, we first calculated the total distance moved on a daily basis for each day that data were available (as opposed to the total tracking duration). We then extracted the mean and standard deviation (SD) of this vector of distance values. It did not make sense to split tracks and remove data gaps for the squared displacement because the initial telemetry point of this metric has to be the capture site. There was a negligible effect of data gaps on calculations of turning angles and so an adjustment for these two movement measures was not necessary.

To check for biases in our data, we also measured three potentially confounding factors that might bias the metrics in Table 2: the number of active tracking days over which observations were made, the total number of fixes per animal, and the number of fixes per animal per day. We tested for pairwise correlations between these factors and our five movement measures before proceeding with the rest of the analysis (Appendices S4 and S5).

We used a multivariate linear modelling approach to test for differences in movement trajectories between locations. We treated the five movement measures as the response variable (represented as a bird by movement measure matrix) and the bird ringing location as the predictor variable of the multivariate model. The multivariate linear model is

$$Y_{(n\times m)} = X_{(n\times k+1)} \times \mathbf{B}_{(k+1\times m)} + \mathbf{E}_{(n\times m)}$$

where Y is a matrix of n birds and m movement metrics; X is a model matrix with columns for k ringing locations (sites); **B** is a matrix of regression coefficients, one column for each response variable; and **E** is a matrix of errors. In R syntax this translates as *lm(cbind(mean_dd*, *sd_dd*, *mean_absang*, *sd_meandisp*, *sd_relang) ~ site)* where each metric is a vector with length 34 or 35 (during the analysis it became apparent that the bird with PTT ID 7713303 was an outlier in the majority of the measures and had a disproportionate effect on the regression results; we, therefore, repeated the regression analysis after removing PTT 7713303 and reported on both results).

Using Wilks' Lambda test statistic (Λ) within the MANOVA, we were able to test if there were differences between group means (sites) for the combination of five movement measures. Following that we used linear hypothesis testing to test for all pairwise differences in the parameters of the multivariate model (e.g. overall response of translocated birds vs. Strandfontein residents). We also extracted the univariate regression results from the analysis (i.e. difference in means between each site for an individual movement measure) to assess the proportion of variation explained (R^2) by each variable and site-level

TABLE 2 Summary of the metrics used to quantify movement paths and the underlying rationale for why they are useful

Metric	Rationale
Mean daily distance moved	Measure how far the animal goes each day, on average; distinguish highly mobile and more sedentary individuals
Standard deviation of daily distance moved	Capture variability in daily distances; distinguish animals with similar daily averages but different movement patterns (e.g. occasional long moves and common medium moves vs. frequent long moves interspersed with very short moves)
Standard deviation of squared displacement	Measure variability in distance from capture site (moult location); distinguish long versus short moves from moult site
Mean absolute turning angle	Distinguish birds that mainly move laterally (East–West) from those that mainly move longitudinally (North–South)
Standard deviation of the relative turning angle	Measure tortuosity in daily movement paths to distinguish birds with very directed movements from those that are more meandering

Note: Calculation of metrics is described in detail by Calenge (2015).

univariate coefficients. The multivariate regression was run using the *lm* function in base R while the MANOVA was run using the *Manova* function and the linear hypotheses using the *linearHypothesis* function, both of which are from the *car* R package (Fox et al., 2012). Given the large differences in magnitude of the movement measure values, we scaled and centred all data (i.e. by subtracting the mean and dividing by the standard deviation) prior to running the linear models. The fact that our sample size was sufficient to distinguish between locations supports the general argument that despite a low sample size of translocated birds, our methods are robust.

3 | RESULTS

3.1 | Movement classification

The NSD analysis of the movement paths of 6 resident Barberspan birds classified eight bursts as migratory, three bursts as mixed migratory and one burst as dispersal. There were four bursts that showed particularly large differences in delta AIC (delta AIC >70) between top model and next best model, illustrating clearly that Barberspan residents exhibit migratory behaviour on a local scale to and from their moult site and have a strong internal incentive to return to it (Table 3, Figure 2a,b, Appendix S4c,e). Model fit varied among the remainder of the bursts which, apart from the single burst in which a bird dispersed, provided good evidence for migratory movements (Appendix S4).

The two translocated birds released at Strandfontein for which we obtained longer time sequences of movement data showed evidence of migratory movements to and from the Strandfontein release site (Figure 2) (see also Appendix S4k,l; see Table 3 for the AIC values of all models displayed in Figure 2). The timing of these movements was, however, not identical to those for birds from the same population that were not translocated. Regardless of its location, a Barberspan bird that had moulted in May would start wing feather moult between April and June. Longer distance movements undertaken by translocated birds between October and January thus suggest a search for a home area and breeding site rather than a moulting location.

3.2 | Qualitative assessment

Visual inspection of the movement trajectories of resident and translocated birds, respectively (Figures 3 and 4), indicated a clear and noteworthy result in relation to our first potential outcome: none of the birds returned to Barberspan or its immediate surroundings during the tracking period. All translocated birds would have had an incentive to return to their familiar nesting and breeding sites (Appendix S1) within two months of being translocated to a new location. Birds for which the tracking devices lasted long enough would have had an even stronger incentive the following year to return to Barberspan to moult.

Subjectively, all of the translocated birds showed some evidence of undertaking longer distance searching movements (Figure 4 and animated visualizations in Appendix S5). One out of the six translocated birds (Egyptian Goose 7713303) moved in a direction roughly towards Barberspan, but this bird may have followed its habitual movement direction. The other translocated birds showed an intriguing and previously unrecorded tendency to fly for long periods over the ocean, potentially mirroring postmoult movements of Barberspan residents to the south or southwest (Figure 3).

Five out of six translocated Egyptian Geese flew across the sea during the tracking period (Figure 4); they turned around after flying for several hours. Egyptian Goose 771703 landed on Dassen Island and spent 32 h there before returning to the mainland. Egyptian Goose 771603 did a loop out to sea, returned to land and then followed the coast until transmission ended. Lastly, Egyptian Goose 771903 left the land between 05:00 and 07:00 on 20 August and turned back towards land around 01:00 on 21 August at a distance of about 300 km from the nearest coast. Distances between successive fixes get smaller and smaller, suggesting an increasingly weary individual and/or that it took breaks on the water. The longest single distance between fixes was 94 km in 2 h, a sustained flight speed of 47 km/h; by the end of the track the distance between fixes was as low as 3.4 km (1.7 km/h) and the bird covered only another 21.5 km after 07:00 on the 21st. The last fix from 771903 was at 17:00 on the 21 August, approximately 188 km from the nearest land. This bird covered about 690 km in 34 h across the open ocean and appears to have died before it could return to the shore. Egyptian Geese are strong fliers and swimmers, being well insulated and often seen sleeping on water, so we can only guess that the waves and wind were too strong for it.

3.3 | Quantitative assessment

3.3.1 | Potential confounding influences on movement metrics

The total observation period for each bird ranged from 64 to 1387 days, with a median of 356 and a mean of 474. Accounting for gaps in telemetry data, the number of active tracking days ranged from 35 to 1150 days, with a median of 269 and a mean of 366. The number of fixes per bird ranged from 283 to 10,854, with a median of 2681 and a mean of 3633. The number of fixes per active day of tracking ranged from 4.9 to 11.7, with a median of 10.3 and a mean of 10. The confounding variables of the total number of active tracking days and number of fixes were not significantly correlated with any of the five movement measures (Appendix S6). The number of fixes per active tracking day was negatively correlated with mean daily distance ($r = -.71$, $p < .05$), SD of daily distance moved ($r = -.73$, $p < .05$) and the SD of mean square displacement ($r = -.48$, $p < .05$; Appendix S6). However, the removal of the outlying bird PTT 7713303 decreased the correlation coefficients of mean daily distance and SD of daily to −0.48 and −0.54, respectively, with a

TABLE 3 Examples of delta (Δ) AIC values of fitted NSD movement models for two consecutive years of movement data from Barberspan birds: nontranslocated (PTT ID 7713201) and translocated (PTT ID 7711703)

Bird ID	Year	Movement classification	Δ AIC
7713201	1	Migrant	0
		Mixed migrant	70
		Disperser	1402
		Resident	1519
		Nomad	1643
7713201	2	Migrant	0
		Disperser	158
		Resident	408
		Nomad	515
7711703	1	Migrant	0
		Mixed migrant	11
		Resident	456
		Disperser	457
		Nomad	523
7711703	2	Mixed migrant	0
		Migrant	12
		Disperser	829
		Resident	861
		Nomad	920

Note: Lower AIC values indicate a better fit.

concurrent increase in *p*-values (Appendix S7). In addition, the correlation with SD of mean square displacement became nonsignificant ($p = .17$) after removing the outlier.

Visualization of mean daily distance and SD of daily distance moved against number of fixes per day (Appendix S6) did not suggest a meaningful relationship for the large majority of the data points. Bonferroni correction for 15 repeated measures (3 confounding factors vs. the 5 Metrics in Table 2) gives an adjusted probability of $p = .003$ for significance, raising the possibility that the observed correlations are a statistical artefact. We thus opted to keep mean daily distance travelled in the analysis, even though it is correlated with the number of fixes per day (as described above), because of its importance as a measure of animal movement.

3.3.2 | Quantitative comparison of movement trajectories

The results of the multivariate linear regression indicated that there was an overall significant difference in movement measures between sites ($\Lambda = 0.06$, $F_{25,94} = 4.26$, $p < .001$). The linear hypothesis tests revealed a significant difference between movement patterns of translocated birds and those of Barberspan, Strandfontein and Voelvlei residents (see Table 4 for all pairwise comparisons). Translocated birds were also significantly different to birds from Lake Manyame and Jozini. There was a significant difference between the movements of resident birds from Barberspan and Strandfontein (Table 4), confirming what we observed from inspecting quantitative and qualitative aspects of the movement data. The movement variables that contributed most strongly to the significance of the multivariate result were mean absolute turning angle, SD of mean squared displacement and SD of the relative turning angle (Figure 5). The R^2 values for univariate linear regressions of these variables ranged from .36 to .62 (see Appendix S8 for all linear regression coefficients and MANOVA results).

There was still an overall significant multivariate difference in movement between sites after removing the outlying bird PTT 7713303 from the analysis ($\Lambda = 0.04$, $F_{25,90} = 4.93$, $p < .001$). However, the difference in movement between translocated birds and, Strandfontein and Voelvlei residents became nonsignificant ($p = .10$ and .08 respectively. See Appendix S9 for all pairwise comparisons with outlier removed). Translocated birds remained highly significantly different to resident Barberspan birds. Mean daily distance ($R^2 = .31$) and SD of daily distance ($R^2 = .46$) also contributed much more strongly to the multivariate result (Appendix S10).

Compared to translocated birds, Barberspan birds appeared on average to travel further with more variability along with distinctly different turning angles. This is especially apparent once the outlier was removed (Appendix S11). Our results, therefore, show distinct differences between the movement patterns of translocated birds and those at the site of origin. In addition, the movements of translocated birds, while accounting for the outlier, seemed to approximate those of Strandfontein resident birds, illustrating how their movements adapt to local landscape features.

4 | DISCUSSION

Overall, the translocation experiment did not support the hypothesis that Egyptian Geese are capable of using environmental or celestial cues to undertake long-distance map-based navigation to determine precisely where they are located relative to a desired endpoint (Table 5). The different directions pursued by translocated birds also suggest a lack of influence of social cues. At the same time, their movement trajectories differed from those of birds that reside in the Western Cape and use Strandfontein (the translocation site) for flightless moult, indicating that movements were not a hardwired response to the local environment and eliminating our third hypothesis. Translocated Egyptian Geese moved mainly west or south after release, as they might have from Barberspan after completing moult. Keeping in mind the limitations of our sample size, we thus tend overall towards explaining the results in light of our second hypothesis based on the evidence summarized in Table 5: translocated birds attempted to move in the manner to which they were accustomed, but were unable to do so due to differences in landscape structure. They, therefore, displayed some flexibility in movement behaviours while being unable to locate (or at least, not returning to)

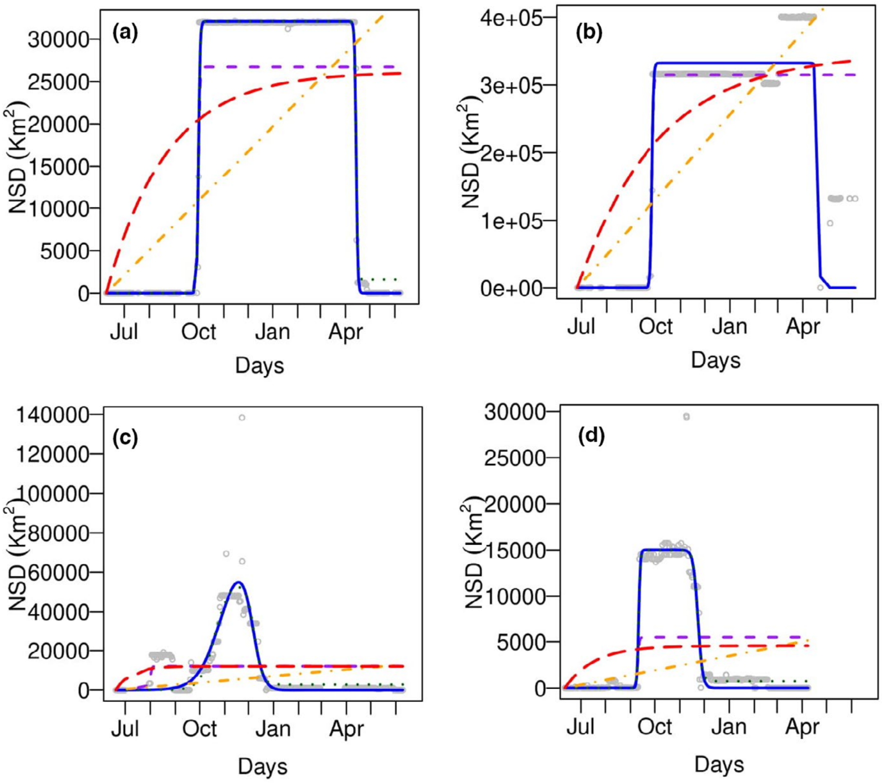

FIGURE 2 Comparison of net squared displacement models for two consecutive years of a Barberspan resident bird (PTT ID 7713201) in (a) and (b), and a translocated bird (PTT ID 7711703) in (c) and (d). Grey dots indicate underlying NSD data points, and coloured lines represent fitted movement models (blue, migratory; black dotted, mixed migratory; purple, dispersal; red, resident; and yellow, nomadic). The migrant model had the highest support in (a), (b) and (c), while a mixed migratory model had the highest support in (d). See Table 3 for a comparison of AIC values

their former breeding and moulting locations at the onset of flightless moult.

We propose that the conflict between learned behaviours and flexible responses to landscape structure led to the expression of a novel mixture of movement patterns in the novel landscape, as illustrated by significant differences in movement patterns between translocated individuals and Egyptian Geese originally tracked from Barberspan and Strandfontein. This is further supported by the results of the net-squared displacement analysis, which indicated the presence of both migratory and mixed migratory strategies in translocated individuals while a migratory strategy was dominant in residents. Alternative explanations are also possible; for example, the birds may have experienced a lower incentive to return to their previous locations than we would assume, and opted to minimize the potential risks of longer distance movement by remaining in suitable habitats in the Cape. However, if risk aversion were the influence that kept translocated birds in the Cape then the observed long-distance movements over the ocean would seem unlikely. We have never seen this kind of behaviour in resident birds from the Cape (Strandfontein and Voelvlei).

The net squared displacement analyses confirmed that Barberspan-moulting Egyptian Geese are genuine moult migrants, moving from a home area to a moult site and back again, as proposed but not formally tested by Cumming et al. (2012). Our analysis suggests that although Barberspan-moulting birds may choose to stay near their moult site beyond the time that is required to moult, they will return to their previous home areas in September in time to nest—providing clear evidence of an incentive to return to a home area. Translocated birds that undertook long-distance dispersive movements appear to have been motivated to return to their original breeding areas, as indicated by evidence of migratory data in translocated birds at a different time from those at Strandfontein; breeding season for Barberspan birds is likely to differ from that in the Cape (Cumming et al., 2016). Nest card data show that Egyptian Geese across southern Africa are dominantly late winter (August–September) breeders (Cumming et al., 2016), so the onset of the breeding season would have provided an incentive for birds that were translocated in June to start trying to find their way back to their partners and nest sites in August. There is no evidence that the climate was significantly different between tracking periods across our sample, and the climates of Strandfontein and Barberspan are in any case very different (e.g. winter vs. summer rainfall), so the likelihood that differences in climate during sampling periods might have driven differences in movement behaviours is extremely low. Further evidence for the lack of a climate trigger for movement is provided by the observation that birds undertake moult migration consistently at the same time between different years, regardless of the weather in that year.

The outcome of the translocation experiment provides evidence that under normal conditions, Egyptian Geese rely on a combination of specific knowledge of the local landscape and learned behaviours (plus potentially, use a sun compass). Consistency in movement paths to and from moult sites, with distinct patterns of behaviour observed in each studied population, suggests a potential for learned route-based navigation. Translocated birds nonetheless retained some individual features of movement behaviour that fitted their original location, as seen in observations of long directional journeys south and west. Our results also provided no

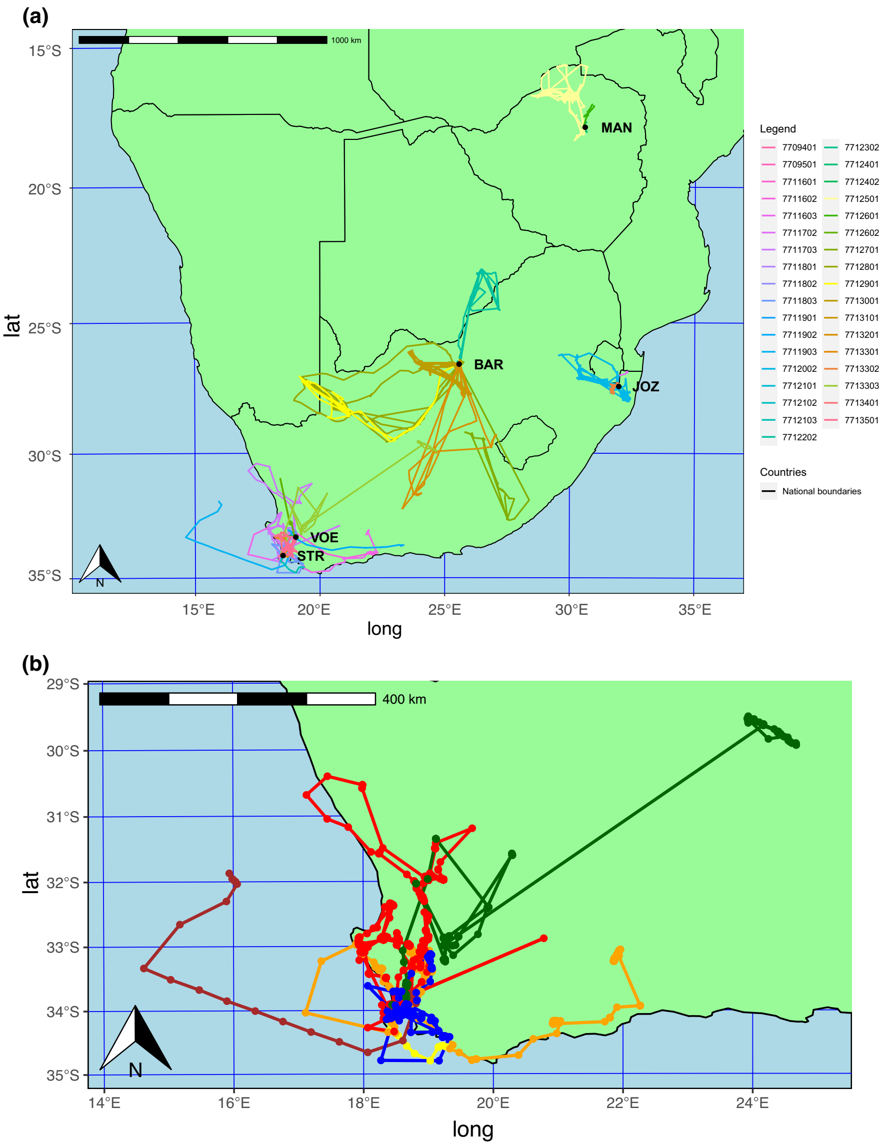

FIGURE 3 Map of southern Africa, showing movement paths analysed in this study from (a) all 29 resident birds and 6 translocated birds; and (b) translocated birds only. Further details for each path are given in Table 1. BAR, Barberspan; BARSTR, birds moved from Barberspan to Strandfontein; JOZ, Jozini Dam; MAN, Lake Manyame; STR, Strandfontein; VOE, Voelvlei

support for the third hypothesis; Egyptian Geese cannot be regarded (or modelled) as automata that respond reflexively to environmental variation. If the transmitters had been operational for longer, we would have been able to test whether the learned component declined over time (i.e. whether movements gradually became better locally adapted, and converged upon those of resident birds) and whether they undertook longer searching movements. However, the fact that Egyptian Geese normally shift their movement patterns through different phases of the calendar year means that at least two years of data from many different birds would be needed for this kind of analysis.

In comparison to our previously published analysis of resident birds (Cumming et al., 2012), this study includes additional sites, translocated birds and a larger sample size of resident birds, as well as a focus on the navigation component of movement patterns rather than on dispersal distances and moult site fidelity. We again found clear differences between the movement paths of individual nontranslocated Egyptian Goose at Strandfontein and Barberspan, despite some individual tracks not including moult migration; and our results also suggest differences between the movement paths of birds at other locations. We lack the sample sizes to test hypotheses about between-site differences rigorously, but it appears that individual birds that reside in a given location learn to use their local landscape effectively (Henry, 2016; Henry et al., 2016) and that some elements of this learned approach may be highly conservative.

For the MEF more generally, our results provide evidence that internal factors (i.e. the urges to breed and to moult) may have a strong influence on the link between navigation capacity and the resulting movement path. This finding has important implications for understanding and predicting the movement responses of animals to environmental change or reintroduction efforts (Batson et al., 2015). In particular, the responses of birds to new environments may be more conservative and less flexible than expected if the role of learned behaviours is not considered. Translocation or displacement field experiments with remotely tracked individuals are commonly performed on migrating species that have inherently strong

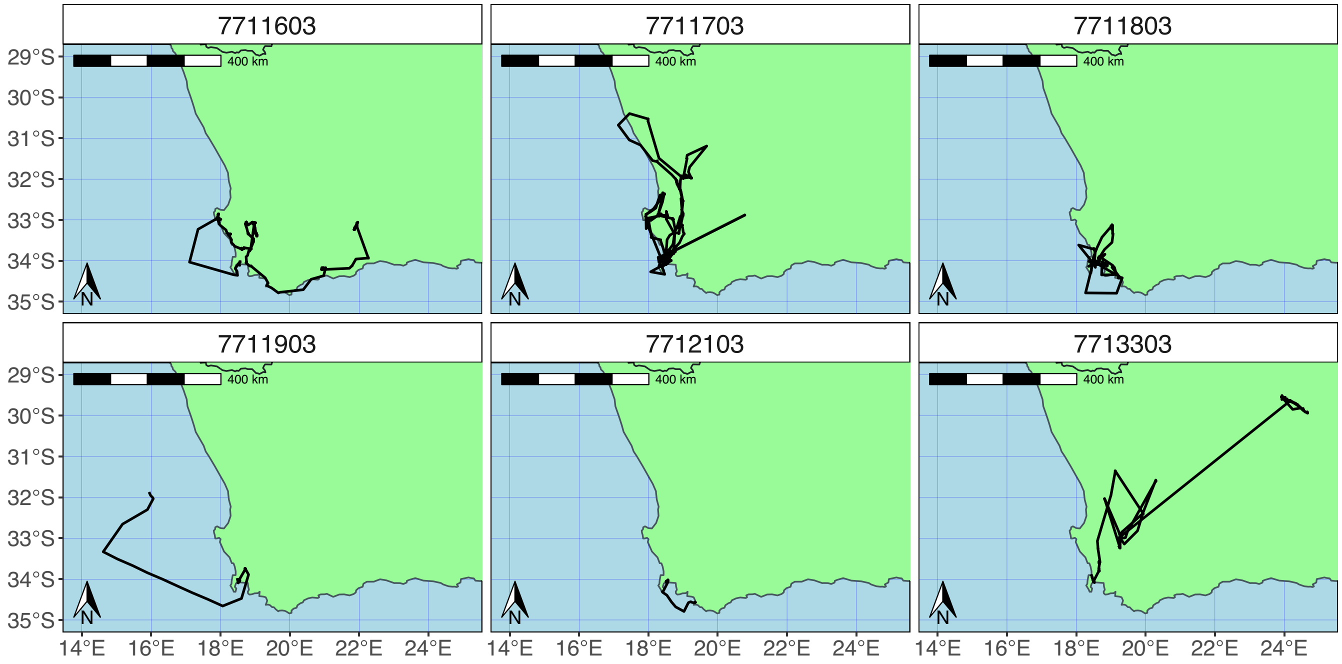

FIGURE 4 Maps showing individual tracks (black lines) of each translocated bird. Numbers correspond to the PTT number given in Table 1

TABLE 4 Pairwise results of linear hypothesis analysis which tests for difference in multivariate coefficients of movement measures using the Wilks' Lambda test statistic (Λ)

	BARSTR	BAR	STR	VOE	MAN
BARSTR					
BAR	**$\Lambda = 0.35$** **$F_{5,25} = 8.98$** **$p < .001$**				
STR	**$\Lambda = 0.61$** **$F_{5,25} = 3.14$** **$p < .05$**	**$\Lambda = 0.42$** **$F_{5,25} = 6.75$** **$p < .001$**			
VOE	**$\Lambda = 0.65$** **$F_{5,25} = 2.71$** **$p < .05$**	$\Lambda = 0.40$ $F_{5,25} = 7.10$ $p < .001$	$\Lambda = 0.89$ $F_{5,25} = 0.59$ $p = .71$		
MAN	$\Lambda = 0.22$ $F_{5,25} = 15.28$ $p < .001$	$\Lambda = 0.39$ $F_{5,25} = 7.30$ $p < .001$	$\Lambda = 0.33$ $F_{5,25} = 9.43$ $p < .001$	$\Lambda = 0.46$ $F_{5,25} = 5.63$ $p < .001$	
JOZ	$\Lambda = 0.22$ $F_{5,25} = 17.01$ $p < .001$	$\Lambda = 0.40$ $F_{5,25} = 7.28$ $p < .001$	$\Lambda = 0.34$ $F_{5,25} = 9.61$ $p < .001$	$\Lambda = 0.47$ $F_{5,25} = 5.44$ $p < .001$	$\Lambda = 0.83$ $F_{5,25} = 0.84$ $p = .45$

Note: The most relevant one-way comparisons are shown in bold.

long-distance navigational capabilities (Holland, 2014; Willemoes et al., 2015). Studies on latitudinal migrants show map-based navigation in birds; depending on the study, displaced birds are often able to relocate their wintering or breeding grounds or rejoin their migration route (Ibarra-Macias et al., 2011; Kennedy & Marra, 2010; Slager et al., 2015; Willemoes et al., 2015). These studies suggest that latitudinal migrants—which include many waterfowl—can use geomagnetic, olfactory and/or celestial cues to determine their position relative to their desired location. Our experimental displacement of a moult migrant thus offers some unique insights into navigation capacity; unlike displaced latitudinal migrants, our study species was clearly unable to navigate "home" from a novel environment. The discrepancies between latitudinal migrants and moult migrants suggest that Egyptian Geese may have a higher reliance than latitudinal migrants on learned responses to the biophysical environment when "deciding" where to move.

The suggestion that moult migrants may navigate differently from classical latitudinal migrants raises an interesting challenge for movement ecology. For the MEF, it implies a clear need to consider the ways in which different influences on movement relate to the continuum of different movement strategies summarized in Figure 1. Intuitively it makes sense that bird populations that live in a less predictable environment with fewer obvious landmarks or geographic constraints may have had to develop different approaches

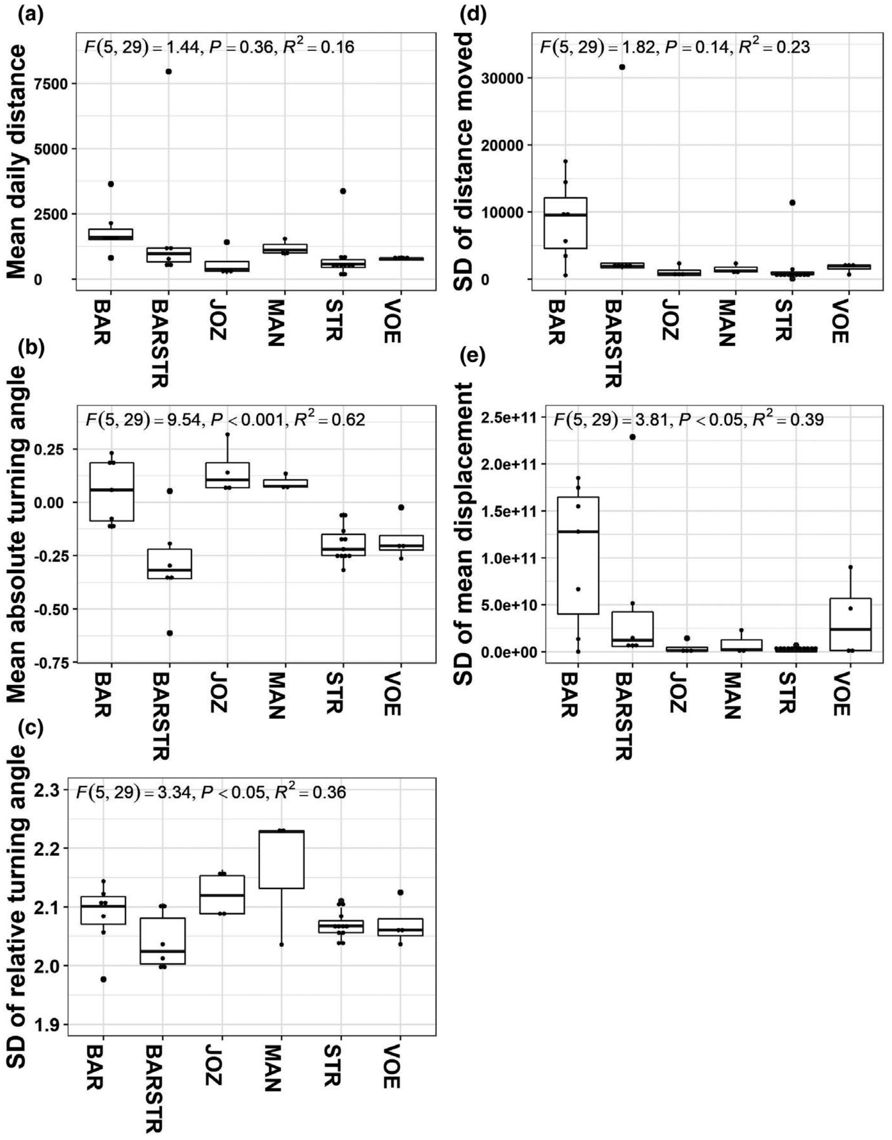

FIGURE 5 Boxplots of individual variables measured to describe and compare the movement path of each bird. These include (a) mean daily distance moved; (b) mean absolute turning angle; (c) standard deviation of relative turning angle; (c) standard deviation of daily distance moved; and (d) standard deviation of mean displacement from the release location (moult site, for residents; Strandfontein, for translocated birds). BAR, Barberspan; BARSTR, birds moved from Barberspan to Strandfontein; JOZ, Jozini Dam; MAN, Lake Manyame; STR, Strandfontein; and VOE, Voelvlei. ANOVA results from univariate linear regression are reported at the top of each panel

to navigation from both residents and latitudinal migrants that exploit more predictable environments and resource pulses (Henry et al., 2016; Roshier et al., 2008; Teitelbaum & Mueller, 2019). Thus, studies of species that move semipredictably in relatively stochastic environments, such as southern Africa and Australia, may be critical for broadening and contextualizing our understanding of animal movement ecology.

Given that wetlands are some of the most threatened ecosystems on earth (Kingsford et al., 2016), our findings have implications for the management and conservation of African waterfowl and more generally for our ecological understanding of population resilience to climate change and habitat modification (Batson et al., 2015). If Egyptian Geese are typical of other African waterfowl species, conservation of individual regional populations *and their learned responses to change* will be important in ensuring the persistence of waterfowl species and the important ecological functions (Reynolds & Cumming, 2015, 2016) and ecosystem services (Green & Elmberg, 2014) that they provide.

Our results also contribute to a deeper understanding of waterfowl biogeography. Egyptian Geese would clearly be capable of crossing the Sahara Desert, but as far as we know they have never established satellite populations in Europe through independent movement. They have more recently been introduced by people to Britain, the Netherlands and the United States, where they have successfully established breeding populations and are spreading (Callaghan & Brooks, 2017; Gyimesi & Lensink, 2012; Sutherland & Allport, 1991). These introductions prove that habitat suitability is not the cause of the failure of Egyptian Geese to naturally expand their range into Europe. It thus appears that conservative learned behaviours may have prevented the further spread of Egyptian Geese into Europe.

More generally, our case study suggests that long-distance navigation capacity may play a role in limiting population expansion. Population and community persistence under environmental change will depend not only on animals being able to cope with new forms of environmental variation, such as the increasingly arid conditions predicted for South Africa (Conradie et al., 2019), but also on their

TABLE 5 Summary of empirical evidence for difference hypotheses and our interpretations of what our results mean for our understanding of the movement ecology of Egyptian Geese

Observation (empirical evidence)	Our interpretation(s) for understanding the movement ecology of Egyptian Geese	Consistent with H1	Consistent with H2	Consistent with H3
Egyptian Geese from different locations show high moult site fidelity between years, often returning to those sites from far away; they then consistently return to their home areas	Egyptian Geese are competent navigators with the capacity to both find remote locations and return from them	X	X	X
Individual Egyptian Geese from different locations exhibit distinct movement paths; these differences are consistent within each individual location	The structure of the landscape in which each population resides entrains an appropriate response at relevant spatial and temporal scales. There is no obvious relationship between movement path properties and either latitude or longitude, as shown by the comparisons of BAR to JOZ and MAN	X	X	X
No translocated birds returned to BAR	Egyptian Geese cannot locate themselves precisely on the earth's surface using environmental cues (e.g. magnetism, sun, stars)		X	X
Translocated BAR birds did not move like STR resident birds	Landscape structure alone does not dictate bird movements. We propose that the obvious interpretation is that there is a strong learned element in observed movement paths/strategies	X	X	
Translocated BAR birds did not move like BAR resident birds	Individuals had sufficient behavioural flexibility to respond to landscape structure. We propose that this means that they are capable of local learning and adaptation, while at the same time being unable to locate Barberspan		X	
Translocated BAR birds released at STR moved a little like residents from nearby sites, including STR and VOE, although their movement patterns were distinct; they were very different from more remote sites (JOZ, MAN)	The movement patterns appear to reflect a balance between learned and flexible responses to a new landscape. This result also proves definitively that despite our small sample sizes, our methods can discriminate successfully between site-specific movement patterns		X	X
Translocated birds showed both migratory and mixed migratory strategies relative to STR, based on net squared displacement	Learning was rapid; in the new environment, the release site was the best approximation to a safe moult site		X	
Evidence of longer distance searching movements in translocated birds	Internal factors such as the desire to moult or breed led birds to seek familiar spaces (or partners) for these activities		X	
Several translocated birds flew extensively over the ocean, a behaviour never seen before in STR resident birds	These movements imply either (1) a lack of flexibility and the possibility of a rigid or faulty internal compass that pushed the birds south instead of north; or (2) a willingness to learn by exploring unfamiliar features		X	X
Higher variability in turning angles of resident birds relative to translocated birds from the same (Barberspan) population	More direct flight implies searching for landmarks rather than for food. Variable turning angles by residents imply the absence of a sun compass or clear cues indicating the best line of travel		X	

Note: The columns at the right indicate support for respectively: H1 (map-based and/or compass-based navigation capacity); H2 (route-based, flexible, primarily local navigation capacity); and H3 (inflexible navigation capacity dominated by learned but hard-wired responses to environment and internal factors). The only consistently supported hypothesis is H2.

being able to modify existing behaviours or unlearn maladaptive behaviours over relatively short time scales. The example of one of our translocated birds dying while attempting to cross the ocean provides a poignant example of how movement strategies that are effective in one location may be fundamentally unsuited to other locations or other conditions.

ACKNOWLEDGEMENTS

We are grateful to the many people who have helped with research on waterbirds over the years. We thank Alexandre Caron, Ngoni Chiweshe, Mduduzi Ndlovu, Gregory Mutumi and David Nkosi. We are also grateful to Sampie van Der Merwe (warden of Barberspan) and the Cape Town City Council for giving us permission to undertake this experiment and facilitating our research.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest in relation to this research.

DATA AVAILABILITY STATEMENT

The Telemetry data are available through Dryad at https://doi.org/10.5061/dryad.jh9w0vtd7 and linked to the R code used to run these analyses at Zenodo repository https://zenodo.org/record/6125750.

ORCID

Graeme S. Cumming https://orcid.org/0000-0002-3678-1326
Dominic A. W. Henry https://orcid.org/0000-0001-7375-141X
Chevonne Reynolds https://orcid.org/0000-0002-2345-7017

REFERENCES

Able, K. P. (2001). The concepts and terminology of bird navigation. *Journal of Avian Biology*, *32*(2), 174–183. https://doi.org/10.1034/j.1600-048X.2001.320211.x

Bastille-Rousseau, G., Potts, J. R., Yackulic, C. B., Frair, J. L., Ellington, E. H., & Blake, S. (2016). Flexible characterization of animal movement pattern using net squared displacement and a latent state model. *Movement Ecology*, *4*(1), 15. https://doi.org/10.1186/s40462-016-0080-y

Batson, W. G., Gordon, I. J., Fletcher, D. B., & Manning, A. D. (2015). Translocation tactics: A framework to support the IUCN Guidelines for wildlife translocations and improve the quality of applied methods. *Journal of Applied Ecology*, *52*(6), 1598–1607.

Bélisle, M., Desrochers, A., & Fortin, M.-J. (2001). Influence of forest cover on the movements of forest birds: A homing experiment. *Ecology*, *82*(7), 1893–1904. 10.1890/0012-9658(2001)082[1893:IOFCOT]2.0.CO;2

Brown, J. I., Lavretsky, P., Cumming, G. S., & Peters, J. L. (2019). Strong population structure and limited gene flow between Yellow-billed Ducks and Mallards in southern Africa. *The Condor*, *121*, 1–10. https://doi.org/10.1093/condor/duz042

Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., & Ericsson, G. (2011). A model-driven approach to quantify migration patterns: Individual, regional and yearly differences. *Journal of Animal Ecology*, *80*(2), 466–476. https://doi.org/10.1111/j.1365-2656.2010.01776.x

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer-Verlag.

Cagnacci, F., Focardi, S., Ghisla, A., van Moorter, B., Merrill, E. H., Gurarie, E., Heurich, M., Mysterud, A., Linnell, J., Panzacchi, M., May, R., Nygård, T., Rolandsen, C., & Hebblewhite, M. (2016). How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. *Journal of Animal Ecology*, *85*(1), 54–68. https://doi.org/10.1111/1365-2656.12449

Calenge, C. (2015). *Analysis of animal movements in R: The adehabitatLT Package*. R Package version n 0.3, 20.

Calenge, C., Dray, S., & Royer-Carenzi, M. (2009). The concept of animals' trajectories from a data analysis perspective. *Ecological Informatics*, *4*(1), 34–41. https://doi.org/10.1016/j.ecoinf.2008.10.002

Callaghan, C. T., & Brooks, D. M. (2017). History, current distribution, and status of the Egyptian Goose (*Alopochen aegyptiaca*) in the contiguous United States. *The Southwestern Naturalist*, *62*(4), 296–300.

Conradie, S. R., Woodborne, S. M., Cunningham, S. J., & McKechnie, A. E. (2019). Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proceedings of the National Academy of Sciences*, *116*(28), 14065–14070. https://doi.org/10.1073/pnas.1821312116

Cumming, G. S., Caron, A., Abolnik, C., Cattoli, G., Bruinzeel, L. W., Burger, C. E., Cecchettin, K., Chiweshe, N., Mochotlhoane, B., Mutumi, G. L., & Ndlovu, M. (2011). The ecology of influenza A viruses in wild birds in southern Africa. *EcoHealth*, *8*(1), 4–13. https://doi.org/10.1007/s10393-011-0684-z

Cumming, G. S., Gaidet, N., & Ndlovu, M. (2012). Towards a unification of movement ecology and biogeography: Conceptual framework and a case study on Afrotropical ducks. *Journal of Biogeography*, *39*, 1401–1411. https://doi.org/10.1111/j.1365-2699.2012.02711.x

Cumming, G. S., Harebottle, D. M., Mundava, J., Otieno, N., & Tyler, S. J. (2016). Timing and location of reproduction in African waterfowl: An overview of >100 years of nest records. *Ecology and Evolution*, *6*(3), 631–646.

Cumming, G. S., & Ndlovu, M. (2011). Satellite telemetry of Afrotropical ducks: Methodological details and assessment of success rates. *African Zoology*, *46*, 425–434. https://doi.org/10.1080/15627020.2011.11407654

Dean, W. R. J., & Siegfried, W. R. (1997). The protection of endemic and nomadic avian diversity in the Karoo, South Africa. *South African Journal of Wildlife Research*, *27*(1), 11–21.

Dodge, S., Weibel, R., Ahearn, S. C., Buchin, M., & Miller, J. A. (2016). *Analysis of movement data*. Taylor & Francis.

Elton, C. S. (1927). *Animal ecology*. Methuen.

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., & Heiberger, R. (2012). *Package 'car'* (p. 16). R Foundation for Statistical Computing.

Gobeil, J. F., & Villard, M. A. (2002). Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos*, *98*(3), 447–458. https://doi.org/10.1034/j.1600-0706.2002.980309.x

Green, A. J., & Elmberg, J. (2014). Ecosystem services provided by waterbirds. *Biological Reviews*, *89*(1), 105–122. https://doi.org/10.1111/brv.12045

Guilford, T., Åkesson, S., Gagliardo, A., Holland, R. A., Mouritsen, H., Muheim, R., Wiltschko, R., Wiltschko, W., & Bingman, V. P. (2011). Migratory navigation in birds: New opportunities in an era of fast-developing tracking technology. *Journal of Experimental Biology*, *214*(22), 3705–3712. https://doi.org/10.1242/jeb.051292

Gyimesi, A., & Lensink, R. (2012). Egyptian Goose *Alopochen aegyptiaca*: An introduced species spreading in and from the Netherlands. *Wildfowl*, *62*(62), 128–145.

Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2303–2312.

Henry, D. A. (2016). *A multi-scale study on the movement ecology of Afrotropical waterbirds*. University of Cape Town.

Henry, D. A., Ament, J. M., & Cumming, G. S. (2016). Exploring the environmental drivers of waterfowl movement in arid landscapes using first-passage time analysis. *Movement Ecology*, *4*(1), 1. https://doi.org/10.1186/s40462-016-0073-x

Hockey, P. A. R., Dean, W. R. J., & Ryan, P. G. (2005). *Roberts' Birds of Southern Africa* (1296 pp.). Russell Friedman Books CC.

Holland, R. (2014). True navigation in birds: From quantum physics to global migration. *Journal of Zoology*, *293*(1), 1–15. https://doi.org/10.1111/jzo.12107

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., & Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences*, *105*, 19060–19065. https://doi.org/10.1073/pnas.0800483105

Ibarra-Macias, A., Robinson, W. D., & Gaines, M. S. (2011). Forest corridors facilitate movement of tropical forest birds after experimental translocations in a fragmented Neotropical landscape in Mexico. *Journal of Tropical Ecology*, 547–556. https://doi.org/10.1017/S0266467411000186

Joo, R., Picardi, S., Boone, M. E., Clay, T. A., Patrick, S. C., Romero-Romero, V. S., & Basille, M. (2020). *A decade of movement ecology*. arXiv preprint arXiv:2006.00110.

Kemink, K., & Kesler, D. (2013). Using movement ecology to inform translocation efforts: A case study with an endangered lekking bird species. *Animal Conservation*, *16*(4), 449–457. https://doi.org/10.1111/acv.12015

Kennedy, C. M., & Marra, P. P. (2010). Matrix mediates avian movements in tropical forested landscapes: Inference from experimental translocations. *Biological Conservation*, *143*(9), 2136–2145. https://doi.org/10.1016/j.biocon.2010.05.025

Kingsford, R. T., Basset, A., & Jackson, L. (2016). Wetlands: Conservation's poor cousins. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(5), 892–916. https://doi.org/10.1002/aqc.2709

Kingsford, R. T., Roshier, D. A., & Porter, J. L. (2010). Australian waterbirds – time and space travellers in dynamic desert landscapes. *Marine and Freshwater Research*, *61*(8), 875–884. https://doi.org/10.1071/MF09088

Kishkinev, D., Anashina, A., Ishchenko, I., & Holland, R. A. (2020). Anosmic migrating songbirds demonstrate a compensatory response following long-distance translocation: A radio-tracking study. *Journal of Ornithology*, *161*(1), 47–57. https://doi.org/10.1007/s10336-019-01698-z

Kishkinev, D., Chernetsov, N., Pakhomov, A., Heyers, D., & Mouritsen, H. (2015). Eurasian reed warblers compensate for virtual magnetic displacement. *Current Biology*, *25*(19), R822–R824. https://doi.org/10.1016/j.cub.2015.08.012

Lensink, R. (1998). Temporal and spatial expansion of the Egyptian Goose *Alopochen aegyptiacus* in the Netherlands, 1967–94. *Journal of Biogeography*, *25*, 251–263. https://doi.org/10.1046/j.1365-2699.1998.252173.x

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.

Milstein, P. L. S. (1975). The biology of Barberspan, with special reference to the Avifauna. *The Ostrich Supplement*, *10*, 1–74.

Milstein, P. L. S. (1993). *A study of the Egyptian Goose Alopochen aegyptiacus*. (Ph.D.). University of Pretoria.

Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature*, *558*(7708), 50–59.

Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P., & Fagan, W. F. (2013). Social learning of migratory performance. *Science*, *341*(6149), 999–1002.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmona, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*, 19052–19059. https://doi.org/10.1073/pnas.0800375105

Ndlovu, M. (2012). *Environmental influences on moult and movement strategies in southern African waterfowl*. Ph.D. Thesis. University of Cape Town.

Ndlovu, M., Cumming, G. S., & Hockey, P. A. (2014). Influence of moult and location on patterns of daily movement by Egyptian Geese in South Africa. *Emu*, *114*(1), 23–29. https://doi.org/10.1071/MU12108

Ndlovu, M., Cumming, G. S., Hockey, P. A. R., & Bruinzeel, L. (2010). Phenotypic flexibility of a Southern African duck during moult: Do northern hemisphere paradigms apply? *Journal of Avian Biology*, *41*, 558–564.

Ndlovu, M., Cumming, G. S., Hockey, P. A., Nkosi, M. D., & Mutumi, G. L. (2013). A study of moult-site fidelity in Egyptian geese, *Alopochen aegyptiaca*, in South Africa. *African Zoology*, *48*(2), 240–249.

Ndlovu, M., Hockey, P. A., & Cumming, G. S. (2017). Geographic variation in factors that influence timing of moult and breeding in waterfowl. *Zoology*, *122*, 100–106. https://doi.org/10.1016/j.zool.2017.04.001

R Core Team (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reynolds, C., & Cumming, G. S. (2015). The role of waterbirds in the dispersal of freshwater cladocera and bryozoa in southern Africa. *African Zoology*, *50*(4), 307–311. https://doi.org/10.1080/15627020.2015.1108164

Reynolds, C., & Cumming, G. S. (2016). Defining functional groups using dietary data: Quantitative comparison suggests functional classification for seed-dispersing waterfowl. *Basic and Applied Ecology*, *17*(4), 333–343. https://doi.org/10.1016/j.baae.2015.12.006

Roshier, D. A., Asmus, M., & Klaassen, M. (2008). What drives long-distance movements in the nomadic Grey Teal *Anas gracilis* in Australia? *Ibis*, *150*(3), 474–484. https://doi.org/10.1111/j.1474-919X.2008.00806.x

Roshier, D. A., Klomp, N. I., & Asmus, M. (2006). Movements of a nomadic waterfowl, Grey Teal *Anas gracilis*, across inland Australia – Results from satellite telemetry spanning fifteen months. *Ardea*, *94*(3), 461–475.

Roshier, D. A., & Reid, J. R. W. (2003). On animal distributions in dynamic landscapes. *Ecography*, *26*(4), 539–544. https://doi.org/10.1034/j.1600-0587.2003.03473.x

Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G., & Fuller, R. A. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment*, *12*(7), 395–402. https://doi.org/10.1890/130237

Slager, D. L., Rodewald, P. G., & Heglund, P. J. (2015). Experimental effects of habitat type on the movement ecology and stopover duration of spring migrant Northern Waterthrushes (*Parkesia noveboracensis*). *Behavioral Ecology and Sociobiology*, *69*(11), 1809–1819. https://doi.org/10.1007/s00265-015-1993-y

Spitz, D. B., Hebblewhite, M., & Stephenson, T. R. (2017). 'MigrateR': Extending model-driven methods for classifying and quantifying animal movement behavior. *Ecography*, *40*(6), 788–799. https://doi.org/10.1111/ecog.02587

Stephens, K., Measey, J., Reynolds, C., & Le Roux, J. J. (2020). Occurrence and extent of hybridisation between the invasive Mallard Duck and native Yellow-billed Duck in South Africa. *Biological Invasions*, *22*, 693–707.

Sutherland, W., & Allport, G. (1991). The distribution and ecology of naturalized Egyptian Geese *Alopochen aegyptiacus* in Britain. *Bird Study*, *38*(2), 128–134.

Teitelbaum, C. S., & Mueller, T. (2019). Beyond migration: causes and consequences of nomadic animal movements. *Trends in Ecology & Evolution*, *34*(6), 569–581. https://doi.org/10.1016/j.tree.2019.02.005

Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y., & Nathan, R. (2020). Cognitive map–based navigation in wild bats revealed by a new high-throughput tracking system. *Science*, *369*(6500), 188–193.

Tsoar, A., Nathan, R., Bartan, Y., Vyssotski, A., Dell'Omo, G., & Ulanovsky, N. (2011). Large-scale navigational map in a mammal. *Proceedings of the National Academy of Sciences*, *108*(37), E718–E724. https://doi.org/10.1073/pnas.1107365108

Underhill, L. G., Tree, A. J., Oschadleus, H. D., & Parker, V. (1999). *Review of ring recoveries of waterbirds in southern Africa*. Avian Demography Unit, University of Cape Town.

van Toor, M. L., Hedenström, A., Waldenström, J., Fiedler, W., Holland, R. A., Thorup, K., & Wikelski, M. (2013). Flexibility of continental navigation and migration in European mallards. *PLoS One*, *8*(8), e72629.

Willemoes, M., Blas, J., Wikelski, M., & Thorup, K. (2015). Flexible navigation response in common cuckoos *Cuculus canorus* displaced experimentally during migration. *Scientific Reports*, *5*, 16402. https://doi.org/10.1038/srep16402

BIOSKETCHES

Graeme Cumming is a landscape ecologist and conservation theorist with strong interests in the impact of spatial heterogeneity on ecological processes. **Dominic Henry** is a quantitative ecologist and field biologist who uses his statistical and birding skills to save endangered species. **Chevonne Reynolds** is an ecologist and keen ornithologist who teaches and researches in animal ecology.

Author Contributions: GSC conceived the project, raised funding, attached tracking devices to the study animals, ran the first statistical analyses, and drafted the first version of the manuscript. DAWH and CR captured and moved the study animals and contributed to writing and revising the manuscript. DAWH ran additional statistical analyses and developed the Zenodo code repository.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Cumming, G. S., Henry, D. A. W., & Reynolds, C. (2022). Translocation experiment gives new insights into the navigation capacity of an African duck. *Diversity and Distributions*, 28, 1034–1049. https://doi.org/10.1111/ddi.13510