

RESEARCH ARTICLE

Functional Ecology



Landscape-dependent time versus energy optimizations in pelicans migrating through a large ecological barrier

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Abstract

1. During migration, birds are often forced to cross ecological barriers, facing challenges due to scarcity of resources and suitable habitats. While crossing such barriers, birds are expected to adjust their behaviour to reduce time, energy expenditure and associated risks.
2. We studied the crossing of the Sahara Desert by the Great White Pelican (*Pelecanus onocrotalus*), a large wetland-specialist. We focused on decisions made by migrating pelicans along different parts of the southbound autumn migration, their response to local environmental conditions and the implications for time and energy optimizations. We compared the observed pelicans' migration routes with simulated 'direct-pass' (shortest, mostly across the desert) and 'corridor-pass' (along the Nile River) routes, and used GPS, body acceleration and atmospheric modelling to compare flight behaviour along the Nile River versus the desert.
3. The observed route was significantly shorter and faster than the simulated corridor-pass route and not significantly different from the simulated direct-pass one. Daily flights over the desert were longer than along the Nile River, with flying time extending to late hours of the day despite unfavourable atmospheric conditions for soaring-gliding flight. Moreover, the pelicans' behavioural response to atmospheric conditions changed according to the landscape over which they flew. Overall, the pelicans showed stronger behavioural adjustments to atmospheric conditions over the desert than along the Nile River.
4. Our findings suggest that migrating pelicans primarily acted as time minimizers while crossing the Sahara Desert, whereas energetic optimization was only considered when it did not substantially compromise time optimization. The pelicans took the almost shortest possible route, only following the Nile River along its south-oriented parts, and frequently staged overnight in the desert far from water, despite being large, wet-habitat specialists. Correspondingly, their behavioural response to atmospheric conditions changed according to the landscape over which they were flying, switching between time (over the desert) and energy (over the Nile River) optimization strategies. Our results suggest that the interaction between landscape and atmospheric conditions depict a flexible, yet primarily time-dominated, migration optimization strategy.

KEYWORDS

animal behaviour, movement ecology, Nile River, pelican, Sahara Desert

1 | INTRODUCTION

Seasonal migration – a widespread phenomenon characterizing many animals – can critically affect individual fitness and population dynamics (Alerstam, Hedenström, & Åkesson, 2003). During seasonal migration, individuals usually undertake a directional, persistent, round-trip journey across a much greater spatial scale compared to their movements in the breeding grounds, passing through large areas that can vary substantially in their environmental conditions (Alerstam et al., 2003; Bauer & Høye, 2014). Migrating individuals are assumed to gain fitness benefits compared to non-migrating ones by maximizing resource availability and minimizing exposure to harsh conditions, both of which vary in a predictable manner across seasons (Alerstam et al., 2003; Shaw & Couzin, 2013). Yet, while successful migration could increase fitness, migrating animals need to cope with many challenges and uncertainties during these journeys, such as ecological barriers that impede movement and various other environmental hazards (Alerstam & Lindström, 1990; Weber & Hedenström, 2000).

Migrating birds are therefore required to make decisions such as which route to take, where and for how long to stop, and how fast to fly (Alerstam, 2001; Horvitz et al., 2014; Weber, Fransson, & Houston, 1999). Over the last three decades, studies examining this decision-making process have been placed in the context of optimal migration theory, which assumes that migrating birds consider three primary factors: their energy budget, the time spent on migration and the associated risks (Alerstam, 2011; Alerstam & Lindström, 1990). Because these factors might contradict each other (but see Harel et al., 2016), optimal bird migration studies have emphasized common trade-offs between these components. For example, migrating birds often face a choice between migratory routes that differ in their weather conditions, food availability, predation risk or other characteristics (Alerstam, 2001). Such differences are pronounced where the breeding and wintering grounds are separated by large ecological barriers – geographical regions or features that prevent or restrict movement of individuals due to the scarcity of food and other resources, the prevalence of harsh environmental conditions, and/or the paucity of suitable or safe habitats – such as large seas, oceans or deserts (Alerstam, 2001; Moreau, 1972; Newton, 2008). Ecological barriers affect different species according to specific-species characteristics such as flight abilities, habitat and food requirements, hence birds' behaviour in face of such barriers varies by species; for example, some birds that cross barriers in straight tracks fly continuously (i.e. non-stop flights) while others intermittently (i.e. combining flights and stopovers) (Gill et al., 2009; Klaassen, Alerstam, Carlsson, Fox, & Lindström, 2011; Schmaljohann, Liechti, & Bruderer, 2007). Migrating birds that cross ecological barriers usually optimize time (i.e. select the fastest route), at the cost of high-energy expenditure and higher mortality risk due to lack of food, exposure to environmental hazards or scarcity of suitable staging habitats (Alerstam, 2001; Strandberg, Klaassen, Hake, & Alerstam, 2010).

Optimizations of energy expenditure and migration time can also change according to the environmental conditions encountered

during barrier crossing (Erni, Liechti, & Bruderer, 2005; Horvitz et al., 2014; Liechti, 1995; Liechti, Hedenström, & Ålerstam, 1994). Changes in wind speed and direction, for example, can affect the energy required for flight and the birds' flying speed, rain may delay migration and thermal (rising air columns) conditions affect birds' abilities to soar (Shepard et al., 2013). Shifting from soaring–gliding to flapping flight is estimated to be 3–12 times more energetically expensive than soaring flight (Norberg, 1996; Videler, 2006). Different findings of birds' adjustments to weather conditions suggest that energy and time minimization strategies might be context-dependent (Harel et al., 2016) and could also vary both within and among species and environments (Erni et al., 2005; Panuccio et al., 2010; Rotics et al., 2018; Sapir, Wikelski, McCue, Pinshow, & Nathan, 2010).

We studied route selection strategies and response to environmental conditions encountered by migrating birds while crossing a large ecological barrier, in the context of time and energy optimizations. Specifically, we used GPS and acceleration data to study Great White Pelicans (*Pelecanus onocrotalus*) migrating over the eastern part of the Sahara Desert's 1,500–2,000 km ecological barrier. In the eastern part of the Sahara Desert, pelicans have the option of following the Nile River during major parts of their migration, a more suitable landscape especially for these large wetland specialists that are adapted to roost and protect themselves in water and may possibly feed in the Nile River. Therefore, the Nile River might act as a corridor for crossing major parts of the long and otherwise inhospitable barrier of the Sahara Desert (Newton, 2008). We hypothesized that pelicans' route and flight characteristics (i.e. flight speed, flight duration and flight mode) when crossing the Sahara Desert would be shaped by energy optimization considerations due to their large body size, long migration distance and restricted suitable habitats along the route (Alerstam & Lindström, 1990). To test this, we first compared the observed pelicans' route with two possible (simulated) routes, suggesting energy or time optimization strategies. Then, we compared the pelicans' flight behaviour between flight segments over the desert and along the Nile River and examined the effect of meteorological characteristics (i.e. wind and thermal condition) on this behaviour. Given our hypothesis, we predicted that pelicans will migrate along the Nile Valley where they can stage in their favoured habitat to safely rest and feed, despite the fact that such route will take longer to complete than the fastest possible one. Regarding flight behaviour, we predicted that the pelicans will reduce energy expenditure by flying more slowly in less suitable atmospheric conditions and by limiting the use of flapping flight, changing their behaviour according to atmospheric conditions regardless of the landscape over which they migrate.

2 | MATERIALS AND METHODS

The Great White Pelican is the heaviest long-range migrant in the Western Palearctic, weighing between 5.5 and 15 kg, with a wing span of 226–360 cm (Elliot et al., 2017). Great White Pelicans' diet is based almost entirely on fish caught while swimming; they feed

mostly in shallow freshwater in inland lakes, ponds, wide rivers and deltas (Elliot et al., 2017; Shmueli, Izhaki, Arieli, & Arad, 2000). They rarely (if ever) forage in saline sea such as the Gulf of Suez (Elliot et al., 2017), and take a detour through the Middle East rather than directly crossing the Mediterranean Sea during migration. They are social, breeding in large colonies, often feed in synchronous flocks and seldom fly alone (Elliot et al., 2017; Hatzilacou, 1996). Furthermore, during migration, they fly and roost in groups of up to 30,000 individuals, gliding in line formations ('V' shaped) (Elliot et al., 2017; Shirihi, 1996).

Pelicans were trapped in Israel during autumn migration and harnessed (using a 'backpack' configuration) with data loggers which collected GPS locations and acceleration data, the later used to distinguish flapping from gliding flight modes (Nathan et al., 2012; Resheff, Rotics, Harel, Spiegel, & Nathan, 2014); tag plus harness constituted 1.5%–2.5% of the bird's body mass (see Appendix S1). Wind velocity and turbulence kinetic energy (TKE), a proxy for convective updraft intensity, were obtained using numerical atmospheric simulations from the Regional Atmospheric Modelling System (Appendix S2).

Migration routes and stopover sites were identified by mapping the GPS locations of every individual. Migration onset latitude was defined as the northernmost latitude after which all daily flights were directional towards the south; the end of migration and beginning of the wintering area were defined as south of the latitude in which directional flights ceased. Routes were compared between pelicans, and segments in which most pelicans' routes overlapped were noted. Mean route was measured by averaging all locations for every 0.5 latitude degrees except for locations of two pelicans at the beginning and end of migration which were substantially different (see Section 3). The number of nights that the pelicans spent at each stopover was counted and the distance from the Nile River was measured to distinguish stopovers at the suitable habitat from stopovers at the desert (including a few observed stops at the Gulf of Suez, a non-suitable habitat due to its salinity). A daily migration flight was defined as a continuous flying period in which a pelican's north to south displacement was at least 50 km. During all daily migration flights, the pelicans flew non-stop between their morning take-off and their landing for night roost.

We compared the average observed pelican migration route to two hypothetical routes representing alternative migration strategies: a straight (shortest) one which means migration mostly over the Sahara Desert, denoted as 'direct-pass' route, and a tortuous one that maximizes migration along the Nile River, denoted as 'corridor-pass' route. These two alternative routes, assumed to represent time versus energy optimizations, respectively, were generated by stochastic simulations. The number of daily migration flights was summed for every pelican which had data throughout the migration route and compared to the number of days it would take a pelican to migrate using these two different hypothetical routes (Figure 1). For each route in each hypothetical scenario, the start and end locations were the same as the real (observed) route, and the simulated



FIGURE 1 Theoretical corridor-pass (Nile River, green) and direct-pass (orthodrome, red) routes and the observed migration routes taken by the pelicans (black). Real routes are semi-transparent thus darker black mean that more pelicans took that route. Migration start and end points are the northernmost and southernmost meeting points of the corridor-pass and direct-pass routes

pelicans could not switch between the two route types but maintained the same route type until the end of their migration. For the simulated direct-pass route, a straight line (orthodrome) was set, with one exception: to avoid unrealistic flights including 200 km over the Red Sea, the route was forced to cross the Gulf of Suez at its easternmost part (Figure 1). For the corridor-pass route, a straight route to the Nile River was first set; then, the route continued by following the river. The number of days required to cross the Sahara Desert was estimated by 10,000 stochastic simulations for each route type. Stochasticity was implemented by randomly choosing a daily distance out of the measured daily distances, then summing daily distances until the modelled pelican reached or crossed the end location. Distributions of the number of flight days required to cross the Sahara Desert were compared between the two route types, and each was also compared to the observed distribution of flight days, using a two-sample Kolmogorov–Smirnov (KS) test.

To test for differences in the pelicans' behaviour when flying over different landscapes, daily migration flights were divided into hourly segments, starting at the first location. This meant that the last segment before landing was always shorter than 1 hr (e.g. a 5 hr and 40 min daily migration flight would have five segments of 1 hr and one segment of 40 min), thus last segments that were shorter than 30 min were excluded from the analysis. Hourly migration flight segments were divided into two landscape groups: (a) Nile – a radius of 30 km around the Nile River's centre and (b) Desert – all other parts, starting at latitude 31.25N. Landscape classification was based on

the changing width of the Nile River along the pelicans migration route, and according to the birds distance from the river when flying along it, and was confirmed with a sensitivity analysis testing different thresholds to define the Nile River landscape (Appendix S3). Segments that had GPS locations over more than one landscape were categorized by the higher number of locations. Complete daily migration flights were categorized as Nile or Desert flights based on the landscape that had the higher number of hourly segments throughout the day. Differences between daily migration flights in total flight time, take-off time (hours after sunrise) and landing time (hours before sunset) were tested using a generalized linear mixed effects model (GLMM) with a gamma distribution (data were not normally distributed), log link function and individual as a random factor. To account for flights that ended earlier because the pelicans reached the Gulf of Suez (see Section 3), differences in daily flight characteristics were tested with and without these flights. To better understand the implications of changes in take-off time, landing time or total flight time on the pelicans flights, atmospheric conditions and flight characteristics (averaged per hour) were plotted against time before sunset.

To understand the energetic implications of flying over the different landscapes, key atmospheric conditions (TKE, tail and crosswinds) and flight characteristics (altitude, flap rate, ground and air speed) during hourly segments were compared between the landscapes. Differences in atmospheric conditions between the Nile and the Desert were tested using a GLMM with a gamma distribution and a log link function for TKE and crosswind and a linear mixed effect model (LMM) for tailwind; all atmospheric condition models included hour as a random factor. The effect of atmospheric conditions and landscape (Nile or Desert) on flight characteristics was tested using GLMMs with a gamma distribution and a log link function for altitude and air speed and a binomial distribution and a logit link function for flap rate; an LMM was used to examine ground speed. These models included hour and individual as random factors and were ranked using a corrected AIC (AICc) score for all possible variable subsets including the atmospheric conditions, landscape and interactions between landscape and each atmospheric condition. Models that had approximately the same weight ($\Delta AICc < 2$, Anderson, 2008; Burnham & Anderson, 2002) were averaged using the 'MuMin' package in R (Barton, 2012).

Sorting and analysis of the data were performed using MATLAB® R2013b (MathWorks®), and statistical analyses were done using R 3.4.2 (R foundation for statistical computing). MATLAB and Google Earth® Pro 7.1.2.2041 were used to map and view GPS tracks. Unless otherwise noted, results are reported by their mean $\pm$ SD.

3 | RESULTS

Migration routes were mapped for 26 pelicans between latitudes 32.1° and 16.7°N. Of these birds, 22 were trapped during the 2 years of study and four additional birds harnessed with transmitters during 2010 and 2012, using the same methods. The

migration routes of all tagged pelicans were similar, especially when crossing the Gulf of Suez and along the Nile River, though one bird made a long stopover at the Nile Delta west of the main route and another ended its migration east of the other pelicans' end location (Figure 1). The pelicans migrated 3 days over the desert before reaching the Nile River, and then followed the river south until it bends west, where they crossed the desert again. When flying along the Nile River, the pelicans often drifted up to 30 km from its centre, hence we set 30 km as a threshold for the corridor-pass route. A total of 119 daily migration flights from 19 different individuals were used for flight characteristics analyses, with 6.4 ± 3.2 migration days per individual pelican, consisting of 4,098 GPS locations and 23,970 acceleration measurements in total. Complete migratory routes were obtained for 18 pelicans; eight of them crossed the Sahara Desert without making stopovers longer than a single night, other birds spending 2–58 nights at the same stopover. Of the 102 stopovers along the migration, 53 were more than 30 km away from the Nile River, and all stopovers longer than a single night occurred on the Nile River. Upon reaching the Gulf of Suez, 13 of the 18 pelicans stopped their daily flight <10 km from the coast ($n = 9$) or on water ($n = 4$), flying an average of 1 hr less than other flight days over the desert and about 35 min less than all other flight days (6.33 ± 1.33 compared to 7.4 ± 1.14 and 6.94 ± 1.63 hr, respectively). The five pelicans that did cross the Gulf of Suez upon arrival did not arrive there earlier than the other 13 birds and did not start their daily flight closer to the Gulf. GPS intervals lower than or equal to 25 min were obtained for 12 pelicans from migration onset to their first encounter with the Nile River and for nine pelicans throughout the migration. The mean migration route flight distance was 1,773 km and the pelicans reached the Nile River after 645 km, spending 48% of their route less than 30 km from the river.

The simulated corridor-pass route was measured at 2,600 km and reached the Nile River after 460 km while the simulated direct-pass route was measured at 1,744 km and reached the Nile River after 1,430 km, following the river for 60 km before leaving it (Figure 1). The observed migration route lasted 7.93 ± 1.28 flight days (ranging 6–10, $n = 18$), while the simulated routes lasted 7.82 ± 1.06 and 11.4 ± 1.27 days (ranging 4–12 and 8–17) for the direct- and corridor-pass routes, respectively (Figure 2). Because the simulated daily migration distance was (randomly) taken from the empirical tracking data in both route types, the overall migration speed was very similar for the two route types (227.2 ± 31.49 and 231.1 ± 26.3 km/day, respectively), emphasizing our focus on decision-making regarding route selection rather than daily migration speed. Despite this clear tendency of the (real) pelicans to migrate as fast as the direct-pass simulated ones, they spent large parts of their migration along the Nile River, while the direct-pass route only crosses it once (at $\sim 18.9^\circ$ N). This was accomplished by flying along the Nile River mostly (or only) along its fairly straight north–south sections (easternmost longitude $\sim 33.9^\circ$ E) and taking shortcuts over the desert to avoid the two large western bends (westernmost longitude $\sim 30.5^\circ$ E; Figure 1).

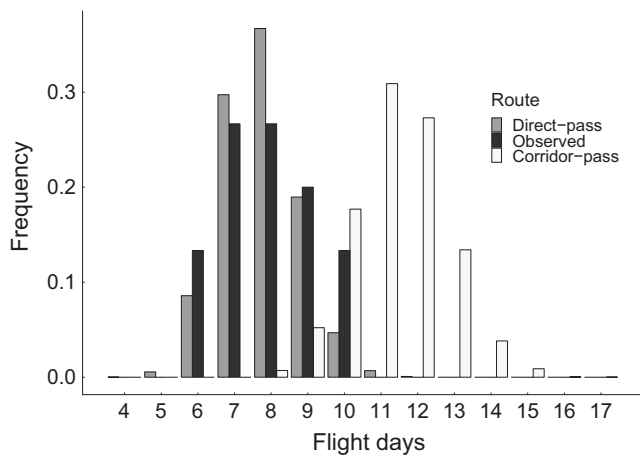


FIGURE 2 Number of flight days needed to cross the Sahara Desert for simulated pelicans taking a direct- or corridor-pass route, and for GPS-tracked pelicans denoted as 'observed' (see Figure 1 for routes)

A significant difference was found between the distributions of flight days of the two simulated routes, and between the simulated corridor-pass and the observed routes (KS; $D = 0.89, 0.81$, respectively, $p < .001$ for both), but no difference was found between the simulated direct-pass and the observed routes (KS; $D = 0.089$, $p = .99$, Figure 2). Landing time was significantly later when landing in the desert compared to along the Nile River, both including ($n = 49, 57$, respectively) and excluding ($n = 37, 57$, respectively) flights that ended at the Gulf of Suez (Table 1). A significant increase in daily hours flown for flights over the desert was found only when disregarding flights that ended at the Gulf of Suez; take-off time was not significantly different in either case (Table 1). Tailwind showed a general decrease throughout the day while crosswind showed the opposite trend and TKE was at a minimum at the end of the day; flap rate was highest at the start and end of the day and ground and air

speed showed a general increase throughout the day with a small decrease at sunset (Figure 3).

For the analysis of landscape effects, a total of 707 one-hour segments ($n = 299, 408$ for Desert and Nile, respectively) of 119 daily migration flights from 19 pelicans were used. Of the nine pelicans with <30 min interval GPS data throughout migration, $54 \pm 9.3\%$ of the segments were over the Nile River. No difference was found in TKE, tail or crosswind between the landscapes (Table 1). The effects of landscape and atmospheric conditions on ground and air speed, altitude and flap rate had 2, 2, 3 and 2 models with $\Delta AICc < 2$, respectively (Appendix Table S1). Model averaging of these models shows that flying along the Nile River had a significant negative effect on flap rate and a significant positive effect on all other flight characteristics (Table 2). Crosswind had a significant positive effect on flap rate and ground and air speed; tailwind had a significant positive effect on ground speed and altitude had a significant negative effect on air speed and flap rate; TKE had a significant positive effect on altitude and a significant negative effect on flap rate (Table 2). The interaction between flying along the Nile River and crosswind had a significant negative effect on flap rate and ground and air speed; the interaction between flying along the Nile River and tailwind had a significant positive effect on flap rate; the interaction between flying along the Nile River and TKE had a significant negative effect on altitude (Table 2, Figure 4).

4 | DISCUSSION

Migrating Great White Pelicans exhibited both time- and energy-optimization strategies when crossing the Sahara Desert in a flexible, yet asymmetric, time-dominated manner. This is reflected first by their tendency to follow the Nile River Corridor only along its north-south sections, while avoiding migration along the Nile in its two large bends to the west (Figure 1). In these sections,

TABLE 1 Comparisons of mean atmospheric conditions (hourly segments) and daily flight characteristics between Desert and Nile flights

Variable	Nile	Desert	t wald	p	df
Turbulent kinetic energy (m/s^2)	1.19	1.34	-1.27	.205	703
Tailwind (m/s)	2.69	2.88	-0.66	.507	694
Crosswind (m/s)	3.22	2.95	1.7	.09	703
Flight hours (hr)	6.64	7.14	-1.45	.148	103
Take-off time (hr after sunrise)	3.26	3.30	-0.16	.870	103
Landing time (hr before sunset)	1.19	0.570	2.55	.011*	103
Without flights that ended at the Gulf of Suez					
Flight hours (hr)	6.64	7.40	-2.09	.036*	91
Take-off time (hr after sunrise)	3.32	3.26	-0.03	.976	91
Landing time (hr before sunset)	1.19	0.37	3.36	<.001*	91

*Significantly different.

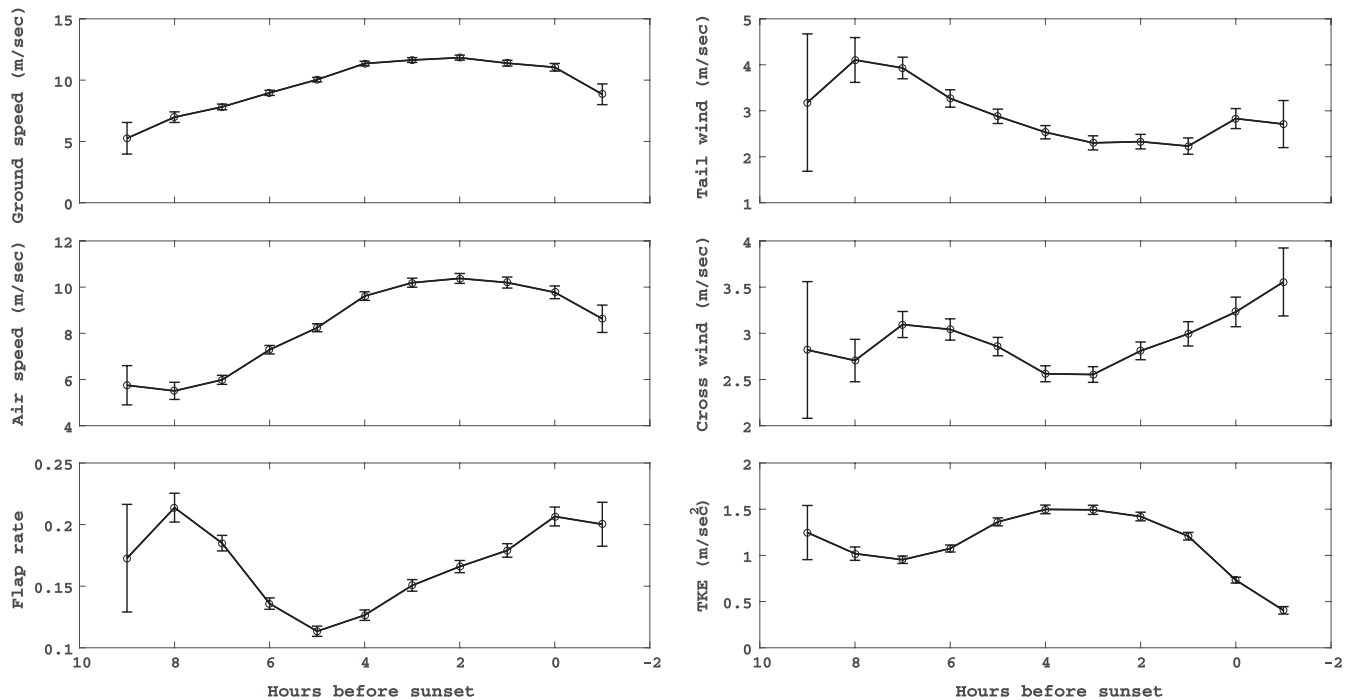


FIGURE 3 Hourly mean values of different flight characteristics (left) and atmospheric conditions (right). Error bars represent $\pm$ standard error

	LS	CW	TW	TKE	LS:CW	LS:TW	LS:TKE
Ground speed	2.64** +	3.7*** +	14*** +	NA	2.69** -	0.63 -	NA
Air speed	2.76** +	12.4*** +	8.44*** -	NA	2.63** -	0.324 -	NA
Altitude	3.53*** +	0.901 +	2.33* +	4.67*** +	NA	1.75 -	3.47*** -
Flap rate	3.56*** -	5*** +	7.63*** -	2.54* -	2.88** -	4.91*** +	1.39 -

TABLE 2 Effects of atmospheric conditions and landscape on flight characteristics

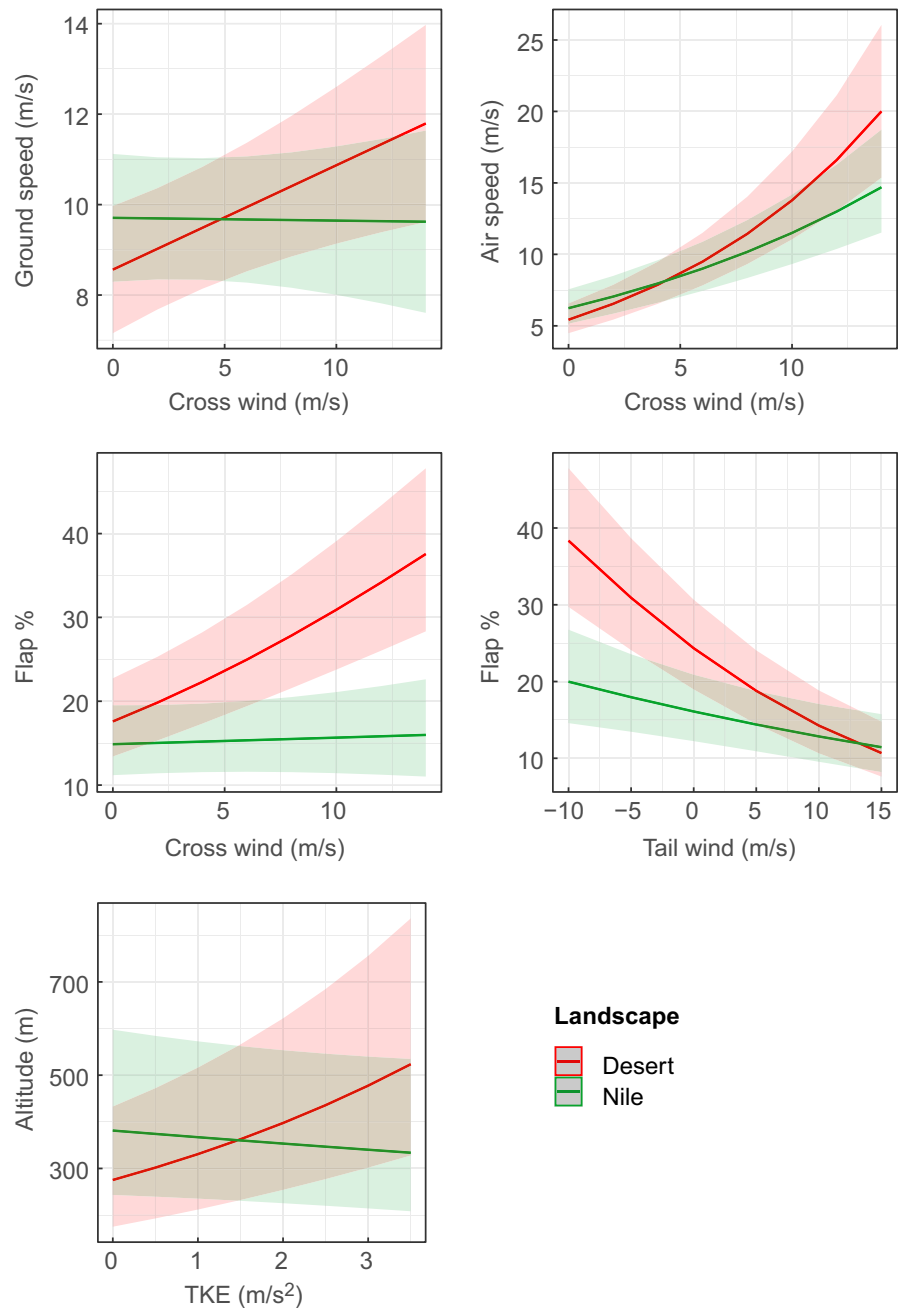
Note: For every predictor, the Z wald is given and p values are denoted as: *.01 < p < .05, **.001 < p < .01, *** p < .001. A+ or - symbol represents whether the predictor's effect was positive or negative; for the landscape (LS) effect, the symbol indicates whether the flight characteristic increased (+) or decreased (-) while migrating over the Nile River compared to the desert. NA indicates that the predictor was not present in any of the best models (Appendix S1). Abbreviations for predictors: LS, landscape, CW, crosswind, TW, tailwind, TKE, turbulence kinetic energy. Interactions are marked with a colon (':').

the pelicans departed from the Nile Corridor and took a shortcut of 300–400 km across the desert. This is also reflected by the comparison of their observed versus simulated migration routes across the Sahara Desert: observed migration duration and route length were nearly the same as the simulated direct-pass route that represent time optimization, but 3.5 days and 830 km shorter (~70%) than the simulated corridor-pass route along the Nile River that represent energy optimization. Furthermore, their response to atmospheric conditions in these two landscape types suggests time- and energy-optimization, respectively, despite similarity in atmospheric conditions in these two contrasting landscapes. This implies that Great White Pelicans migrating 1,744 km to cross the

Sahara Desert act primarily as time optimizers, switching to energy optimization only when this strategy does not compromise time optimization in a substantial manner. This finding negates our hypothesized energy-optimized migration, excepted for the heaviest long-distance avian migrant of the Western Palearctic which is also an obligatory wet-habitat specialist.

This flexible yet time-dominated migration optimization strategy is manifested in a more in-depth exploration of their chosen route. The pelicans optimized time by making two key decisions while crossing the Sahara Desert: (a) to cross the Gulf of Suez and to continue SSW to the Nile, and (b) to make a shortcut across the desert (rather than follow the Nile's western bend) in northern Sudan.

FIGURE 4 Effects of atmospheric conditions on flight characteristics, categorized by the effect over the desert and the effect along the Nile River, as calculated by the mixed effects models (Table 2)



Considering the average daily travel distance, crossing the Gulf of Suez shortened migration by 220 km compared to the simulated 'corridor-pass' route, hence saved one migratory day. Similarly, by crossing the desert later in northern Sudan, the pelicans migrated 500 km and 2 days less than the simulated 'corridor-pass' birds. Remarkably, their 858 km southward migration along the Nile, comprising nearly half (48%) of the total cross-Sahara migration journey, resulted in extending the total route length by only 29 km (1.6%) and migration duration by only a few hours compared to the simulated direct-pass pelicans, predicted to migrate only 60 km (3% of the total route) over the Nile. Similarly, while flying along the Nile River, pelicans' daily flights were shorter and they spent less energy during these days, but their ground and air speeds were higher than

over the desert, resulting in no significant time loss. The total route length, flight speed and flight energetics indicate that the pelicans switched to energy optimization over the Nile River without compromising time optimization. The pelicans also switched to energy optimization upon arrival to the Gulf of Suez, delaying their migration on this occasion, but only by a few hours. Although the Gulf of Suez is <30 km wide at the crossing location, the pelicans' decision not to cross it is probably because thermals are weak over water (Pennycuik, 2008), thus they avoided expending extra energy by delaying their migration.

The finding that over the desert daily migration flights lasted longer (excluding flight days that ended at the Gulf of Suez) and ended closer to sunset compared to flights over the Nile River cannot be

explained by differences in atmospheric conditions (Table 1). While flying for more hours per day could shorten the total number of migration days, thermal (TKE) and wind conditions are less suitable for soaring–gliding flight closer to sunset (Figure 3), thus landing closer to sunset entails higher energy expenditure due to elevated flapping rate. This strategy is predicted (and was documented) for smaller soaring birds when food is not available at the next stopover (Stark & Liechti, 1993; Vansteelant et al., 2015). However, this is not expected for large soaring birds such as pelicans, due to higher energetic costs of switching from soaring to flapping flight (Hedenström, 1993). Interestingly, take-off time did not differ between landscapes, perhaps because taking-off entails high-energy expenditure, especially for large birds, thus pelicans took-off only when atmospheric conditions were sufficiently suitable for soaring flight. At the end of the day, migrating pelicans are already airborne, and hence can soar and glide as long as thermals are still available (Pennycuik, 2008). Such prolonged flights imply that pelicans compromise energy optimization while acting as time optimizers over the desert.

Although flapping flight is energetically expensive, especially for large species (Hedenström, 1993; Rayner, 1988; Spaar, 1997), birds tend to increase their flap rate in less suitable atmospheric conditions to reduce drift (Panuccio et al., 2010; Vansteelant et al., 2015) or to increase speed (Rotics et al., 2016; Spaar, 1997). Furthermore, drift induced by crosswinds can also be reduced by flying faster (Harel et al., 2016; Sapir, Horvitz, Dechmann, Fahr, & Wikelski, 2014) at the cost of increased energy expenditure (Liechti, 2006; Pennycuik, 2008). Accordingly, we found that pelicans increased their flap rate with stronger crosswinds, weaker tailwinds and weaker thermals (TKE). However, the wind-induced increase in flap rate only occurred over the desert and not along the Nile River, indicating that the pelicans increased their effort to fly faster and to avoid wind drift only over the desert. Air speed also increased with stronger crosswinds over both landscapes, but only over the desert did this lead to higher ground speed, while along the Nile River, ground speed remained constant. The differences in the pelicans' adjustments to changing atmospheric conditions between the landscapes further suggest that they act as time minimizers that (strongly) compromise energy optimization over the desert, while acting as energy optimizers without substantially compromising time optimization over the Nile River Corridor.

Increase in flight altitude is expected to allow birds to fly faster, either because winds are stronger at higher altitudes in case of tailwinds (Liechti, 2006) or because it allows soaring birds to glide at a steeper angle (hence faster) with a lower risk of reaching the ground compared to gliding from a lower altitude (Horvitz et al., 2014). However, due to their high wing loading, pelicans can utilize only relatively strong thermals (Pennycuik, 2008; Shamoun-Baranes, Leshem, Yom-Tov, & Liechti, 2003). Soaring birds likely engage in a rather complex decision-making process regarding the altitude at which they should depart from a thermal (Harel & Nathan, 2018), yet such analysis was not possible in the current study due to the lack of sufficiently long high-resolution GPS tracks. Nevertheless, we found that thermal strength (estimated by TKE) is positively correlated with flight altitude over the desert, but not along the Nile River where

the pelicans kept an almost constant altitude and seemed to refrain from taking advantage of stronger thermals to fly faster. This further implies a time minimization strategy over the desert at the cost of higher energy expenditure, while over the Nile River the pelicans compensated not utilizing the thermals by flying faster.

An important limitation of this study is the lack of consideration of the social behaviour typical of the study species. Great White Pelicans exhibit a strong tendency to remain in social groups during all stages of their life cycle and especially during migratory flights (Elliot et al., 2017; Hatzilacou, 1996). Group feeding can increase energy intake (and shorten feeding time) by effective social feeding (Clark & Mangel, 1986), and group formation flight can reduce energy expenditure, as evident by a 11%–14.5% reduction in heart rate found for Great White Pelicans flying in formation compared to flying alone (Bajec & Heppner, 2009; Weimerskirch, Martin, Clerquin, Alexandre, & Jiraskova, 2001). Currently, with a few exceptions of studies of trained groups of birds (Portugal et al., 2014; Weimerskirch et al., 2001), such social effects are practically impossible to disentangle in studies of migrating birds. In our study, we documented only two occasions in which two tracked birds flew in the same flock and only for 2 or 3 days. In another study on white storks, a six-fold larger tagging effort also yielded relatively few cases of tagged birds flying in the same flock (Rotics et al., 2016). This implies that a very intensive (hence impractical) tagging effort would be required to reveal social interactions among GPS-tracked wild birds in most species (but see Dhanjal-Adams et al., 2018). We also note that our findings do not necessarily reflect the behaviour of pelicans during spring migration or during other periods of the annual cycle as energy and time optimizations can greatly vary across seasons and in different contexts (Harel et al., 2016; Mellone et al., 2014; Zhao et al., 2017). Future studies should also tackle the proposition that time and energy considerations can be moulded through carry-over effects between different parts of the annual cycle (Marra, Cohen, Loss, Rutter, & Tonra, 2015).

The finding that pelicans exhibit different behaviours over different parts of the migration route corresponds to previous results from other soaring birds (Klaassen, Strandberg, Hake, & Alerstam, 2008; Mellone et al., 2014; Vansteelant et al., 2015). Furthermore, our findings on the decisive role of atmospheric conditions in shaping flight characteristics of migrating birds are in general agreement with previous studies of other soaring birds, including other pelican species (Efrat, Harel, Alexandrou, Catsadorakis, & Nathan, 2018; Gutierrez Illan, Wang, Cunningham, & King, 2017). However, our results show how the interaction between landscape and atmospheric conditions modulates migratory optimization considerations, suggesting that the landscape over which birds migrate can affect their migratory behaviour and response to atmospheric conditions, even without landscape-induced changes in the atmospheric conditions. Shmueli et al. (2000) estimated that upon departure from Israel, migrating Great White Pelicans can cover 1,051–1,620 km in 4.8 days, according to fat stores found in pelicans' stomachs during autumn migration stopover in Israel. This 1,051–1,620 km range was calculated for alternative mean daily migration distances of 219 or 338 km/day, the former lies much closer to our data (228 km/day). Shmueli et al.

assumed that migrating pelicans take the shortest route – equivalent to our simulated direct-pass route – to their wintering grounds at the Sudd swamps of southern Sudan, without feeding along the way in the Nile River or elsewhere and without making longer than overnight stops. They noted that although their estimated migration range falls short of the Sudd area, pelicans that overwintered in Israel had a much higher fat load than those that migrated to Africa, and with such a higher fat store they could have migrated 1,600–2,464 km to reach the vicinity of the Sudd area within 7.3 days. Our study shows that all pelicans reached the Nile River long before they reached the Sudd area, after flying 719 km for 3.33 days on average. This implies that the lower bound (1,051–1,620 km) of Shmueli's et al. estimate better reflects the energy constraints of migrating pelicans, suggesting that these birds are forced to refuel at the Nile River to accomplish their cross-Sahara migration. Indeed, some pelicans stopped-over for up to 58 consecutive days on the Nile River, hence feeding there must be possible, at least at some points on their route.

Overall, our study reveals that Great White Pelicans crossing the Sahara Desert engage in both time and energy optimization, as long as the former is not compromised by the latter in a substantial manner, suggesting that time optimization plays a primary role. This conclusion contradicts the predicted energy optimization for such large, wetland specialist species. Importantly, our study divulged frequent shifts among opposing landscape-specific migration strategies, reflecting a plastic response to atmospheric conditions. We thus suggest that migratory optimization strategies are affected not only by the species characteristics and environmental conditions, but also by the landscape over which the species migrates. We call for further integration of movement data and environmental modelling to further improve our understanding of the mechanisms underlying the response of animals to their environments across multiple spatial and temporal scales.

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AUTHORS' CONTRIBUTIONS

R.E., O.H. and R.N. conceived the ideas and designed methodology; R.E. and O.H. collected the data and R.E. analysed the data; R.E. and R.N. led the writing of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data used in this study are stored in Movebank Data Repository <https://doi.org/10.5441/001/1.hs79pk45> (Efrat, Hatzofe, & Nathan, 2019).

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