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Movement patterns of lesser flamingos *Phoeniconaias minor*: nomadism or partial migration?

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Waterbirds in stochastic environments exhibit nomadism in order to cater for the unpredictable availability of water resources. Lesser flamingos *Phoeniconaias minor* have long been thought to be nomadic waterbirds. In southern Africa, conservation efforts for lesser flamingos are hampered by a lack of knowledge about their movement trajectories. To investigate their movement ecology in southern Africa, we fitted GPS–GSM transmitters to 12 adults and tracked their movements over four years, from March 2016 to February 2020. Net squared displacement (NSD) was used in nonlinear least squares models classifying trajectories as nomadic, migratory, mixed-migratory, home range restricted or dispersal movement types. Data from eight of the 12 birds met the criteria for the NSD analysis. Model success was good; only 8 out of 120 (6.7%) movement type models failed to reach convergence. Goodness of fit statistics from the NSD models supported migratory and mixed migratory movement types (concordance criteria coefficient (CC) = 0.78) for more than half of the annual trajectories investigated (57.2%). Dispersal, home range-restricted and nomadic movements best described 28.6, 9.5 and 4.8% of annual trajectories, respectively, but all resulted in a mean CC of < 0.4 and thus did not fit observed NSD patterns as well as the migratory movement types. We then used nonlinear mixed effects models to account for annual and individual differences in migration parameters. Variation in the timing and duration of all migrations were more important than variation in migration distance, indicating well-established summer and winter 'ranges' and routes between Kamfers Dam (South Africa) and Sua Pan (Botswana). We propose that lesser flamingos in central southern Africa may be partial migrants, not true nomads, as most of their movements followed a regular, repeated pattern between two primary locations.

Keywords: dispersal, Etosha Pan, Kamfers Dam, lesser flamingo, migration, net squared displacement, nomadism, *Phoeniconaias minor*, Sua Pan

Conserving highly mobile species is difficult, because they require protection over large geographical areas at the source, destination and over the course of their long-range movements (Runge et al. 2014). It is especially challenging to plan and implement conservation strategies for animals that move erratically over vast areas, such as those that exhibit nomadic movements in response to stochastic environmental changes (Cottee-Jones et al. 2016). Because of their ability to fly, birds are some of the most mobile animals on the planet; some coastal birds undergo the longest migrations on record (Egevang et al. 2010, Battley et al. 2012). In migratory land birds, long distance movements of Palearctic and Nearctic species have also been well documented (McKinnon et al. 2013) and the multiple threats to these migrants have been the subject of international conservation plans for some time (CMS 1979). Specific plans have been established for migratory waterfowl (e.g. the African Eurasian Waterbird Agreement – AEWA), but implementing these actions is complicated for birds with less predictable movements. Waterfowl in arid environments provide good examples of the above, as they have been shown to be nomadic (Kingsford et al. 2010, Henry et al. 2016, Pedler et al. 2018).

Movement types can be placed into different categories, such as those described by Teitelbaum and Mueller (2019). Bunnefeld et al. (2011) provided conceptual models for five broad categories, namely nomadic, migratory, mixed migratory, dispersal and home range restricted movements. Classifying movement types this way may not, however, be accurate at all spatial and temporal scales. Birds previously thought to be nomadic sometimes show predictable movements

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for a part of the year (Watson and Keren 2019), while some species exhibit partial migration, where individuals of a species thought to be migratory sometimes overwinter at their breeding grounds (Townsend et al. 2018).

These patterns are most effectively detected by means of global positioning system (GPS) or satellite telemetry, advances in which have revolutionised our ability to track the trajectories of animal movement paths (Kays et al. 2015). In this context trajectory is as a sequence of time-stamped locations from which we can derive inferences about animal movement behaviour (Teimouri et al. 2018). The choice of movement trajectory is driven by certain environmental cues and the behavioural responses to these cues ultimately impact the fitness of individual animals (Cattarino et al 2016). In temperate environments, these cues take the form of zeitgebers, usually changes in temperature and photoperiod, which regulate the circannual rhythms in birds, including decisions about when to migrate (Gwinner 1996). Because environmental cues are less predictable in stochastic environments, we expect the movement paths of nomadic waterbirds inhabiting arid areas to show more significant intraspecific variation in both spatial and temporal patterns of displacement from a source location. In the field of movement ecology, such a source location would usually be a nesting site, or the place where an individual was captured and fitted with a tracking device.

Some Afrotropical waterbirds in the arid regions of southern Africa seem able to anticipate the distribution of favourable resources before they become available, which favours a hypothesis of prescient movement over that of reactive movement (Henry 2015). This implies an intimate knowledge of local waterbodies and their expected quality at a given time, contradicting the assumption of randomness in the movements of what are thought to be nomadic species. Movements may thus be migratory but conditional, i.e. different patterns are displayed by individuals over time (Fieberg et al. 2008).

There is evidence for an innate navigational capability in wide-ranging, solitary birds (de Grissac et al. 2016). Many inland waterbirds are more gregarious, moving around in groups. Gregarious species are thought to use the presence and activities of conspecifics as a mechanism of patch choice for optimal foraging and nest site selection (Fernández-Chacón et al. 2013), thus movements are based, to some extent, on social learning. The mechanisms behind the movements of gregarious inland waterbirds are unknown in the arid parts of southern Africa.

Considering the above, the lesser flamingo *Phoeniconaias minor* makes for an interesting model on which to investigate movement patterns of highly gregarious Afrotropical waterbirds. In southern Africa it inhabits environments that are unpredictable in terms water occurrence, and with fluctuating quality in terms of hydrochemistry (McCulloch et al. 2008), supporting a reactive movement strategy and nomadism. Looking at a larger scale, very small gene flow between the East African population and other, seemingly isolated populations in southern Africa and India is facilitated by only a few individuals per generation (Zaccara et al. 2011, Parasharya et al. 2015), which also supports a nomadic movement strategy. However, being the world's most numerous species of flamingo (Ogilvie and Ogilvie 1986), aspects such as the phenology of their movements and navigation are probably influenced by social learning, which points to a prescient movement strategy typical of migrants.

The lesser flamingo is considered Near Threatened by the International Union for Conservation of Nature and Natural Resources (BirdLife International 2018), and it appears under the same category on regional lists (Anderson 2015, Simmons et al. 2015). Despite their relatively large numbers there are concerns that the species is susceptible to population declines should their specialised breeding and feeding habitat be compromised. Decreases in lesser flamingo populations across Africa (Simmons 1996, Childress et al. 2008) are attributed to the degradation of key breeding and feeding sites through pollution, altered hydrology and the subsequent decrease in water quality (Hill et al. 2013), salt and soda ash extraction, and human disturbance (Childress et al. 2008, Anderson 2015). Collisions with power lines are also frequently recorded, especially in South Africa and India (Tere and Parasharya 2011).

The correct classification of the movement patterns employed by lesser flamingos may have consequences for the planning and implementation of interventions for managing anthropogenic threats. If they are nomadic, then all conservation efforts should aim to protect the few key breeding and feeding sites, as these are the only sites for which we can predict regular flamingo presence. Alternatively, if southern African lesser flamingos migrate between these areas in predictable patterns, then movement corridors can be identified and added to current conservation plans, and interventions can be timed to account for temporal differences in flamingo densities. The aims of this study were to track and classify the spatiotemporal characteristics of southern African lesser flamingo movements, and to test the nomadic movement paradigm. We based our investigation on the movement paths and telemetry data from GPS-tagged adult birds.

Methods

Study area

The focus of our study was the inland population of lesser flamingos within southern Africa. The southern African population contains roughly 50 000 lesser flamingos (Simmons 1997), although irruptive influxes sometimes result in numbers far beyond this estimate (Simmons 1996). Three of the five current breeding locations of the species are contained within the study area (Fig. 1). The first, Sua Pan, forms a large (3400 km^2) part of the Makgadikgadi Pans complex in Botswana and is the most prolific breeding site for the species in the region (McCulloch and Borello 2000). The Makgadikgadi Pans are the relics of a massive lake (Lake Makgadikgadi) that once covered much of what is now known as the Kalahari Basin in Botswana (Cooke 1979). The two biggest pans, Ntwetwe Pan and Sua Pan, were connected as recently as the beginning of the previous century, according to evidence from old Baobab trees (Riedel et al. 2012). Etosha Pan is situated in northern Namibia, approximately 1000 km northeast of Sua Pan. At nearly 5000 km^2, Etosha Pan can support large numbers up to 1 million flamingos when conditions are suitable (Berry 1972). Breeding does

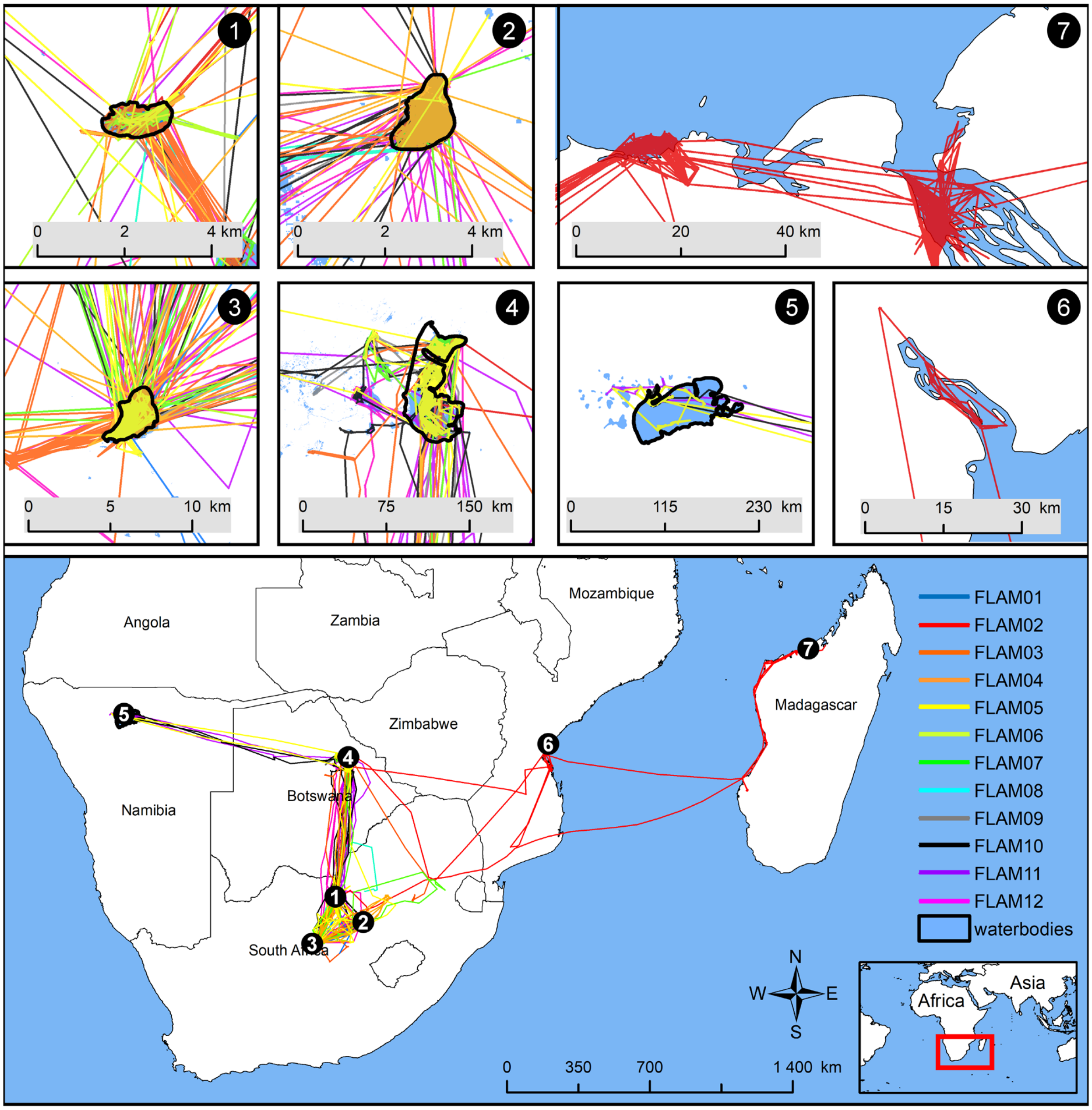

Figure 1. A map of southern Africa and the study area, including some waterbodies regularly visited by flamingos. The numbers indicated on the map refer to capture sites 1) Delareyville and 2) Allanridge in South Africa and other places mentioned in this paper: 3) Kamfers Dam in South Africa, 4) Sua Pan in Botswana, 5) Etosha Pan in Namibia, 6) Beira in Mozambique and 7) Mahajanga in Madagascar.

not occur regularly, and when it does the nests and nestlings are often at risk from rapidly evaporating water levels (Simmons 1996, Versveld 2010). The third site, Kamfers Dam, is an artificial reservoir near Kimberley, South Africa. Here there has been some breeding success on an artificial island (Anderson 2008, Anderson 2015) and recently (2018/2019) nesting also occurred on other sections of the dam. With a fluctuating population regularly exceeding 20 000 birds, Kamfers Dam is an important feeding site for the species in southern Africa.

The study area included two flamingo capture sites in South Africa, a salt pan at the Henk Joubert Nature Reserve near Delareyville (26°70′3″S, 25°45′6″E), North West Province, and a pan near the town of Allanridge (27°76'9''S, 26°64'7''E) in the Free State Province of South Africa.

Capturing and tracking flamingos

The captures were completed in three field trips on the following dates: 1–2 March 2016 and 26–28 May 2016 (Delareyville), and 11–12 November 2016 (Allanridge). Trapping and tagging lesser flamingos followed general methods employed by Childress et al. (2004) and Childress and Jarrett (2005). Twelve lesser flamingos were captured; six at Delareyville and six at Allanridge. They were caught around their legs using slipknot nooses made from 0.5 mm clear monofilament line attached to 50 m lengths of nylon rope, forming a sunken 'trap line'. Captured flamingos were processed at a mobile bird ringing station hidden in the treeline surrounding the waterbodies. We followed the guidelines for using morphological measurements to sex birds contained within Childress et al. (2005). GPS–GSM satellite tracking devices ('duck' model, ECOTONE Telemetry, Gdynia, Poland) were attached to the birds by means of Teflon backpack harnesses. The devices weighed 30 g, which was a mean of 1.5% (1.3–1.7%) of the mass of the 12 captured birds. In addition to the tracking devices, the flamingos were fitted with alphanumerically unique stainless-steel rings (SAFRING). Flamingos were captured and handled under South African ordinal permits from the North West Dept. Rural, Environmental and Agricultural Development (permit no. HQ 02/16-004 NW) and the Free State Dept. Economic Development, Tourism and Environmental Affairs (permit no. 01/35851).

Data analyses

The number of daily GPS location fixes varied significantly both within and among individual flamingos, largely due to differences in GSM signal strength within the study area. To account for the inconsistent frequency of recorded fixes, we resampled the data to include one fix per day for the identification of broad movement types of annual trajectories. Net squared displacement (NSD) was used to classify individual flamingo movements into five main types, namely: nomadic, migratory, mixed-migratory, dispersal and home range restricted movements. NSD is a measure of the squared distance between the starting location of an animal's trajectory and a subsequent relocation. Plotting NSD over time produces a curve that can be modelled to fit a variety of theoretical movement patterns, as demonstrated by Bunnefeld et al. (2011), Papworth et al. (2012), Beatty et al. (2013) and de Grissac et al. (2016) (Fig. 2). In addition to determining movement patterns of populations, the NSD method can also model movement patterns of individuals (Börger and Fryxell 2012) and has been found to be superior to home range overlap and cluster methods when quantifying smaller scale differences in movement patterns (Cagnacci et al. 2016).

Using NSD as a response, we applied the model functions for different movement types by Bunnefeld et al. (2011) and de Grissac et al. (2016) to create theoretical movement models for flamingos. The most basic movement model is that of sedentary flamingo movements, hereafter referred to as 'home range' movements for parity with the above-mentioned studies. Home range movements show some variation around a core area, and ultimately produce an NSD close to the original value for a given period. Thus NSD = 0 at time = 0 (days since departure) and NSD ≈ 0 at 0 + time t. NSD for a theoretical flamingo home range model is therefore constant and can be considered an intercept model (Table 1, Eq. 1). It has been shown that when animals move in a random walk, NSD increases linearly from source over time (Börger et al. 2008). Nomadic flamingo movements were thus considered a linear model that increases with time (Table 1, Eq. 2).

A dispersal pattern can be modelled using an asymptote of NSD signifying settlement in a new area. This is akin to a logistic curve, thus the theoretical NSD model for dispersing flamingos is a single sigmoid function (Table 1, Eq. 3).

A basic migratory pattern can be demonstrated using NSD over time by considering a trajectory where individuals depart one seasonal range to move to another, and then return to the exact departure point. The departure and temporary settlement in a seasonal range is similar to the dispersal function, but the return journey mirrors the first half of the curve. We thus considered a basic theoretical flamingo migration model to be a double sigmoid function, eventually returning to NSD ≈ 0 (Table 1, Eq. 4).

A more complicated migratory pattern has been identified whereby a migrating individual nearly completes a full migration but settles upon its return at a location that is different to the original departure point. There is thus a second

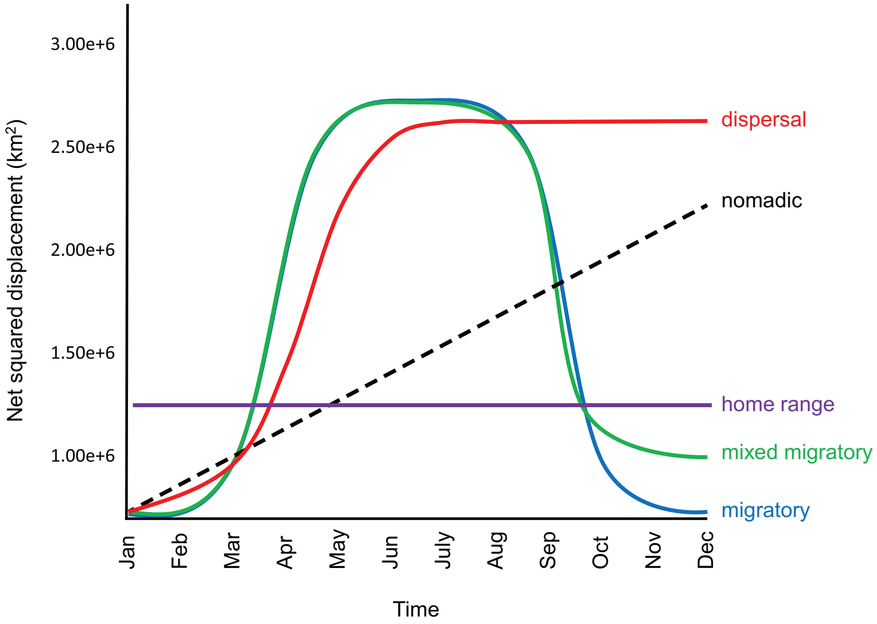

Figure 2. Theoretical patterns of net squared displacement over time for different movement types, adapted from Bunnefeld et al. (2011) and de Grissac et al. (2016).

Table 1. Equations of model functions for different lesser flamingo movement types, as defined defined by Bunnefeld et al. (2011). β and c are constants, t is the time since start of a trajectory, asym is an asymptote reached for a displacement, θ is the inflection point of a dispersal or migration movement, a and b signify different seasonal movements, and φ is a scale parameter that dictates the shape of the curve.

Model no.	Equation	Movement type
1	$\text{NSD} = c$	home range
2	$\text{NSD} = \beta \times t$	nomadic
3	$\text{NSD} = \dfrac{\text{asym}}{1 + \exp\left(\dfrac{\theta - t}{\varphi}\right)}$	dispersal
4	$\text{NSD} = \dfrac{\text{asym}}{1 + \exp\left(\dfrac{\theta_a - t}{\varphi_a}\right)} + \dfrac{-\text{asym}}{1 + \exp\left(\dfrac{\theta_b - t}{\varphi_b}\right)}$	migration
5	$\text{NSD} = \dfrac{\text{asym}_a}{1 + \exp\left(\dfrac{\theta_a - t}{\varphi_a}\right)} + \dfrac{-\text{asym}_b}{1 + \exp\left(\dfrac{\theta_b - t}{\varphi_b}\right)}$	mixed migration

NSD asymptote at play. For flamingos we considered mixed migration to be a similar model structure to a basic full migration, but with differences in seasonal asymptotes (Table 1, Eq. 5).

Because we wanted to quantify annual differences between NSD models for individual flamingos, separate trajectories were prepared for 365 day periods starting on $t_{(1)} = 13$ November for 2016/2017, 2017/2018 and 2018/2019. This particular date was chosen as a starting point as the last individual was fitted with a tracking device on the previous day, and because the entire sample, including the birds captured months before at Delareyville, was present at Allanridge during that time. Three flamingos were omitted from the dataset entering NSD analyses, as they did not survive one full trajectory to satisfy model parameters ($t < 365$).

Nonlinear least squares (nls) models were fitted to NSD equations for the movement types described in Table 1 (migratory, mixed migratory, home range, nomadic and dispersal) using the *nls* function in R (ver. 3.5.3, <www.r-project.org>). A nonlinear approach was appropriate for this analysis because the movement type curves (Fig. 2) did not fit linear models, barring the model describing nomadism. Separate models were fit to annual individual lesser flamingo trajectories, and model parameters were constrained to $0 \leq t \leq 365$. The concordance correlation coefficient (CC) was used to extract goodness of fit values of competing movement type models for annual trajectories. Huang et al. (2009) demonstrated the advantage of using CC over traditional measures such as Akaike's information criterion (AIC, Burnham and Anderson 2002) and improved on Lin's (1989) original CC equation to cater for nlme models. In the case of our study, CC was a measure of the agreement between observed and predicted NSD values extracted from movement type models. CC values ranged between −1 and 1, with 1 representing a perfect agreement of predicted NSD values to those recorded by the lesser flamingos and −1 was a perfect negative agreement, while CC values close to 0 corresponded to a poor agreement and CC values ≤ 0 indicate a lack of model fit (Huang et al. 2009). Only models with a fit of CC > 0.5 were considered candidates for describing lesser flamingo movement types.

From the individuals identified as migrants (including both migratory and mixed migratory types), we then constructed a priori nonlinear mixed effects models (nlme – Pinheiro et al. 2019) using different combinations of model parameters. These included fixed effects entering the migration model formula in Table 1, i.e. migration distance (asym), the timing (θ_a) and duration (φ_a) of summer migration, and the timing (θ_b) and duration (φ_b) of winter migration. The nlme models were ranked using CC and Akaike weights, while only those within < 2 ΔAIC were considered well supported (Burnham and Anderson 2002). Population-level migration parameters were extracted from the coefficients of the fixed effects of the most parsimonious nlme model, after Bunnefeld et al. (2011).

All statistical analyses were performed on R (ver. 3.5.3, <www.r-project.org>), while all visual inspections and mapping of the data was done on ArcMap 10.7.1. Statistical significance was considered at $\alpha = 0.05$, and results are reported as mean ± standard deviation, or mean (range) where appropriate.

Results

Telemetry data and general movements

A total of 84 696 GPS fixes were received from the satellite-tagged lesser flamingos (n = 12), which culminated in a mean of 7442 (1990–10 794) fixes per individual, including those recorded prior to day one for the analysis of NSD, 13 November 2016. On this day all twelve lesser flamingos were present at Allanridge. The lesser flamingos spent an average of 67.7% (9.8–89.9%) of their total days at two locations: Kamfers Dam and Sua Pan (Fig. 1). Mapping the trajectories of the twelve lesser flamingos revealed a narrow passage of movement between Kamfers Dam and Sua Pan. Three lesser flamingos (FLAM05, FLAM10 and FLAM11) moved to Etosha Pan in Namibia, using Sua Pan as a turning point in their trajectories. One female, FLAM02, left continental Africa soon after being fitted with a tracking device, crossing the Indian Ocean over the Mozambican Channel to settle on the north coast of Madagascar for two years before returning to Mozambique in 2018. From there she made a westward round trip to Sua Pan, settling once again along the Mozambican coast south of Beira (Fig. 2). FLAM02 was the only satellite-tagged individual that moved to the coast; all others remained within an inland area south and east of 15.62°E, 18.54°S near Etosha Pan, north of Kalkfontein Dam in the Free State Province of South Africa (25°25'E; 29°54'S), and west of Blinkpan near Chrissiesmeer, near the border between South Africa and Swaziland30°33'E, 26°34'S). In South Africa, most (94.3%) of flamingo relocation fixes were recorded from the Free State, Northern Cape and North West Province.

Nine of the twelve flamingos survived long enough to be tracked for 365 days, all of which visited Sua Pan on at least

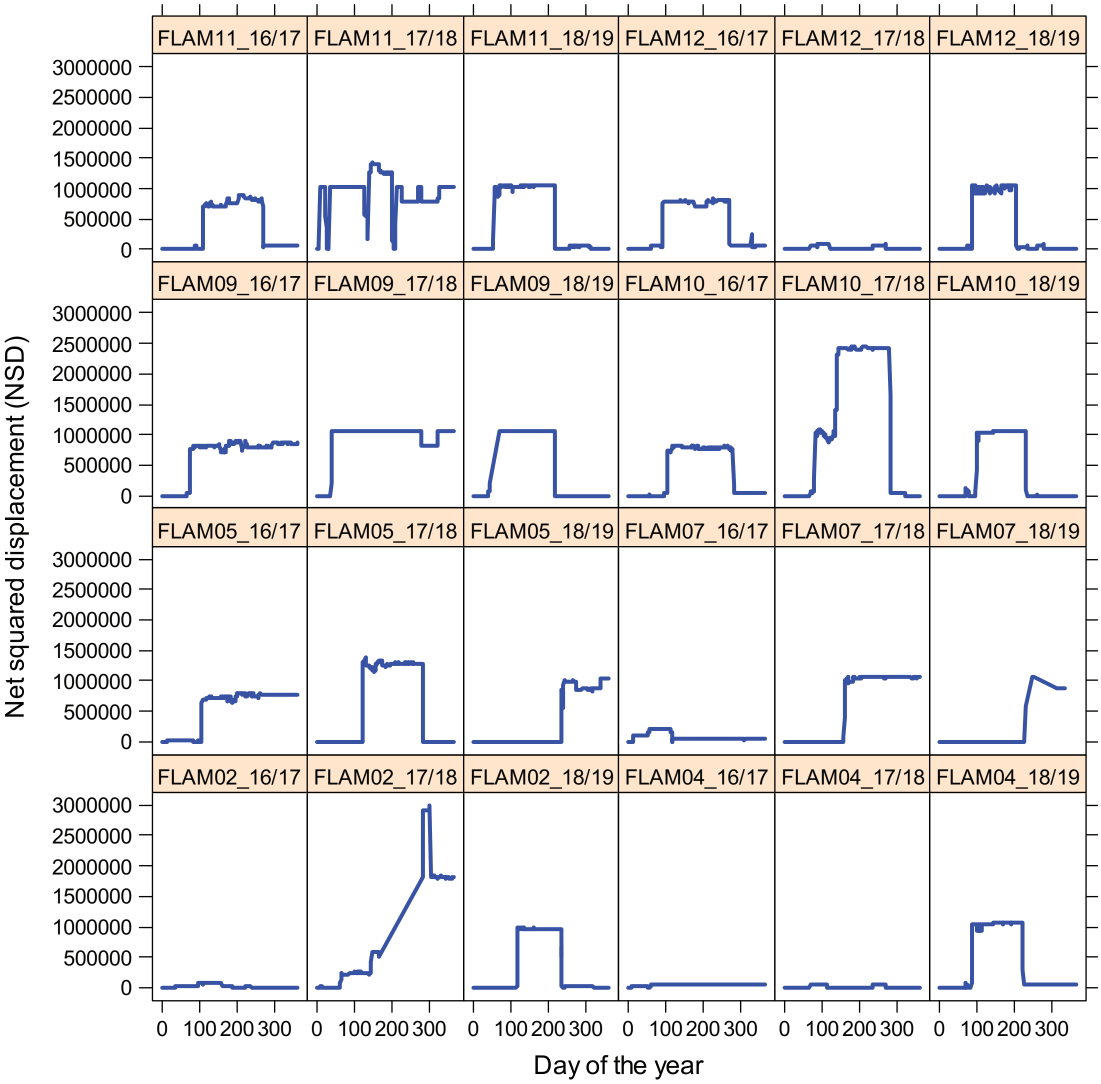

Figure 3. Daily net squared displacement, NSD (in kilometres) for annual trajectories of eight individual GPS-tracked lesser flamingos for the years 2016/2017, 2017/2018 and 2018/2019. Day one was 13 November 2016, following the capture of the last bird in the sample.

one occasion. Eight of the nine provided three full trajectories from three consecutive years' relocation fixes between 13 November 2016 and 12 November 2019. The 24 annual trajectories entering the analysis of movement patterns included a total of 8266 fixes. Data acquisition from birds in areas with poor GSM signal did not satisfy the requirement of one fix per day for 25% of the annual trajectories; fixes were received from a mean of 344.42 (232–365) days per year.

Classification of movement types

The six annual lesser flamingo trajectories with < 1 location fix per day did not suffer from a lack of resolution when quantifying net squared displacement; movements were simple and significant enough to result in clear patterns of NSD for most annual trajectories (Fig. 3). For three out of 24 trajectories (12.5%), nonlinear least squares models resulted in low concordance correlation coefficients across all movement types, indicating a poor model fit to observed NSD patterns (Table 2). We failed to achieve convergence for the more complex models (migratory and mixed-migratory types) for three of the remaining 21 trajectories (14.3%). Mean CC values were highest, and very similar, for mixed migratory ($CC = 0.78 \pm 0.23$) and migratory ($CC = 0.78 \pm 0.28$) movement types. Other models resulted low average CC values of 0.38, 0.32 and 0.22 for the dispersal, nomadic and home range movement types, respectively. Despite the high CC value, the mixed migratory type was the best model for only 14.3% of annual trajectories with at least one adequate fit to movement models. Most of the other trajectories were classified as migratory (42.9%), followed by dispersal (28.6%) movements, while home range and nomadic movements best described only 9.5% and 4.8% of annual trajectories, respectively. NSD commonly reached asymptotes near 1 million km^2, thus corresponding to a net displacement distance close to 1000 km (Fig. 4).

Variation in annual movements

Fourteen of 17 nonlinear mixed effects models evaluated for differences in fixed effects achieved convergence. Of these,

Table 2. Concordance correlation coefficients describing the goodness of fit of nonlinear least squares models of lesser flamingo net squared displacement, as related to different movement types. Trajectories were collected from eight GPS-tagged individuals over three years: 2016/2017, 2017/2018 and 2018/2019, with day one set to 13 November. Only models with a fit of CC > 0.5 (bold text) were considered candidates for describing flamingo movement types. Models with asymptote distance out of range are indicated by an asterisk. Trajectories without a clear fit to any of the movement types are labelled 'no fit'.

Track	Dispersal	Migratory	Mixed-migratory	Nomadic	Home range	Best model
FLAM02_16/17	0.145	0.465	0.438	0.153	**0.665**	Home range
FLAM04_16/17	0.056	0.769*	0.700*	0.509	**0.784**	Home range
FLAM05_16/17	**0.977**	0.933	0.967	0.800	0.000	Dispersal
FLAM07_16/17	0.365	0.060	0.476	0.336	0.000	No fit
FLAM09_16/17	**0.930**	0.892*	0.968*	0.697	0.000	Dispersal
FLAM10_16/17	0.034	**0.895**	0.609	0.038	0.000	Migratory
FLAM11_16/17	0.038	**0.848**	0.794	0.012	0.000	Migratory
FLAM12_16/17	0.001	**0.955**	0.889	0.001	0.000	Migratory
FLAM02_17/18	**0.951**	0.897	0.877	0.904	0.024	Dispersal
FLAM04_17/18	0.020	0.580*	0.673*	0.412	0.373	No fit
FLAM05_17/18	0.026	**0.979**	0.945	0.062	0.000	Migratory
FLAM07_17/18	**0.978**	0.940	0.932	0.860	0.000	Dispersal
FLAM09_17/18	**0.895**	0.738	0.836	0.321	0.000	Dispersal
FLAM10_17/18	0.383	**0.970**	0.968	0.039	0.000	Migratory
FLAM11_17/18	0.379	0.553	0.579	**0.649**	0.011	Nomadic
FLAM12_17/18	0.034	0.112	0.154	0.044	0.255	No fit
FLAM02_18/19	0.000	**0.911**	0.854	0.000	0.000	Migratory
FLAM04_18/19	0.049	**0.968**	0.958	0.051	0.000	Migratory
FLAM05_18/19	0.973	0.958	**0.989**	0.810	0.000	Mixed-migratory
FLAM07_18/19	**0.929**	0.000*	0.000*	0.276	0.000	Dispersal
FLAM09_18/19	0.071	0.660	**0.662**	0.032	0.000	Mixed-migratory
FLAM10_18/19	0.033	**0.769**	0.765	0.032	0.000	Migratory
FLAM11_18/19	0.662	0.950	**0.981**	0.235	0.000	Mixed-migratory
FLAM12_18/19	0.090	**0.929**	0.892	0.078	0.001	Migratory
Mean	**0.376**	**0.775**	**0.778**	**0.306**	**0.088**	
SD	**0.407**	**0.277**	**0.225**	**0.318**	**0.216**	

only two appeared in the 95% confidence set of competing models, and only one model was within < 2 ΔAIC and was thus considered a competitor for the highest ranked model (Table 3). The highest ranked, most parsimonious model resulted in an Akaike weight of 0.62, more than twice that of the competing model (Akaike weight = 0.30). The top model accounted for individual variation in all fixed effects barring the asymptotic distance, and thus predicted that the timing and duration of all (summer and winter) migrations varied among individual flamingos. The next best model (Akaike weight 0.30) accounted for variation in the timing and asymptotic distance of all (summer and winter) migrations, but no variation in the duration of all migrations.

Migration parameters

Annual migration parameters of fixed effects extracted from the most parsimonious nlme model are presented in Table 4. Mean annual asymptotic distance was 1159.5 km (1069.4–1296.3 km). The midpoint of annual summer migration was day 103.0 (87.1–115.1), i.e. 23 February (8 February–8 March), while the midpoint of winter migration was day 248.5 (229.5–282.1), i.e. 19 July (30 June–22 August). The mean annual duration was 1.6 (1.5–1.8) days and 2.0 (1.1–2.8) days for summer and winter migrations, respectively.

Discussion

In this study we presented evidence of migratory and mixed-migratory movements in southern African lesser flamingos. This study was the first to track lesser flamingos via satellite telemetry from capture sites in South Africa, however southern African lesser flamingos have formed a part of one previous tracking study; McCulloch et al. (2003) tracked a smaller sample of adults captured in the Makgadikgadi Pans. Many previous bird tracking studies have demonstrated more extensive movements of dispersing fledglings compared to regular, home range-restricted movements of adult birds (Newton 2010, Péron and Grémillet 2013). Migration in long-lived species is, to some extent, genetically programmed (Newton 2010), thus juveniles can usually find their own way upon their first trip. Lesser flamingos seem to fly in groups (Ogilvie and Ogilvie 1986) so there may also be some element of social learning from conspecifics. Assuming these naïve juveniles followed adults on their initial dispersal flights, it is probable that we have not recorded all adult movement corridors, particularly heading west from Kamfers Dam to the west coast of South Africa and Namibia. However, barring the extensive movement of FLAM02 to Madagascar, the coverage of movements made by adult flamingos in this study closely matches that of the flamingos tracked more than a decade ago by McCulloch et al. (2003), adding further support to our hypothesis of regular, known migration routes.

The Euclidian distance between Kamfers Dam and the northern part of Sua Pan most commonly visited by the satellite-tagged lesser flamingos (Nata Sanctuary) is 930 km, thus the NSD asymptote equalling 1 000 000 km^2 is well supported by a direct, purposeful movement between these two waterbodies, without much longitudinal variation in the routes flown. The first capture site, Delareyville and

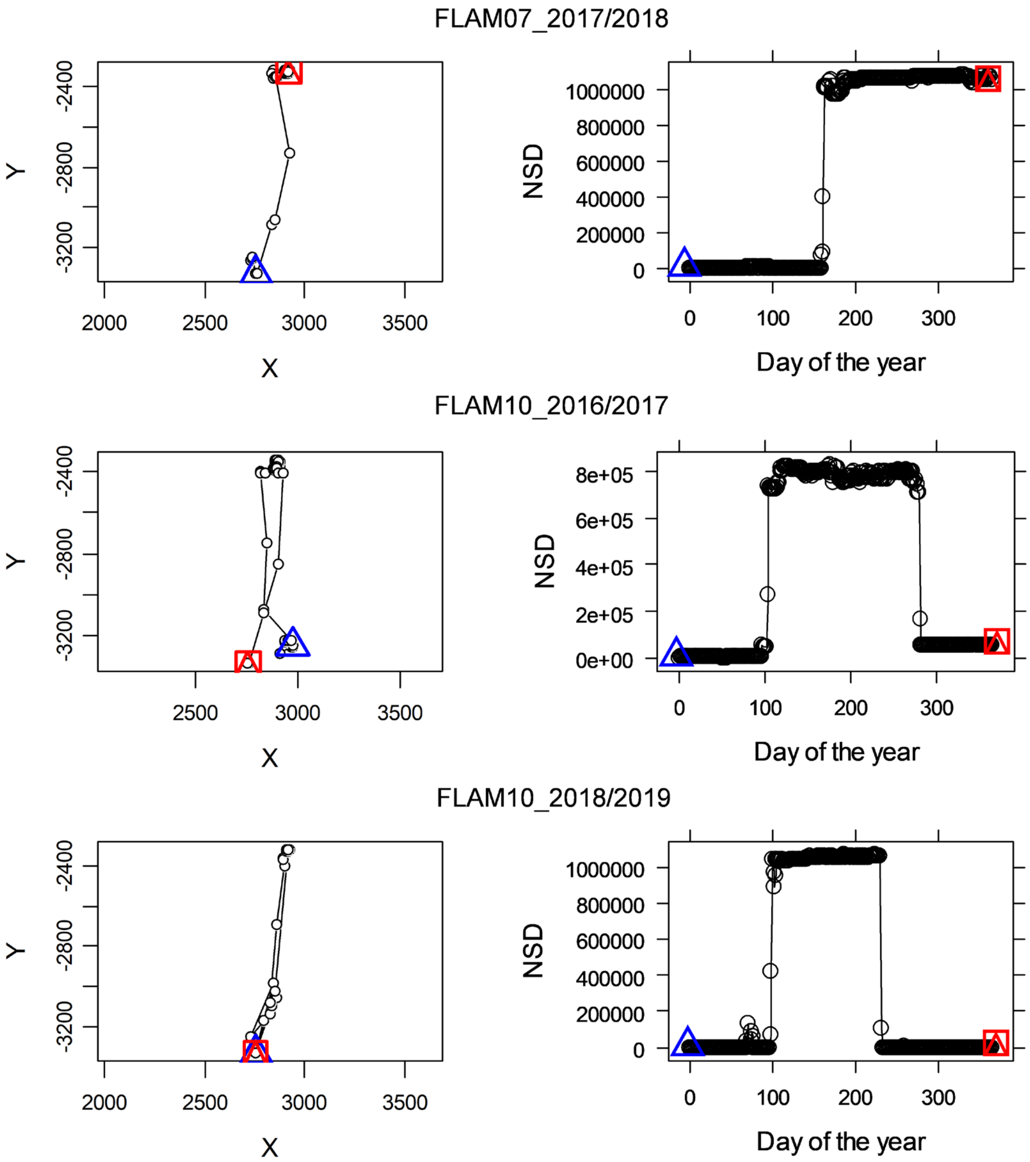

Figure 4. Examples of trajectories (left) and corresponding time series of net squared displacement (right) illustrating dispersal (top), mixed migratory (middle) and migratory (bottom) movement patterns from the annual trajectories of selected lesser flamingos. Blue triangles and red squares represent starting locations on day 1 and end locations on day 365, respectively.

Table 3. Candidate nonlinear mixed effects models describing lesser flamingo migrations. 'Distance' refers to the model asymptote, in kilometres from the starting location. 'Timing' refers to the date in days since the start of the annual trajectory (13 November) of the midpoint of migrations, while 'duration' corresponds to half of the time in days spent migrating. AIC = Akaike's information criterion, LogLik = Log likelihood, ΔAIC = delta AIC, ω = AIC weight, CC = Concordance correlation coefficient.

No.	Model	AIC	logLik	ΔAIC	ω	CC
1	No variation in distance of (all) migrations	2967.34	−1467.67	0.00	0.62	0.80
2	No variation in the duration of (all) migrations	2968.79	−1472.40	1.45	0.30	0.78
3	No variation in the timing and duration of summer migrations	2971.50	−1473.75	4.16	0.07	0.78
4	No variation in the duration of summer migrations	2979.49	−1473.75	12.15	0.001	0.78
5	No variation in distance of (all) migrations, and the timing and duration of summer migration	3005.22	−1490.61	37.88	<0.000	0.78
6	No variation in the distance of (all) migrations and the timing of summer migration	3005.29	−1490.64	37.95	<0.000	0.77

Table 4. Migration parameters for fixed effects from the most parsimonious nonlinear mixed effects model describing lesser flamingo migrations over three years. Distance refers to the model asymptote, in kilometres from the starting location, 'timing' refers to the date, in days since the start of the annual trajectory (13 November) of the midpoint of migrations, while 'duration' corresponds to half of the time in days spent migrating.

	2016/2017		2017/2018		2018/2019	
Migration parameters:	coeff	SE	coeff	SE	coeff	SE
Distance (km)	1 296.25	106.72	1 112.88	36.66	1 069.41	24.96
Timing of summer migration (days since start)	115.12 (08 Mar)	2.71	106.64 (27 Feb)	2.70	87.14 (08 Feb)	1.70
Timing of winter migration (days since start)	229.48 (30 Jun)	5.56	282.11 (22 Aug)	0.61	233.86 (04 Jul)	1.99
Duration of summer migration (days)	1.59	0.18	1.76	2.32	1.54	0.14
Duration of winter migration (days)	2.78	0.29	1.10	0.53	2.25	0.16

the series of pans in the vicinity, including Baberspan and Leeupan, represent the only regular stop on route between Kamfers Dam and Sua Pan. This result again supports the previous findings of McCulloch et al. (2003) and Amat et al. (2005), who highlighted the importance of smaller wetlands as stopover sites between waterbodies supporting major flamingo populations.

The previous paradigm of nomadism as a major movement strategy in lesser flamingos should be reconsidered given our results, as it was the least frequently selected movement type from a well published and frequently practiced modelling procedure using NSD. Results from the nonlinear mixed effects models do, however, caution against population-level conclusions because of individual differences in the timing and duration of migration movements. These individual differences were not, however, found for all fixed effects, e.g. migration distance (NSD asymptote). Our interpretation of these results is that: 1) flamingos migrate between a 'northern inland range' in Botswana/Namibia and a 'southern inland range' in South Africa, with Kamfers Dam and Sua Pan being the most important waterbodies in these two areas, 2) there are individual differences in the timing of migrations, although the lesser flamingos generally conduct their northerly movement in summer and then return in winter and 3) most, but not all lesser flamingos migrate every year. The lesser flamingos of inland southern Africa may thus be partial migrants and not true nomads.

As with previous tracking studies, we were unable to confirm the much-debated connectedness of the southern and East African populations by means of satellite tracking in this study. However, given the present but infrequent gene flow of a few individuals per generation (Zaccara et al. 2011, Parasharya et al. 2015), it is likely that some, but not regular nomadic behaviour exists to facilitate the connection through wandering individuals. It is likely that future tracking studies will also fail to capture these movements without a significantly larger sample, thus the genetic evidence presented by the above authors should be considered sufficient unless a considerable financial investment is made toward a more substantial tracking effort. We believe, however, that we have captured the general and regular movement patterns of adult lesser flamingos of the inland southern African population, supporting and building on the previous study by McCulloch et al. (2003). We were unable to obtain data about breeding events at Sua Pan and Etosha Pan for our period of study and believe that such information would be valuable in confirming migration in the classical sense of movements between a breeding and non-breeding range. Breeding events have recently been recorded for lesser flamingos at Kamfers Dam after a gap of some years following the initial successful use of the artificial island reported by Anderson (2008). Whether the continued use of Kamfers Dam as a breeding location will result in shifts in regional movement patterns remains unclear and would be of interest for future studies.

The contribution and potential application of these data are clear regarding power line mitigation. This paper is the first output of a larger project investigating the movement ecology of lesser flamingos and its implications for mitigation measures aimed at reducing power line collisions in southern Africa. While power line collisions have not been a specific focus of this paper, the classification of lesser flamingo movements as migratory (and mixed migratory) affects the proactive mitigation sensitivity maps for distribution and transmission overhead power lines (Pretorius and Hoogstad 2016). Migratory behaviour assumes regular routes between well-known areas of frequent use, and that these routes vary little over space and time. When and where birds may be exposed to the threat of power line collision therefore becomes more predictable. In the case of southern African lesser flamingos, a regular migratory pattern has emerged, and the migratory route has been mapped. The timing of migration varies between individuals, but population-level movements have revealed a seasonal trend. Birds migrating north to Sua Pan from Kamfers Dam do so via stopover sites such as Baberspan near Delareyville. From there they conduct non-stop directed flights within a narrow corridor of movement, spanning 90 km at its widest point.

The identification of the most important waterbodies for lesser flamingos, and the routes connecting them, allows for better informed conservation interventions such as the implementation of power line mitigation measures. Moreover, using GPS tracking technology in conjunction to remote sensing links finer-scale patterns of habitat use with broader-scale movement types, allowing for accurate spatial mapping of potential flamingo occurrence according to both resource availability and the predictability of movements (Pretorius and Leeuwner 2019). A repeat of the analytical methods employed in this study at different spatial and temporal scales may reveal that different movement patterns become more likely given, 1) the spatial scale-dependent connectedness of resources and 2) the temporal scale-dependent detectability of irregular, nomadic movements.

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