Timing rather than movement decisions explains age-related differences in wind support for a migratory bird

Cristina Rueda-Uribe [a, *] [iD], Patrik Byholm [b, c] [iD], Ulrik Lötberg [d] [iD], Natalie Isaksson [e] [iD], Martin Beal [a] [iD], Sara Raj Pant [a], Susanne Åkesson [a, *]

[a] Department of Biology, Centre for Animal Movement Research, Lund University, Ecology Building, Lund, Sweden
[b] Novia University of Applied Sciences, Ekenäs, Finland
[c] Organismal and Evolutionary Biology, University of Helsinki, Helsinki, Finland
[d] BirdLife Sweden, Mörbylånga, Sweden
[e] Environmental Research Institute, North Highland College, University of the Highlands and Islands, Thurso, U.K.

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Migratory birds must make complex decisions to use wind to their advantage during flight and increasing flight performance is particularly important while crossing ecological barriers. Age-related differences in how birds deal with wind have suggested experience improves necessary skills in gaining positive wind support. However, differences in wind support between age groups over ecological barriers have rarely been tested, and our understanding of how birds acquire related skills is lacking. We compared wind support achieved by adult and subadult Caspian terns, *Hydroprogne caspia*, during southward and northward crossings of the Sahara Desert by quantifying air-to-groundspeed ratios (AGR). We also tested possible underlying causes of lower subadult wind support in comparison to adults by calculating optimal AGR altitudes and fitting step selection functions in response to wind direction and speed. We found no difference between age groups in autumn, when young were flying with adults, but subadults had lower wind support during their first solo northward crossings. Adults departed northwards from wintering areas earlier in the year and encountered more favourable wind conditions than subadults, yet both age groups made similar movement decisions in relation to wind. Consequently, differences in performance are better explained by timing of passage rather than movement skills. Our findings highlight the influence of wind seasonality over the Sahara on migratory behaviour and raise questions about the evolution and ontogeny of migratory timing in relation to wind patterns and other factors that may determine departure decisions.

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Studies of age-related differences in migratory performance have given insights into how morphological, physiological and behavioural adaptations for migration have a genetic basis but can also depend on learning and improve with age (Åkesson et al., 2021). How animals accomplish complex migratory feats may alter the balance between the costs and benefits of this natural phenomenon (Alerstam & Lindström, 1990), and lower survival in early life stages may be explained by the lower ability of naïve individuals to manage challenging conditions compared to experienced adults (Sergio et al., 2019). For example in migratory birds, to have favourable wind support, defined as the assistance of a bird's

displacement in relation to the ground by moving airflows, individuals must time their departure according to wind conditions (Åkesson & Hedenström, 2000; Erni et al., 2002; Gill et al., 2014; Sjöberg et al., 2015) and make several in-flight decisions related to altitude selection, airspeed, heading and route choice (Åkesson et al., 2016; Åkesson & Hedenström, 2000, 2007; Chapman et al., 2011; Hedenström & Åkesson, 2017; Sjöberg & Nilsson, 2015). Favourable wind support reduces flight costs (Hedenström & Alerstam, 1995) and can substantially increase flight speed (Liechti & Bruderer, 1998). The efficient use of wind support may therefore enable different migratory strategies between seasons, such as achieving the speeds needed to perform fast migrations to return to breeding grounds in spring (Åkesson & Bianco, 2021; Lopez-Ricaurte et al., 2021). Also, wind is correlated with changes in migratory behaviours including daily speed, flight altitude and

* Corresponding authors.
  E-mail addresses: cristinaruedauribe@gmail.com (C. Rueda-Uribe), susanne.akesson@biol.lu.se (S. Åkesson).

hours dedicated to flight (Rueda-Uribe et al., 2022; Shamoun-Baranes et al., 2003). Furthermore, regional wind patterns may shape migratory routes (Vansteelant et al., 2017), even favouring longer but lower cost paths that are possibly selected for (Felicísimo et al., 2008; Kranstauber et al., 2015) particularly while crossing ecological barriers such as the Sahara Desert (Åkesson et al., 2016; Norevik et al., 2020). Ultimately, unfavourable wind support over inhospitable landscapes may directly decrease survival rates (Loonstra et al., 2019) or could possibly have carryover effects (Marra et al., 2015) on reproductive success in the following breeding seasons due to late arrival (McNamara et al., 1998; Kokko, 1999) and lowered body condition (Descamps et al., 2011).

Accumulating evidence has shown age-related differences in how birds use winds during migration. For example, comparisons between age groups and studies tracking individuals at different ages have revealed that adults often deal better with drift than juveniles (Sergio et al., 2014; Thorup et al., 2003). Also, tracking data have shown that young birds take several months to reach the same migration speeds as adults (cf. Lane et al., 2021), suggesting that a learning phase may be necessary to overcome challenging weather and wind conditions (Weimerskirch et al., 2006). However, few studies on migrating birds have compared wind support between age groups (but see Nourani et al., 2020) and none have tested possible underlying mechanisms that lead to age-related differences in wind support, despite the obvious importance of wind for flight performance (Hedenström & Alerstam, 1995; Liechti, 2006) and its possible role as a selective agent in bird migration (Alerstam, 1979; Alerstam et al., 2003).

In this study we analysed GPS tracks of autumn and spring crossings of the Sahara Desert by adult and subadult Caspian terns, *Hydroprogne caspia*. We chose to focus on Sahara crossings because gaining positive wind support may be particularly important for fast, efficient flights over areas with little to no foraging habitat and harsh climatic conditions. The desert is a major ecological barrier for migratory birds that fly between Europe and sub-Saharan Africa (Bairlein, 1988), and previous research has proposed that positive wind support is necessary for migratory birds to successfully fly over such a large expanse of unsuitable habitat (Liechti, 2006). First, we compared the wind support acquired by adults with that of subadults to test whether age differences are relevant for migratory flight performance in relation to wind conditions over ecological barriers. Young Caspian terns born in the Baltic Sea migrate together with adults during their first journey (Byholm et al., 2022; Jozefik, 1969), which occurs in autumn when they fly south to wintering areas in the Iberian Peninsula, Sahel and Nile River Delta (Byholm et al., 2020; Rueda-Uribe et al., 2021; Shiomi et al., 2015). In spring, adults migrate back to the Baltic while young birds stay in wintering areas. Some subadults perform first partial return migrations in their second or third year of life (Kilpi & Saurola, 1984; Rueda-Uribe et al., 2021), departing on average 3 months later than adults (Rueda-Uribe et al., 2021). For these subadults, those spring migrations represent their first solo crossings of the Sahara. Because young migrate with adults in the autumn and likely imitate and receive guidance from adults (Byholm et al., 2022), we predicted that there should be no differences in wind support during southward crossings between age groups. In contrast, if experience plays an important role in gaining positive wind support over this ecological barrier, subadult Caspian terns should have lower wind support than adults in northward crossings because they are migrating without adult guidance for the first time and their experience is limited compared to that of adults. Alternatively, if the skills required for adequate wind support are innate, we expected to find no differences in wind support between age groups for both southward and northward crossings.

We also tested whether differences in flight performance between adults and subadults during the northward crossing of the Sahara were related to inexperienced flight decisions or wind conditions encountered during the timing of passage, since subadults leave wintering grounds later than adults (Rueda-Uribe et al., 2021). For this, we analysed differences between adults and subadults in selecting optimal flight altitudes and taking horizontal movement steps in relation to wind speed and direction. Additionally, we compared encountered wind conditions at simulated steps between adults and subadults to explore the role of wind seasonality on barrier-crossing flights. If subadults still need to learn how to optimally use wind to gain support during migratory flights, we predicted that flight performance will be better explained by differences in movement decisions between age groups rather than by wind seasonality.

METHODS

Data Acquisition and Preparation

Autumn and spring Sahara crossings were recorded by 15 and 20 g GPS−GSM/3G devices (Ornitela) attached on Caspian terns in 10 breeding sites in Sweden and Finland, as part of a conservation project (Lötberg et al., 2022; Rueda-Uribe et al., 2021). From the project data set, tracks from individuals that successfully crossed the Sahara Desert during migration were selected. Birds that migrated together in family groups were removed (two juveniles and one adult). This resulted in a study sample size of 13 adult and 10 first-year Caspian terns (Table A1). Birds were captured either with walk-in spring traps (adults) or by hand prior to fledging (first-year birds). GPS devices were mounted on their lower backs with Teflon leg-loop harnesses, as described in Rueda-Uribe et al. (2021), that on average represented 3.32% of birds' body mass and never surpassed 4.35% (Table A2). The tracking devices recorded geographical position, altitude, instantaneous groundspeed and heading every 5 min (or up to 2 h if the battery was low).

We processed the tracks to exclude low-quality relocations (satellite number < 4 and dilution of precision (DOP) ≥ 10). Then, we manually segmented migratory tracks to only include flights over the Sahara Desert. We defined the start of barrier-crossing flights as a continuous increase in instantaneous groundspeed and altitude (starting over 10 km/h and 10 m above the ground, that were continuous or kept increasing at least over 1 h and clearly evidenced sustained flight) and the end as a decrease in these two variables once the desert had been crossed. Note that our main interest was in flights over the desert, but some birds flew nonstop over the Sahara and Mediterranean Sea while others stopped on the North African coast before or after crossing the desert. We considered that if birds are flying over the Mediterranean Sea as they do over the desert (nonstop and at high altitudes and speeds), then the sea is part of the ecological barrier crossing; thus, we preferred to include complete flights that from now on we refer to as Sahara−Mediterranean crossings.

We further processed flight tracks by excluding altitude measurements greater than 6500 m above sea level (considered outliers, less than 0.3% of data; see Fig. A1) or relocations resulting from abrupt altitude changes over a maximum climb rate of 0.85 m/s, with the purpose of filtering unreliable altitude recordings and improbable altitude jumps during flight (Fig. A2). The maximum climb rate threshold (m/s) was obtained from the flight power curve with set body measurements (mass $= 633$ g, wing span $= 1276$ mm and wing area $= 613$ cm^2, average values calculated in Rueda-Uribe et al., 2021) using the R package 'afpt' (Heerenbrink, 2020; see Fig. A3). Climb rates greater than 0.85 m/s represented 4% of data points resulting from previously described

filters, and omitting 4% of the lowest descent rates values resulted in removing negative vertical speeds under −0.88 m/s.

In addition, we identified flight bursts within individual flight tracks to deal with sequential autocorrelation in our models. Flight bursts are defined as sequential relocations with equal sample rate and were identified using the R package 'amt' (Signer et al., 2019). Autocorrelation among residuals was tested by inspecting estimated autocorrelation functions by time lag plots created with the 'acf' function in R, and subsequently accounted for by including individual flight bursts as random effects in models.

Flight Performance in Relation to Wind

We tested whether inexperienced subadults and experienced adults gained different wind support during their Sahara−Mediterranean crossings during autumn and spring migration by comparing air-to-groundspeed ratios (AGR). Following Åkesson et al. (2016), values for AGR greater than 1 indicate that birds are not receiving wind support for their movement relative to the ground, whereas AGR values lower than 1 reveal wind support for horizontal movement. We calculated airspeed as the difference between groundspeed and tail wind for each relocation. Groundspeed was calculated as the ellipsoidal distance covered between two relocations divided by time, and the distance was measured using the package geosphere (Hijmans, 2019). Wind data were obtained at a $0.25° \times 0.25°$ grid resolution in the ERA5 hourly data on single levels downloaded from the Copernicus Climate Change Service (Hersbach et al., 2018; https://climate.copernicus.eu/). To match the temporal scale of wind data, tracks were resampled into 60 min intervals (with a 5 min tolerance) and assigned to the closest hour. U and v components of wind were annotated on tracks during periods when birds were flying (instantaneous groundspee-d > 10 km/h, Klaassen et al., 2012) to the nearest corresponding pressure level in 50 hPa intervals (1000−450 hPa). Then we calculated tail wind flight assistance using the R package 'RNCEP' (Kemp, van Loon, et al., 2012). Tail wind was calculated from the equation $fa_{tail\ wind} = y \cos θ$ (Kemp, Shamoun-Baranes, et al., 2012), where fa is tail wind flight assistance, y is the wind speed and $θ$ is the angular difference between the direction of the bird's movement and the wind. Differences in wind support (AGR) were tested with linear mixed-effects models, using age as the explanatory variable and individual, flight bursts within individual flight tracks and year as random intercepts. Additionally, the speed (km/h), duration (h) and path tortuosity of Sahara−Mediterranean crossings are also reported and differences between age groups were tested with t tests. To estimate path tortuosity, we calculated the straightness index using the R package 'amt' (Signer et al., 2019).

Possible Explanations for Differences in Flight Performance

We then tested whether differences in adult and subadult performance in northward Sahara−Mediterranean crossings were related to altitude selection, horizontal movement decisions or timing. To test whether adults were flying at optimal altitudes for wind support more frequently than subadults, we calculated AGR as if birds were flying one pressure level below or above their actual altitude and compared these values with the AGR at observed altitudes for each relocation. Rather than considering the complete range of pressure levels as possible altitudes birds could select at each relocation, we included only the immediately adjacent pressure levels (i.e. a difference of 50 hPa, which approximately equates to 500 m), as such not allowing for unrealistic changes in altitude that would disregard biologically plausible maximum climb/descent rates. If a bird was at the altitude with the lowest AGR compared to the two adjacent pressure levels, the relocation was

assigned a value of 0 (optimal altitude for wind support), and if it deviated from the optimal AGR it was given a value of 1 (nonoptimal altitude for wind support). In this way, the selection of optimal or nonoptimal altitude for wind support measured as AGR was included as the response variable in a binomial linear mixed-effects model, with age group as explanatory variable and individual, flight bursts within individual flight tracks and year as random intercepts.

Besides differences in altitude selection in response to wind conditions, subadults and adults could make different horizontal movement decisions, which can be quantified by the turning angle and length of each step. We fitted step selection functions (Avgar et al., 2016; Fieberg et al., 2021), with average wind speeds and directions during Sahara crossings at the median pressure levels experienced by individual birds (see Table A3) at the end of observed and simulated steps as environmental covariates. First, tracks were resampled to 60 min intervals (with a 5 min tolerance). Then, for each relocation within individual tracks, 100 random steps were generated from the fitted gamma and von Mises distributions of observed step lengths and turning angles of the individual's track, respectively. Both observed and random steps were annotated with wind speed and direction data downloaded from the Copernicus Climate Change Service as described above. Conditional logistic regression models for each individual ($N = 23$) were then fitted with observed and simulated steps, which, respectively, represent the selected and available but not selected movement step at each relocation. Included fixed effects were wind direction, wind speed, movement variables (cosine of turning angles, step lengths and natural logarithm step lengths) and all possible interactions between movement variables and wind covariates. Observed and simulated available locations from steps were grouped and indicated as strata in the models (Fieberg et al., 2021). For track resampling, simulation of random steps and model fitting we used the 'amt' package in R (Signer et al., 2019). After models were fitted, we tested for differences in the significance of fixed effects between adults and subadults with t tests.

Finally, how birds use wind to their advantage could be the result of available wind conditions (speed and direction) instead of differences in their in-flight decision making. To test whether adult and subadult Caspian terns experience variable wind conditions because they cross the Sahara and Mediterranean at different times of the year, we used wind covariates at simulated steps as a measure of the available wind conditions during northward crossings. We tested for differences between age groups in terms of available wind speed and the angular difference between the mean heading of each individual track and mean available wind direction. Differences in wind speed were assessed with linear mixed-effects models, using age as explanatory variable and individual, flight bursts within individual flight tracks and steps as random intercepts. Direction averages were calculated using the R package 'circular' (Agostinelli & Lund, 2017) and the difference between age groups was checked with a t test. All mixed-effects models in this study were fitted using the package 'lme4' in R (Bates et al., 2015) and residuals were checked with the DHARMa package in R (Hartig, 2020).

Ethical Note

Caspian terns are a species of conservation interest in the Baltic Sea and tagging with GPS has taken place as part of efforts to designate Important Bird and Biodiversity Areas (IBAs) in the region and identify areas for species-specific conservation action (i.e. protection of important foraging areas; Lötberg et al., 2022). All birds were handled under permit and standard procedures to minimize stress to the birds were followed (i.e. placement in a bird

bag, handling time minimized as far and as safely as possible). A small proportion of birds at any one visit to a colony were tagged with GPS (see Table A2), as this should suffice to measure behaviours of interest while minimizing any potential adverse effects on the population (Geen et al., 2019; Soanes et al., 2013). Average total handling time (including GPS deployment) was 18 (5 SD) min and GPS devices represented on average 3.32% (0.44 SD) of bird body mass (Table A2). After handling, all birds flew well and showed no sign of stress or injury, and all adults migrated successfully and nested in the following breeding seasons. Additionally, as far as possible at colonies with surveillance video cameras (Lötberg et al., 2022), tagged adults were monitored after colony visits and those observed behaved as normal (no noticeable difference to that of nontagged partner). GPS devices are not designed to fall off because they continue generating tracking data for researching migratory behaviour and movement across years. These studies will be presented in future publications.

Tagging and ringing of birds in breeding colonies was led by U.L. and P.B., who each has more than 10 years of experience handling seabirds and have personal ringing permits no. 710 from the Naturhistoriska riksmuseet in Sweden and 2604 from the Finnish Ringing Centre in Finland, respectively. Permits to trap and deploy GPS tracking devices on Caspian terns in Finland were issued by the Regional State Administrative Agency for Southern Finland (ESAVI/1068/04.10.07/2017) and the Centre for Economic Development, Transport and the Environment in Southwestern Finland (VARELY/875/2017). Permits to work in protected areas in Finland were issued by the Centre for Economic Development, Transport and the Environment in Southern Ostrobothnia (EPOELY/1830/215). Permission to track Caspian terns in Sweden was given by Malmö-Lunds djurförsöksetiska nämnd (M470-12, M72-15, M74-20) to SÅ. Permission to capture and ring Caspian terns in Sweden was given by the Swedish Environmental Protection Agency and the Swedish Ringing Office to U.L. (NV-03567-16). Permits to visit protected areas where the colonies are situated were given by the responsible County Administration Boards. The permit to visit Stenerna and Hållet was given to U.L. and that for Furö was given to Tommy Larssson. A special permit was given to catch birds within Rödkallen-Söräspens Nature reserve (521-4026-18).

RESULTS

There was no difference in performance between the age groups during southward autumn crossings of the Mediterranean–Sahara, but experienced adults flew straighter routes, at faster speeds and with greater wind support than less experienced subadults on northward crossings (Fig. 1). In autumn, both adults and subadults flew over the desert during late September to early December, in less than 2 days, at similar speeds, with no difference in path tortuosity and maintaining AGR values mostly under 1 (Table 1, Fig. 1a). In contrast, spring crossings were performed by adults and subadults at different times of the year. Adults departed on average on 13 April (SD = 10 days/range 2 April–3 May), whereas subadults left on average on 16 July (SD = 25 days/range 3 June–3 September). Adult northward spring crossings were faster, as they were performed at higher speeds and followed straighter paths than those of subadults (Table 1). On their first spring northward crossings, subadults had higher AGR than experienced adults, notably surpassing the AGR threshold of 1, which indicates wind was not supporting horizontal movement (Fig. 1a, Table A4). Models testing for differences between age groups in AGR or deviation from optimal AGR altitude did not show autocorrelation when individual flight bursts were included as random effects (Fig. A4). In all cases the variable 'year' as a random factor failed to explain any observed variation, so it was removed to avoid model

singularity (see Fig. A5 for average wind speed across years in the study area).

However, we found no age-related differences in altitude or step selection in relation to wind during northward desert crossings. On average, 30% (SD = 18) and 29% (SD = 1) of subadult and adult relocations were at optimal AGR altitudes, respectively. The binomial model used to test whether adults more frequently selected altitudes with optimal AGR than subadults during spring did not show a significant difference between age groups (age coefficient estimate = −0.67 (−1.47–0.17 95% confidence interval, CI), $t = −0.67$, $P = 0.09$; Fig. 1d, Tables A4 and A5). Deviation from optimal AGR was low for both age groups, with 95% of relocations being within a 0.49% and 0.60% difference for adults and subadults, respectively (Fig. 1c). Additionally, on northward crossings there were no differences in P values between age groups for any of the fixed effects of the step selection functions (Fig. 1b; t tests: all $P > 0.05$; see Tables A6 and A7). Environmental covariates (wind speed and direction), movement variables and interactions included in step selection functions were not significant for most tracked individuals (52–91% of individuals had nonsignificant P values; see Fig. A6).

In terms of the wind conditions that were available during northward crossings, there was a significant difference in the wind speeds that adults and subadults could have encountered along the route since simulated steps for subadults had lower available wind speeds (Fig. 2). In terms of the absolute difference between mean heading and available wind direction, this difference was lower for adults (42.69°) than subadults (79.76°) but it was not statistically significant ($N = 23$, $t_{13.05} = −1.79$, $P = 0.1$; Table A8).

DISCUSSION

Our findings confirm the prediction that inexperienced subadult Caspian terns have similar wind support to experienced adults during southward crossings of the Sahara Desert but less wind support in their first solo northward crossings. This pattern may suggest there is an experience-based learning process related to gaining positive wind support; however, we found little difference between age groups in flight movement decisions in relation to wind despite subadults having less wind support, lower speed and less straight flight paths during northward crossings. Both adults and subadults had on average only around 30% of relocations at optimal AGR altitudes, yet the deviation from calculated optimal AGR values was small (within 0.6%). In terms of the evaluated step selection functions, there was variation between individuals in the effects of wind speed, direction and movement variables but no clear pattern of differences between age groups. Instead, lower subadult flight performance in relation to wind is most likely due to seasonal changes in wind conditions. The timing of departure of adults coincides with higher wind speeds and directions that are closer to their overall heading, whereas subadults cross the desert on average 3 months later, when wind speeds are lower and on average blowing at 80° angular differences to birds' overall directions.

The variation we found in available wind conditions according to the time of year strongly highlights the importance of environmental factors for explaining age-related differences in flight performance over a major ecological barrier. Atmospheric changes in the air masses that converge in the Intertropical Convergence Zone (ITCZ) combined with its latitudinal displacement result in wind seasonality that is also related to the precipitation regimes of the region (Matthew & Ayoola, 2020). Birds may respond to regional variation in wind patterns resulting from the seasonal position of the ITCZ, as has recently been shown in migratory Eleonora's falcons, *Falco eleonorae*, which make detours to gain wind support while flying over the Sahara and Sahel (Vansteelant et al., 2021).
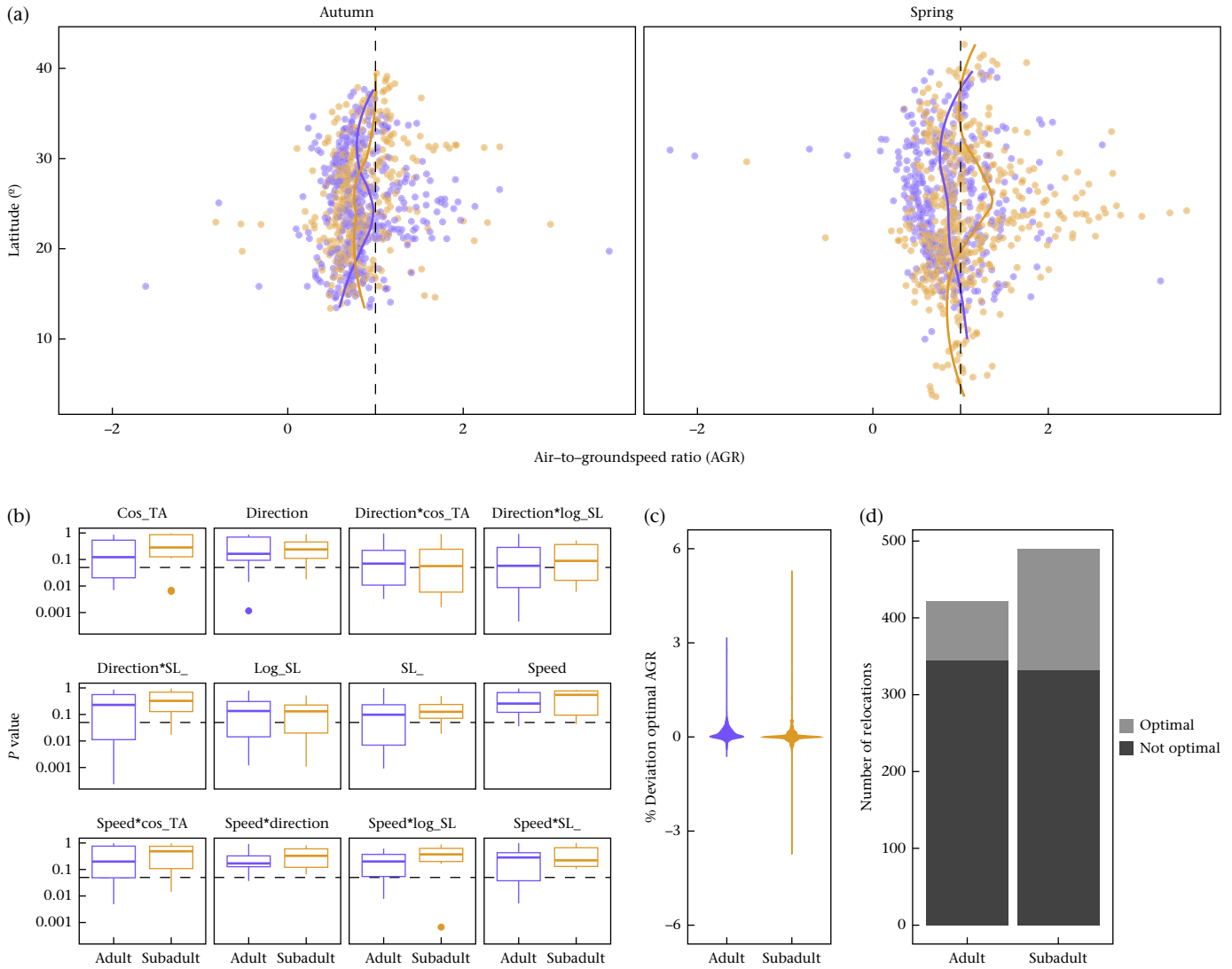
Figure 1. Wind support experienced by 13 adult (purple) and 10 subadult (orange) Caspian terns during crossings of the Mediterranean Sea and Sahara Desert. (a) Observed air-to-groundspeed ratios (AGR) for resampled 1 h relocations in autumn and spring migration according to latitude, with smoothed lines (gam method from ggplot geom_smooth). Vertical dashed lines represent AGR of 1. AGR values greater than 1 indicate that birds are not receiving wind support for their movement relative to the ground, whereas AGR values lower than 1 reveal wind support for horizontal movement. (b) Box plots showing the distribution of *P* values for all fixed effects of each individual in models of step selection functions during spring northward crossings. Box plots represent the median with middle thick lines, first and third quartiles at hinges of the box, 1.5 times the interquartile range with vertical lines and outliers with points. Dashed horizontal line shows *P* value of 0.05, which was a priori determined as the significance threshold. Cos_TA = cosine of turning angles, direction = wind direction, SL_ = step length, log_SL = natural logarithm of step length, speed = wind speed. (c) Violin plots of percentage deviations of resampled 1 h relocations of observed AGR from optimal AGR calculated in comparison to adjacent pressure levels. Negative values indicate optimal AGR altitudes were below observed flight altitudes and positive above. Two extreme outliers of subadult values with −14.2 and 9.9% deviation from optimal AGR were excluded from the graph. (d) Number of resampled 1 h relocations that were at an optimal AGR altitude in comparison to adjacent pressure levels to the observed flight altitude during northward crossings in spring.

Table 1
Average values for the speed, duration and path tortuosity measured as straightness for Sahara–Mediterranean crossings of 13 adult and 10 subadult Caspian terns during autumn and spring

Season	Performance variable	Adult	Subadult	*t*	*df*	*P*
Autumn	Speed (km/h)	55 (12)	50 (10)	1.33	23.58	0.196
	Duration (h)	41 (12)	47 (14)	−1.07	19.72	0.299
	Straightness	0.91 (0.05)	0.89 (0.04)	1.06	20.33	0.301
Spring	**Speed (km/h)**	66 (14)	40 (12)	5.05	23.41	**<0.001**
	Duration (h)	40 (14)	61 (26)	−2.38	14.80	**0.031**
	Straightness	0.95 (0.04)	0.88 (0.05)	3.57	17.21	**0.002**

Standard deviations are shown in parentheses. Results of *t* tests to compare differences between age groups are also included and significant variables and *P* values are highlighted in bold.
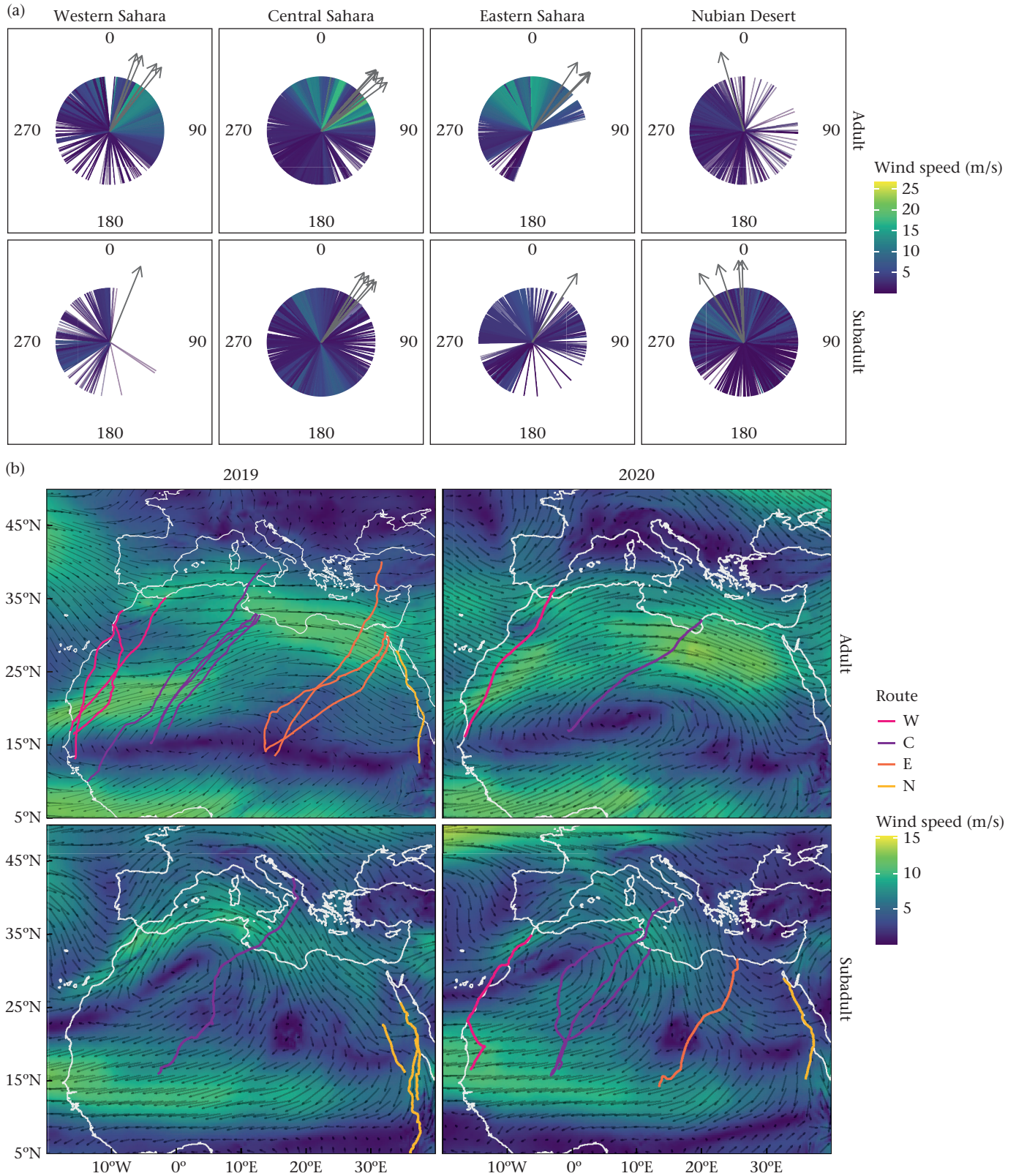
Figure 2. Available wind speed and direction for 13 adult and 10 subadult Caspian terns during northward crossings of the Sahara Desert and Mediterranean Sea, calculated from simulated steps. (a) Observed wind speed and direction at each simulated step. The coloured lines represent available wind conditions along individual birds' paths. Wind speed in m/s is shown according to the colour scale legend. Lines point from the centre outwards to indicate wind direction in degrees (0° = N). Grey arrows show the average direction of individual birds. (b) Maps of monthly mean wind speed and direction at 700 hPa (ca. 3000 m above sea level, close to the average median altitude of 2370 m above sea level during crossings) for the study area, during April (adult migration; mean departure date: 13 April) and July (subadult migration; mean departure date: 16 July) in 2019 and 2020. The four different routes used in the crossings are shown: western Sahara (W), central Sahara (C), eastern Sahara (E) and Nubian Desert (N). Note that the colour scales for wind speed in (a) and (b) use the same colour scale, but differ slightly since (a) shows observed wind conditions at simulated steps while (b) shows monthly mean wind conditions for each map cell.

Mechanisms that are possibly used by birds to adjust flight behaviour to wind currents have been proposed in relation to visual cues (Åkesson, 1993; Serres et al., 2019), although the use of advantageous airflows could have evolved through increased survival along certain routes, even if birds are incapable of individually sensing or predicting wind patterns (Erni et al., 2005; Kranstauber et al., 2015). Similarly, the evolution of the timing of departure from wintering areas could be related to the seasonality of wind patterns over the Sahara. Traditionally, departure timing in spring for Afro-Palearctic migrants has been linked to the scheduling of annual cycles and the timely arrival at breeding sites (Kokko, 1999). However, the importance of timing for age-related differences in the performance of Caspian terns during Sahara—Mediterranean crossings hints at the possible costs that could arise if adults delayed their departure. Low wind support over an ecological barrier such as the Sahara could directly increase mortality (Loonstra et al., 2019) and decrease reproductive success if birds reach breeding sites late or in bad physical condition (Descamps et al., 2011).

The rapid acquisition of adult-like vertical and horizontal movement skills by subadult birds we report here contrasts with studies that have shown improvement of migratory performance to be a gradual, life-long process (Campioni et al., 2020; Sergio et al., 2014). Rather, our findings coincide with examples that have shown young birds can deal with complex wind conditions, such as juvenile great frigatebirds, *Fregata minor*, compensating for wind drift when in sight of land (Wynn et al., 2020). How subadult Caspian terns have gained skills to make movement decisions over their first solo Sahara—Mediterranean crossings remains unclear. In social species, such as Caspian terns, learning through experience may be complemented by imitating and following leaders (Berdahl et al., 2018; Byholm et al., 2022; Mellone et al., 2016; Mueller et al., 2013), possibly accelerating improvements in performance and allowing young birds to complete their first return solo migrations. For example, there is evidence that white storks, *Ciconia ciconia*, located in rear positions of flocks follow those individuals that are ahead to detect columns of rising air, which enable soaring migrants to gain altitude and cover distances with lower energy expenditure (Flack et al., 2018). In the case of Caspian terns, young follow adults during autumn migration (Jozefik, 1969) and depend on receiving guidance from adults to survive their first migratory flight in autumn (Byholm et al., 2022). So when subadults cross the greatest ecological barrier of their migratory route by themselves for the first time during their first northward spring migration, they have already flown all the way from the Baltic Sea in the company of adults in their first autumn and are starting their second or third year of life (Kilpi & Saurola, 1984; Rueda-Uribe et al., 2021). In other words, they have already experienced migration and the crossing of the Sahara, during which they could have learned from experienced conspecifics, and they have practised flight capabilities during prolonged stays in wintering areas, since subadults crossing the desert northwards in their third year of life have remained in their wintering grounds for over a year.

An alternative explanation is that the skills Caspian terns need for dealing with atmospheric conditions while migrating over ecological barriers do not require a learning process but are innate (Berthold, 1996). To separate innate and learning processes in this study system, an experimental approach or an analysis of tracking data from consecutive years as individuals age is needed (as in Campioni et al., 2020). It would be particularly interesting to study how subadults may shift their timing of passage as they age to match that of adults, and whether they gain positive wind support with the more advantageous wind conditions in April—May over the Sahara. Furthermore, with more data to compare adults that are flying solo with those that accompany young during southbound crossings of the Mediterranean—Sahara ecological barrier, possible costs of migrating in family groups and differences between the sexes, as suggested by Byholm et al. (2022) for this species, could be discerned.

Another question that arises from our findings is: why do subadults cross the desert in June—September, when wind conditions are less favourable compared to when adults depart in April? We consider five different and nonexclusive hypotheses for late subadult departure in spring that may be tested in future research. First, it may be that subadults are still inexperienced in choosing optimal departure dates. Timing of departure seems to be endogenously regulated in some migratory birds (Conklin et al., 2013; Vardanis et al., 2011) but other species have shown individual flexibility in timing of departure (Vardanis et al., 2016). Subadult Caspian terns may be naïve in their decision to depart, performing crossings in unfavourable conditions that could lead to high mortality during desert crossings (Klaassen et al., 2014) and low survival in early life stages (Sergio et al., 2019), although there are still no published data on Caspian tern mortality, survival or body condition to address the possible costs of having low wind support over the desert. Conversely, a second explanation could be that subadults may be less motivated to depart as early as adults and migratory performance may have a greater effect on fitness for breeding individuals, since arrival date and body condition when birds reach breeding grounds may affect reproductive success (Descamps et al., 2011). Timely arrival of adult Caspian terns to breeding grounds in the Baltic Sea is achieved through fast spring migration with a reduced number of stopovers and less time spent at stopovers (Rueda-Uribe et al., 2021; Shiomi et al., 2015). Similarly, a third factor could be the high costs for subadults of arriving too early in spring to the Baltic Sea. Harsh conditions such as low temperatures or lower fish abundance, with possibly no benefit from reproductive output and less experience in dealing with these challenges in comparison to adults, could delay subadult departure from wintering grounds and shape their avoidance of these northern breeding locations during their first years of life.

A fourth option may be that subadult Caspian terns are responding to other environmental cues for departure, such as precipitation regimes. In the Sahel, the rainy season begins around May and peaks in July and August (Zwarts et al., 2009), which roughly coincides with the departure of adults and subadults, respectively. For subadults, the benefits of exploiting the rainy season and an associated surge in food sources may outweigh the costs of flying over the desert with low wind support. Precipitation patterns and resulting vegetation greenness in the Sahel have been shown to affect the timing of Sahara crossings (e.g. Robson & Barriocanal, 2011; Tøttrup et al., 2008) and spring arrivals (e.g. Gordo & Sanz, 2008) for migratory birds. Studies with barn swallows, *Hirundo rustica*, have additionally given evidence of age-related differences in migratory timing as a response to vegetation greening (measured as the normalized difference vegetation index, NDVI), since more experienced individuals delayed arrival times in breeding quarters when ecological conditions in wintering areas improved. In contrast, adult Caspian terns may be less responsive to fluctuations in precipitation because they return to their breeding colonies in the Baltic to reproduce, so the timing of arrival is important. Except for a few cases (Byholm, n.d.), subadults do not return or arrive too late at breeding areas in the Baltic Sea in the year they perform their first northward migration (Rueda-Uribe et al., 2021; Shiomi et al., 2015). Of the 10 subadults included in this study, only two returned to the Baltic while the rest remained in their wintering grounds or performed partial return migrations to locations near the Mediterranean Sea. This leads us to our fifth and last possible explanation: competition between adults and subadults in the wintering areas may lead to adults or even resident Caspian terns dominating diminishing resources and relegating

subadults to lower quality feeding areas as the Sahel gets drier from October until April. Through either indirect or direct competition, it may be that subadults have not been able to accumulate sufficient fuel when adults depart in April, and may need more time, food (which becomes more available or abundant with the arrival of the rainy season) or lower competition as bird densities in the Sahel decrease (Zwarts et al., 2009). Little is known about the potential for intraspecific competition in the Sahel to affect migration, and this is an interesting subject for future studies.

In conclusion, our study reveals that age-related differences in wind support over a major ecological barrier may be explained by environmental conditions encountered as a result of timing choices rather than the in-flight movement decisions of a long-distance migratory bird species that may learn through experience and social mechanisms (Berdahl et al., 2018). We foresee that further technological advances and tracking studies of individuals as they age will continue to shed light on the cues and processes that are important in learning migratory skills (as in Wynn et al., 2020), particularly in relation to dealing with varying winds. It has been repeatedly suggested that migratory feats such as the crossing of the vast Sahara Desert could not be possible without the support of the wind, and that wind patterns largely determine migratory routes (reviewed in Liechti, 2006; Shamoun-Baranes et al., 2017). Surprisingly, the question of how birds acquire such skills remains largely unknown. Our results highlight the importance of wind seasonality and timing for birds to be able to have positive wind support over challenging landscapes, revealing that timing of departures from wintering areas could also have evolved from the use of favourable winds at a certain time of the year. An analysis extended to other parts of migratory routes (ie. not only the Sahara Desert and Mediterranean Sea) or a comparison with Caspian terns that winter north of this ecological barrier (Rueda-Uribe et al., 2021) could shed light on the relative importance of gaining positive wind support over different geographical regions and landscapes. Finally, our findings give way to more questions about late subadult spring departures from sub-Saharan wintering sites that could be investigated by evaluating fitness effects of wind support during migration and analysing departure cues such as the ecological conditions at wintering sites.

Author Contributions

U.L., P.B. and S.Å. designed the project of tracking the migration of Caspian terns. U.L. and P.B. led fieldwork to capture the birds and deploy GPS tags and C.R., N.I., S.R.P. and M.B. participated in fieldwork. C.R., U.L., S.R.P., P.B. and S.Å. planned and discussed the research questions to include in this study. CR did all the data preparation and analyses, created the figures and wrote the first draft of the manuscript with input from all coauthors. All authors read and approved the final manuscript.

Data Availability

Data are stored in the Centre for Animal Movement Research at Lund University in Sweden (www.canmove.lu.se) and are available on request.

Declaration of Interest

The authors declare that they have no competing interests.

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Appendix

Table A1
Location of 10 breeding sites in Sweden and Finland and number of individuals by colony of tracked Caspian terns over Sahara–Mediterranean crossings used in this study

Country	Breeding colony	Latitude	Longitude	*N*
Sweden	Furö	57.286500	16.611420	3 adults/4 subadults
	Rödkallen	65.326070	22.346780	4 adults/1 subadult
	Stenarna	60.634400	17.923770	1 adult/2 subadults
Finland	Gävskärskobben	62.309082	21.274697	1 adult
	Girsberget	62.197383	21.369013	1 adult
	Granlundsberget	62.355902	21.192540	1 adult
	Knappelbådan	62.223509	21.287340	1 adult/1 subadult
	Kaldhamn	62.178761	21.320507	1 subadult
	Ingströmsberget	62.327478	21.227117	1 adult
	Gubbstenen	62.500584	21.100989	1 subadult

Table A2
Body mass, weight of attached GPS device, GPS device as a percentage of body mass and total handling time for each individual Caspian tern tracked in this study

ID (colour ring)	Body mass (g)	GPS mass (g)	GPS as % of body mass	Total handling time (min)
MH3	585	20	3.42	30
U40	530	20	3.77	19
UA00	620	20	3.23	20
UA01	680	20	2.94	32
UA04	570	20	3.51	21
UA90	530	20	3.77	18
UA92	530	20	3.77	19
F9M	460	20	4.35	14
FA04	630	20	3.17	15
FA05	680	20	2.94	24
FA07	720	20	2.78	17
FA11	670	15	2.24	20
A75	560	20	3.57	13
AC75	570	20	3.51	13
C31	700	20	2.86	13
PUC	620	20	3.23	10–20
PUU	660	20	3.03	10–20
PUH	635	20	3.15	10–20
PUA	625	20	3.20	10–20
NPY	510	20	3.92	10–20
TYW	570	20	3.51	10–20
PUP	600	20	3.33	10–20
PLZ	615	20	3.25	10–20

Note that for seven individuals total handling time was not recorded, but a range is given.

Table A3
Dates and pressure level used for wind data raster layer from the ERA5 hourly data on single levels downloaded from Copernicus Climate Change Service (Hersbach et al., 2018) for each individual Caspian tern in integrated step selection functions

ID (colour ring)	Age	Start date	End date	Median hPa	Selected hPa
MH3	Adult	4 Apr 2020	6 Apr 2020	745.00	750
U40	Subadult	1 Jul 2020	3 Jul 2020	705.70	700
UA00	Adult	2 Apr 2019	5 Apr 2019	794.69	800
UA01	Adult	11 Apr 2019	13 Apr 2019	701.33	700
UA04	Subadult	22 Jul 2020	24 Jul 2020	751.89	750
UA90	Subadult	4 Jul 2020	8 Jul 2020	993.60	1000
UA92	Subadult	24 Jun 2020	27 Jun 2020	785.56	800
F9M	Subadult	3 Jun 2020	4 Jun 2020	586.37	600
FA04	Adult	20 Apr 2019	21 Apr 2019	677.42	700
FA05	Adult	21 Apr 2019	22 Apr 2019	707.75	700
FA07	Adult	30 Apr 2019	1 May 2019	727.16	750
FA11	Adult	15 Apr 2020	17 Apr 2020	616.89	600
A75	Subadult	16 Jul 2019	21 Jul 2019	873.17	900
AC75	Subadult	26 Jul 2019	30 Jul 2019	799.13	800
C31	Adult	2 Apr 2019	4 Apr 2019	696.98	700
PUC	Adult	3 May 2019	4 May 2019	760.52	750
PUU	Adult	7 Apr 2019	9 Apr 2019	720.96	700
PUH	Adult	14 Apr 2019	18 Apr 2019	779.86	800
PUA	Adult	14 Apr 2019	16 Apr 2019	794.49	800
NPY	Subadult	3 Sep 2019	4 Sep 2019	773.27	750
TYW	Subadult	21 Jul 2020	25 Jul 2020	1012.13	1000
PUP	Adult	4 Apr 2019	6 Apr 2019	932.35	950
PLZ	Subadult	2 Aug 2019	4 Aug 2019	819.44	800

Table A4
Results of linear mixed-effects models for wind support variables in Sahara—Mediterranean crossings of 13 adult and 10 subadult Caspian terns

Response variable	Season	Explanatory variable	Estimate	CI	SE	t	P
Air-to-groundspeed ratio (AGR)	Autumn	Intercept	0.8220	0.7191—0.9270	0.0562	14.6146	<0.001
		Age (subadult)	−0.0306	−0.1702 to 0.1062	0.0752	−0.4069	0.684
	Spring	Intercept	0.9159	0.6843—1.1472	0.1184	7.7314	<0.001
		Age (subadult)	**0.3161**	**-0.0024 to 0.6278**	**0.1603**	**1.9724**	**0.049**
Deviation from optimal AGR altitude	Spring	Intercept	1.4858	0.8963—2.0834	0.2873	5.172	<0.001
		Age (subadult)	−0.6744	−1.47 to 0.1733	0.3939	−1.712	0.087
Available wind speed	Spring	Intercept	8.9655		1.0517	8.5249	<0.001
		Age	**−3.6953**		**1.5475**	**2.3878**	**0.017**

CI: confidence interval. All models included age as a fixed effect and movement bursts nested within individual as a random intercept effect. Since available wind speed was obtained from simulating 100 steps for each observed movement step, this model also included steps as a random effect. Models of AGR and available wind speed had Gaussian distributions while the deviation from optimal AGR altitude was investigated with a binomial model, where a value of 0 indicated that a bird was at its optimal altitude for lower AGR in comparison to the adjacent pressure levels and a value of 1 indicated the bird was not at an optimal altitude. Significant explanatory variables ($P < 0.05$) are highlighted in bold. See Table A5 for variance and standard deviation of random effects. Southward crossings of the desert were performed in autumn and northward crossings in spring.

Table A5
Variance and standard deviation of random effects included in linear mixed-effects models of wind support variables

Response variable	Season	Random effects	Variance	SD
Air-to-groundspeed ratio (AGR)	Autumn	ID*burst	0.0991	0.3147
		ID	0.0032	0.0569
		Residual	0.0957	0.3094
	Spring	ID*burst	0.2297	0.4793
		ID	0.0552	0.2350
		Residual	0.1257	0.3546
Deviation from optimal AGR altitude	Spring	ID*burst	0.5600	0.7484
		ID	0.3837	0.6194
Available wind speed	Spring	Step*burst	7.2116	2.6854
		ID*burst	9.6148	3.1008
		ID	8.6183	2.9357
		Residual	0.5593	0.7479

See description of Table A3 and methods section for more information about the models used.

Table A6
Results of t tests to compare P values of fixed effects included in integrated step selection models between 13 adult and 10 subadult Caspian terns over Sahara—Mediterranean northward crossings

Fixed effect	t	df	P
Speed	0.51607	19.172	0.612
Direction	−0.057367	19.876	0.955
Speed*direction	0.66653	20.259	0.513
Speed*cosine of turning angles	0.43862	19.277	0.666
Speed*step length	0.63602	18.865	0.532
Speed*log step length	1.514	16.663	0.149
Direction*cosine of turning angles	0.056053	19.066	0.956
Direction*step length	0.77905	17.768	0.446
Direction*log step length	−0.31012	20.384	0.760

Direction = wind direction, speed = wind speed.

Table A7
Results of step selection functions fitted to individual northwards Sahara–Mediterranean crossings of 13 adult and 10 subadult Caspian terns

ID (colour ring)	Age	Model likelihood	Variable	Observed estimate	Expected estimate	SE	z	P
MH3	Adult	4.29E+01	Speed	−8.75	0.00	6.35	−1.38	0.17
			Direction	480.00	3.E+208	196.00	2.45	0.01
			SL_	−41.50	0.00	27.50	−1.51	0.13
			Log_SL	66.90	1.E+29	27.30	2.45	0.01
			Cos_TA	758.00		327.00	2.32	0.02
			Speed*direction	−1.88	0.15	1.84	−1.02	0.31
			Speed*SL_	1.78	5.93	1.24	1.43	0.15
			Speed*log_SL	−0.87	0.42	0.75	−1.15	0.25
			Speed*cos_TA	10.50	4.E+04	5.34	1.97	0.05
			Direction*SL_	8.31	4.E+03	18.10	0.46	0.65
			Direction*log_SL	−30.20	0.00	15.90	−1.90	0.06
			Direction*cos_TA	−481.00	0.00	192.00	−2.51	0.01
U40	Subadult	15.91	Speed	−1.23	0.29	2.01	−0.61	0.54
			Direction	0.80	2.21	5.16	0.15	0.88
			SL_	−12.60	0.00	18.60	−0.68	0.50
			Log_SL	8.54	5.E+03	10.50	0.81	0.42
			Cos_TA	−0.51	0.60	5.77	−0.09	0.93
			Speed*direction	0.33	1.40	0.34	0.97	0.33
			Speed*SL_	0.00	1.00	2.02	0.00	1.00
			Speed*log_SL	−0.17	0.84	1.13	−0.15	0.88
			Speed*cos_TA	0.04	1.04	0.67	0.06	0.96
			Direction*SL_	−0.27	0.76	5.11	−0.05	0.96
			Direction*log_SL	1.82	6.19	2.84	0.64	0.52
			Direction*cos_TA	−1.88	0.15	1.62	−1.16	0.25
UA00	Adult	49.78	Speed	−2.88	0.06	1.50	−1.91	0.06
			Direction	−26.70	0.00	8.21	−3.25	0.00
			SL_	−75.70	0.00	22.90	−3.31	0.00
			Log_SL	28.80	3.E+12	8.89	3.24	0.00
			Cos_TA	−2.25	0.11	4.28	−0.53	0.60
			Speed*direction	0.39	1.48	0.40	0.97	0.33
			Speed*SL_	1.08	2.95	1.37	0.79	0.43
			Speed*log_SL	−0.61	0.54	0.69	−0.89	0.37
			Speed*cos_TA	1.38	3.96	0.65	2.13	0.03
			Direction*SL_	40.00	2.E+17	10.90	3.68	0.00
			Direction*log_SL	−14.20	0.00	4.05	−3.50	0.00
			Direction*cos_TA	−4.46	0.01	1.71	−2.60	0.01
UA01	Adult	3.36E+01	Speed	−8.49	0.00	4.05	−2.10	0.04
			Direction	−3.39	0.03	9.98	−0.34	0.73
			SL_	−103.00	0.00	39.70	−2.59	0.01
			Log_SL	38.80	7.E+16	16.70	2.32	0.02
			Cos_TA	2.97	19.50	4.78	0.62	0.53
			Speed*direction	−0.41	0.66	0.30	−1.38	0.17
			Speed*SL_	12.90	4.E+05	4.71	2.73	0.01
			Speed*log_SL	−4.25	0.01	2.21	−1.92	0.05
			Speed*cos_TA	−1.35	0.26	1.05	−1.29	0.20
			Direction*SL_	2.02	7.54	12.40	0.16	0.87
			Direction*log_SL	−1.48	0.23	5.37	−0.28	0.78
			Direction*cos_TA	2.06	7.86	1.39	1.49	0.14
UA04	Subadult	19.2	Speed	−1.11	0.33	5.41	−0.21	0.84
			Direction	−6.51	0.00	4.05	−1.61	0.11
			SL_	−17.00	0.00	24.20	−0.70	0.48
			Log_SL	8.13	3.E+03	12.60	0.64	0.52
			Cos_TA	7.63	2.E+03	6.69	1.14	0.25
			Speed*direction	0.66	1.93	0.36	1.84	0.07
			Speed*SL_	3.49	32.80	5.87	0.60	0.55
			Speed*log_SL	−1.67	0.19	3.05	−0.55	0.58
			Speed*cos_TA	−1.09	0.34	1.42	−0.77	0.44
			Direction*SL_	3.32	27.60	4.02	0.83	0.41
			Direction*log_SL	−1.64	0.20	2.08	−0.79	0.43
			Direction*cos_TA	3.26	26.00	1.13	2.87	0.00
UA90	Subadult	3.15E+01	Speed	−0.18	0.84	0.38	−0.47	0.64
			Direction	2.27	9.67	0.96	2.37	0.02
			SL_	−7.13	0.00	3.03	−2.35	0.02
			Log_SL	3.56	35.30	1.33	2.68	0.01
			Cos_TA	0.15	1.16	0.91	0.17	0.87
			Speed*direction	−0.06	0.94	0.13	−0.46	0.64
			Speed*SL_	0.04	1.05	0.18	0.25	0.80
			Speed*log_SL	−0.01	0.99	0.03	−0.48	0.63
			Speed*cos_TA	−0.01	0.99	0.14	−0.05	0.96
			Direction*SL_	−2.29	0.10	0.96	−2.39	0.02
			Direction*log_SL	1.22	3.40	0.45	2.75	0.01
			Direction*cos_TA	0.05	1.05	0.23	0.23	0.82
UA92	Subadult	30.06	Speed	−4.54	0.01	2.77	−1.64	0.10
			Direction	5.00	148.00	3.82	1.31	0.19

Table A7 (*continued*)

ID (colour ring)	Age	Model likelihood	Variable	Observed estimate	Expected estimate	SE	z	P
			SL_	−28.70	0.00	16.50	−1.75	0.08
			Log_SL	14.00	1.E+06	8.10	1.72	0.08
			Cos_TA	−7.33	0.00	5.53	−1.33	0.19
			Speed*direction	−0.20	0.82	0.20	−0.99	0.32
			Speed*SL_	3.81	45.10	2.67	1.43	0.15
			Speed*log_SL	−1.57	0.21	1.27	−1.24	0.22
			Speed*cos_TA	2.17	8.78	1.45	1.50	0.13
			Direction*SL_	−0.86	0.42	3.95	−0.22	0.83
			Direction*log_SL	1.90	6.72	2.12	0.90	0.37
			Direction*cos_TA	−3.19	0.04	1.41	−2.26	0.02
F9M	Subadult	3.52E+01	Speed	−0.71	0.49	1.21	−0.59	0.56
			Direction	−0.27	0.76	2.24	−0.12	0.90
			SL_	−17.70	0.00	8.41	−2.11	0.04
			Log_SL	5.08	160.00	3.81	1.33	0.18
			Cos_TA	−1.47	0.23	7.32	−0.20	0.84
			Speed*direction	0.48	1.61	0.26	1.85	0.07
			Speed*SL_	1.28	3.58	0.79	1.62	0.10
			Speed*log_SL	−0.36	0.70	0.42	−0.84	0.40
			Speed*cos_TA	−0.19	0.83	0.93	−0.21	0.84
			Direction*SL_	−2.69	0.07	2.12	−1.27	0.20
			Direction*log_SL	2.06	7.87	0.82	2.53	0.01
			Direction*cos_TA	3.43	30.80	1.45	2.37	0.02
FA04	Adult	1.72E+02	Speed	−0.52	0.59	1.51	−0.35	0.73
			Direction	24.80	6.E+10	10.40	2.37	0.02
			SL_	−18.00	0.00	5.98	−3.01	0.00
			Log_SL	3.42	30.40	3.35	1.02	0.31
			Cos_TA	−3.56	0.03	3.77	−0.94	0.35
			Speed*direction	−1.92	0.15	0.95	−2.03	0.04
			Speed*SL_	−0.67	0.51	0.68	−0.98	0.33
			Speed*log_SL	1.71	5.52	0.95	1.79	0.07
			Speed*cos_TA	2.31	10.10	1.05	2.20	0.03
			Direction*SL_	−4.78	0.01	8.23	−0.58	0.56
			Direction*log_SL	11.30	8.E+04	4.97	2.27	0.02
			Direction*cos_TA	2.19	8.94	4.86	0.45	0.65
FA05	Adult	5.81E+01	Speed	−1.33	0.27	3.11	−0.43	0.67
			Direction	−110.00	0.00	105.00	−1.05	0.29
			SL_	−41.10	0.00	24.80	−1.66	0.10
			Log_SL	−12.30	0.00	18.40	−0.67	0.50
			Cos_TA	−142.00	0.00	83.30	−1.71	0.09
			Speed*direction	−2.25	0.11	1.83	−1.23	0.22
			Speed*SL_	3.25	25.90	1.27	2.56	0.01
			Speed*log_SL	−1.95	0.14	0.94	−2.07	0.04
			Speed*cos_TA	−0.69	0.50	2.23	−0.31	0.76
			Direction*SL_	−60.00	0.00	23.70	−2.54	0.01
			Direction*log_SL	92.70	2.E+40	30.80	3.01	0.00
			Direction*cos_TA	247.00	2.E+107	94.50	2.61	0.01
FA07	Adult	2.81E+01	Speed	2.37	10.70	3.15	0.75	0.45
			Direction	8.64	5650.00	49.10	0.18	0.86
			SL_	−74.80	0.00	40.40	−1.85	0.06
			Log_SL	68.70	7.E+29	33.30	2.06	0.04
			Cos_TA	80.00	6.E+34	51.80	1.54	0.12
			Speed*direction	−1.54	0.22	1.01	−1.52	0.13
			Speed*SL_	−1.45	0.24	1.70	−0.85	0.39
			Speed*log_SL	1.23	3.42	1.17	1.05	0.29
			Speed*cos_TA	0.61	1.84	2.29	0.27	0.79
			Direction*SL_	60.90	3.E+26	29.00	2.10	0.04
			Direction*log_SL	−57.90	0.00	24.20	−2.40	0.02
			Direction*cos_TA	−70.40	0.00	38.80	−1.81	0.07
FA11	Adult	22.7	Speed	−18.60	0.00	21.30	−0.88	0.38
			Direction	100.00	3.E+43	260.00	0.39	0.70
			SL_	158.00	2.E+68	168.00	0.94	0.35
			Log_SL	−173.00	0.00	126.00	−1.38	0.17
			Cos_TA	−735.00	0.00	285.00	−2.58	0.01
			Speed*direction	−14.20	0.00	9.31	−1.53	0.13
			Speed*SL_	−4.07	0.02	11.10	−0.37	0.71
			Speed*log_SL	4.98	145.00	8.45	0.59	0.56
			Speed*cos_TA	35.30	2.E+15	19.70	1.80	0.07
			Direction*SL_	−145.00	0.00	105.00	−1.39	0.16
			Direction*log_SL	141.00	2.E+61	87.20	1.62	0.11
			Direction*cos_TA	252.00	2.E+109	206.00	1.22	0.22
A75	Subadult	4.39E+01	Speed	−0.35	0.70	0.19	−1.83	0.07
			Direction	−0.17	0.84	0.24	−0.69	0.49
			SL_	−1.58	0.21	0.94	−1.68	0.09
			Log_SL	0.67	1.95	0.20	3.27	0.00

Table A7 (*continued*)

ID (colour ring)	Age	Model likelihood	Variable	Observed estimate	Expected estimate	SE	z	P
			Cos_TA	0.49	1.63	0.49	1.00	0.32
			Speed*direction	0.06	1.06	0.04	1.47	0.14
			Speed*SL_	0.22	1.25	0.14	1.54	0.12
			Speed*log_SL	−0.09	0.91	0.03	−3.40	0.00
			Speed*cos_TA	0.06	1.06	0.09	0.61	0.54
			Direction*SL_	0.02	1.02	0.20	0.12	0.91
			Direction*log_SL	−0.06	0.95	0.03	−1.98	0.05
			Direction*cos_TA	−0.51	0.60	0.16	−3.15	0.00
AC75	Subadult	1.60E+01	Speed	−3.17	0.04	1.88	−1.69	0.09
			Direction	−4.75	0.01	2.51	−1.89	0.06
			SL_	−13.90	0.00	10.20	−1.37	0.17
			Log_SL	5.34	209.00	4.45	1.20	0.23
			Cos_TA	−7.26	0.00	2.69	−2.70	0.01
			Speed*direction	−0.08	0.93	0.30	−0.25	0.80
			Speed*SL_	2.40	11.00	1.98	1.21	0.23
			Speed*log_SL	−0.86	0.42	0.91	−0.95	0.34
			Speed*cos_TA	2.23	9.30	0.91	2.45	0.01
			Direction*SL_	4.83	125.00	3.02	1.60	0.11
			Direction*log_SL	−2.32	0.10	1.36	−1.71	0.09
			Direction*cos_TA	0.80	2.23	0.68	1.18	0.24
C31	Adult	2.77E+01	Speed	6.97	1.E+03	5.03	1.39	0.17
			Direction	−17.40	0.00	10.40	−1.68	0.09
			SL_	−63.50	0.00	23.50	−2.70	0.01
			Log_SL	43.70	9.E+18	16.70	2.61	0.01
			Cos_TA	133.00	8.E+57	50.40	2.64	0.01
			Speed*direction	0.53	1.70	0.26	2.09	0.04
			Speed*SL_	6.86	952.00	2.46	2.79	0.01
			Speed*log_SL	−4.72	0.01	1.77	−2.66	0.01
			Speed*cos_TA	−14.40	0.00	5.11	−2.81	0.00
			Direction*SL_	−14.90	0.00	5.41	−2.75	0.01
			Direction*log_SL	10.50	4.E+04	4.00	2.62	0.01
			Direction*cos_TA	31.40	4.E+13	10.70	2.94	0.00
PUC	Adult	26.65	Speed	−9.05	0.00	8.00	−1.13	0.26
			Direction	−474.00	0.00	340.00	−1.39	0.16
			SL_	−374.00	0.00	313.00	−1.19	0.23
			Log_SL	303.00	5.E+131	223.00	1.36	0.17
			Cos_TA	−44.50	0.00	216.00	−0.21	0.84
			Speed*direction	9.08	9.E+03	4.89	1.86	0.06
			Speed*SL_	−0.07	0.93	4.90	−0.01	0.99
			Speed*log_SL	2.23	9.30	4.35	0.51	0.61
			Speed*cos_TA	−2.00	0.14	3.90	−0.51	0.61
			Direction*SL_	278.00	8.E+120	256.00	1.09	0.28
			Direction*log_SL	−245.00	0.00	190.00	−1.29	0.20
			Direction*cos_TA	63.00	2.E+27	211.00	0.30	0.77
PUU	Adult	2.65E+01	Speed	0.56	1.74	3.92	0.14	0.89
			Direction	−48.10	0.00	32.70	−1.47	0.14
			SL_	−0.68	0.51	27.00	−0.03	0.98
			Log_SL	10.10	3.E+04	24.00	0.42	0.67
			Cos_TA	−57.20	0.00	21.20	−2.70	0.01
			Speed*direction	−0.17	0.85	1.52	−0.11	0.91
			Speed*SL_	0.67	1.95	1.45	0.46	0.64
			Speed*log_SL	−0.57	0.57	1.03	−0.55	0.58
			Speed*cos_TA	−0.12	0.89	3.05	−0.04	0.97
			Direction*SL_	−10.50	0.00	16.70	−0.63	0.53
			Direction*log_SL	1.44	4.22	14.20	0.10	0.92
			Direction*cos_TA	59.50	7.E+25	23.40	2.55	0.01
PUH	Adult	2.11E+01	Speed	4.15	63.73	2.68	1.55	0.12
			Direction	−2.14	0.12	3.27	−0.65	0.51
			SL_	8.22	4.E+03	7.12	1.15	0.25
			Log_SL	−0.88	0.41	3.31	−0.27	0.79
			Cos_TA	1.71	5.52	10.28	0.17	0.87
			Speed*direction	0.23	1.26	0.24	0.99	0.32
			Speed*SL_	−4.16	0.02	2.00	−2.08	0.04
			Speed*log_SL	1.05	2.85	0.79	1.33	0.18
			Speed*cos_TA	−0.49	0.61	2.11	−0.23	0.82
			Direction*SL_	2.28	9.82	1.90	1.20	0.23
			Direction*log_SL	−0.99	0.37	0.92	−1.07	0.29
			Direction*cos_TA	−0.16	0.85	2.75	−0.06	0.95
PUA	Adult	1.22E+01	Speed	0.34	1.40	6.13	0.06	0.96
			Direction	−6.50	0.00	39.60	−0.16	0.87
			SL_	−54.00	0.00	41.30	−1.31	0.19
			Log_SL	38.90	8.E+16	26.00	1.49	0.14
			Cos_TA	41.60	1.16E+18	29.20	1.43	0.15
			Speed*direction	0.16	1.17	1.37	0.12	0.91
			Speed*SL_	6.05	425.00	5.64	1.07	0.28

Table A7 (*continued*)

ID (colour ring)	Age	Model likelihood	Variable	Observed estimate	Expected estimate	SE	z	P
			Speed*log_SL	−4.43	0.01	3.46	−1.28	0.20
			Speed*cos_TA	−5.70	0.00	3.68	−1.55	0.12
			Direction*SL_	−20.20	0.00	42.60	−0.47	0.64
			Direction*log_SL	15.20	4.E+06	25.30	0.60	0.55
			Direction*cos_TA	26.70	4.E+11	19.50	1.37	0.17
NPY	Subadult	39.01	Speed	−6.05	0.00	26.90	−0.23	0.82
			Direction	−51.20	0.00	49.50	−1.04	0.30
			SL_	−444.00	0.00	244.00	−1.82	0.07
			Log_SL	191.00	9.E+82	114.00	1.68	0.09
			Cos_TA	−2.41	0.09	44.60	−0.05	0.96
			Speed*direction	−0.85	0.43	1.21	−0.70	0.49
			Speed*SL_	10.50	3.E+04	27.40	0.38	0.70
			Speed*log_SL	6.17	479.00	16.80	0.37	0.71
			Speed*cos_TA	5.57	262.00	8.90	0.63	0.53
			Direction*SL_	61.90	8.E+26	57.70	1.07	0.28
			Direction*log_SL	−24.70	0.00	26.90	−0.92	0.36
			Direction*cos_TA	1.41	4.10	14.10	0.10	0.92
TYW	Subadult	29.9	Speed	0.08	1.08	0.34	0.23	0.82
			Direction	−0.30	0.74	0.33	−0.90	0.37
			SL_	−1.14	0.32	0.98	−1.16	0.24
			Log_SL	0.12	1.13	0.10	1.23	0.22
			Cos_TA	1.13	3.09	0.71	1.60	0.11
			Speed*direction	0.05	1.05	0.11	0.45	0.65
			Speed*SL_	0.36	1.43	0.22	1.59	0.11
			Speed*log_SL	−0.04	0.97	0.03	−1.39	0.16
			Speed*cos_TA	−0.29	0.74	0.18	−1.64	0.10
			Direction*SL_	−0.67	0.51	0.36	−1.85	0.06
			Direction*log_SL	0.10	1.11	0.04	2.63	0.01
			Direction*cos_TA	0.87	2.38	0.28	3.09	0.00
PUP	Adult	8.87E+01	Speed	−3.23	0.04	1.68	−1.92	0.05
			Direction	3.50	33.00	2.50	1.40	0.16
			SL_	−25.10	0.00	8.62	−2.91	0.00
			Log_SL	15.10	4.E+06	4.89	3.09	0.00
			Cos_TA	7.99	3.E+03	3.59	2.23	0.03
			Speed*direction	0.27	1.31	0.18	1.52	0.13
			Speed*SL_	2.56	13.00	1.38	1.85	0.06
			Speed*log_SL	−2.03	0.13	0.94	−2.16	0.03
			Speed*cos_TA	−0.42	0.66	0.71	−0.59	0.55
			Direction*SL_	−6.66	0.00	2.52	−2.65	0.01
			Direction*log_SL	3.73	41.80	1.31	2.85	0.00
			Direction*cos_TA	3.06	21.40	1.21	2.53	0.01
PLZ	Subadult	2.40E+01	Speed	1.90	6.69	0.94	2.01	0.04
			Direction	2.51	12.27	1.59	1.57	0.12
			SL_	3.18	24.08	2.59	1.23	0.22
			Log_SL	−1.84	0.16	0.73	−2.50	0.01
			Cos_TA	−3.11	0.04	1.14	−2.73	0.01
			Speed*direction	−0.65	0.52	0.41	−1.58	0.11
			Speed*SL_	−0.70	0.50	0.57	−1.24	0.22
			Speed*log_SL	0.16	1.18	0.12	1.30	0.19
			Speed*cos_TA	0.60	1.82	0.26	2.29	0.02
			Direction*SL_	−1.57	0.21	1.76	−0.89	0.37
			Direction*log_SL	1.00	2.72	0.59	1.69	0.09
			Direction*cos_TA	1.04	2.84	0.70	1.50	0.13

cos_TA = cosine of turning angles, direction = wind direction, SL_ = step length, log_SL = natural logarithm of step length, speed = wind speed.

Table A8
Differences between mean track and available wind directions for 13 adult and 10 subadult Caspian terns in Sahara–Mediterranean northward crossings

ID (colour ring)	Age	Route	Mean track direction (°)	Mean available wind direction (°)	Difference (°)
MH3	Adult	c	42.36	22.15	20.21
U40	Subadult	C	33.34	10.25	23.09
UA00	Adult	E	41.72	299.83	101.89
UA01	Adult	W	23.14	72.09	48.94
UA04	Subadult	E	327.10	19.95	52.86
UA90	Subadult	W	341.72	300.97	40.75
UA92	Subadult	C	343.74	272.35	71.39
F9M	Subadult	C	358.91	348.41	10.49
FA04	Adult	C	53.81	354.00	59.80
FA05	Adult	C	31.64	225.29	166.34
FA07	Adult	W	45.04	337.76	67.27
FA11	Adult	W	19.16	319.13	60.04
A75	Subadult	N	33.05	309.54	83.51
AC75	Subadult	C	22.10	259.66	122.43
C31	Adult	E	42.38	217.89	175.50
PUC	Adult	C	40.12	320.68	79.44
PUU	Adult	E	44.03	55.48	11.45
PUH	Adult	C	49.36	45.05	4.31
PUA	Adult	W	39.11	27.34	11.76
NPY	Subadult	N	34.86	36.76	1.90
TYW	Subadult	N	356.27	294.30	61.97
PUP	Adult	N	35.54	31.27	4.27
PLZ	Subadult	N	43.99	331.05	72.93

Directions are in degrees, with 0° = north and circular means were calculated with the package 'circular' in R (Agostinelli & Lund, 2017). Routes taken during the crossings are indicated with letters: western Sahara (W), central Sahara (C), eastern Sahara (E) and Nubian Desert (N).
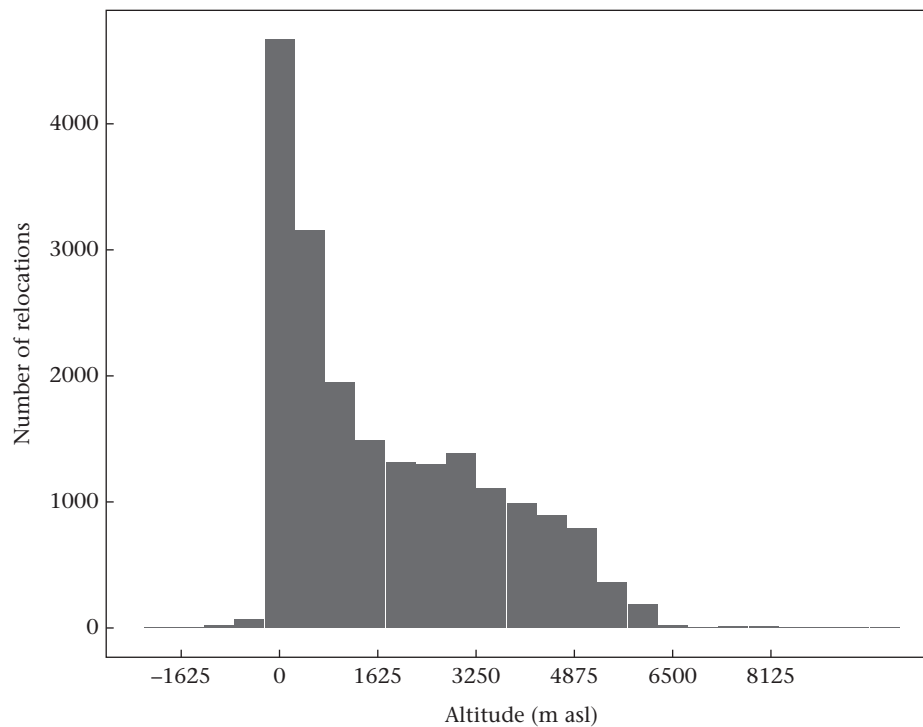

Figure A1. Distribution of altitudes recorded by GPS devices attached to 13 adult and 10 juvenile Caspian terns over Sahara–Mediterranean crossings in autumn and spring, after excluding low-quality relocations (satellite number < 4 and dilution of precision (DOP) ≥ 10). Measurements over 6500 m above sea level (asl; fewer than 0.3% of relocations) were considered outliers caused by imprecise recordings from GPS devices.
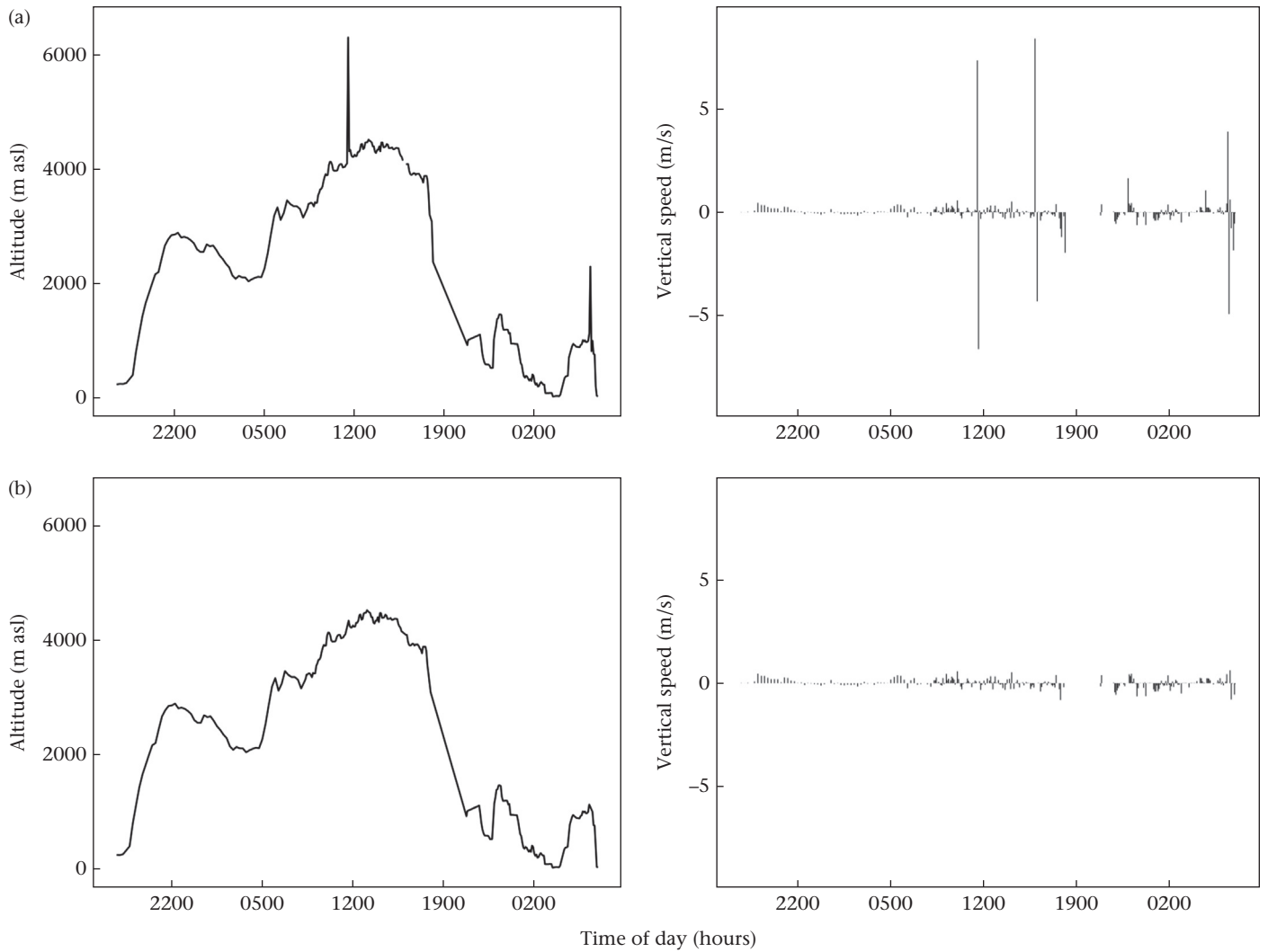
Figure A2. Example flight of a Caspian tern in a Sahara–Mediterranean crossing to show altitudes (m above sea level, asl) as recorded by GPS devices and vertical speeds between consecutive relocations (a) before and (b) after excluding altitude outliers and climb rates greater than 0.85 m/s and descent rates under −0.88 m/s. Altitudes over 6500 m above sea level in the first panel are not shown in the graph.
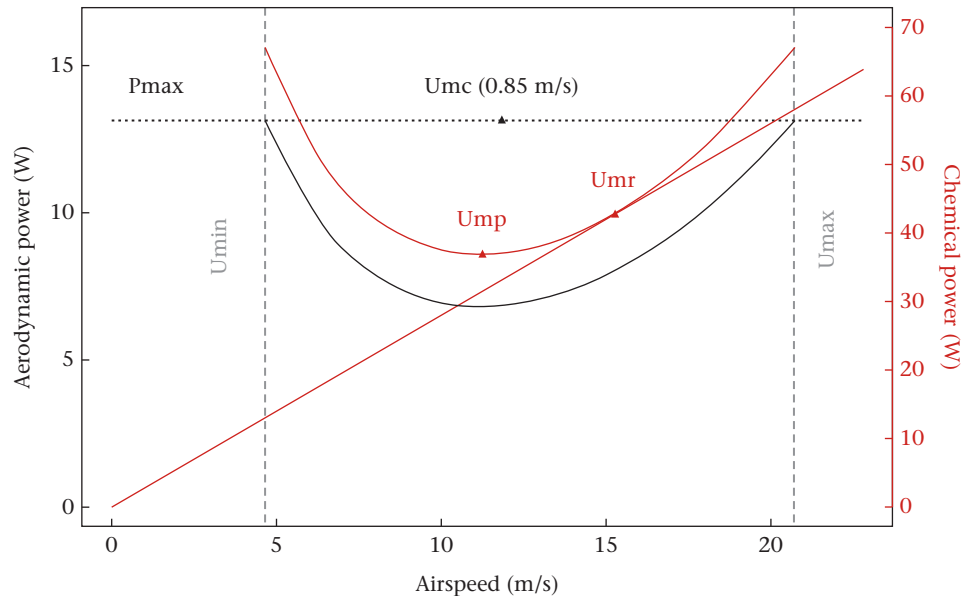
Figure A3. Flight power curve for Caspian tern with set body measurements (mass = 633 g, wing span = 1276 m and wing area = 613 cm^2). The maximum estimated climb rate is 0.85 m/s. Pmax = maximum power, Umax = maximum speed power, Umin = minimum speed power, Umc = maximum climb rate power, Umr = maximum range power, Ump = minimum flight power. Pmax is represented by the horizontal dashed line and Umc by the black triangle. Curve was generated using the R package 'afpt' (Heerenbrink, 2020).
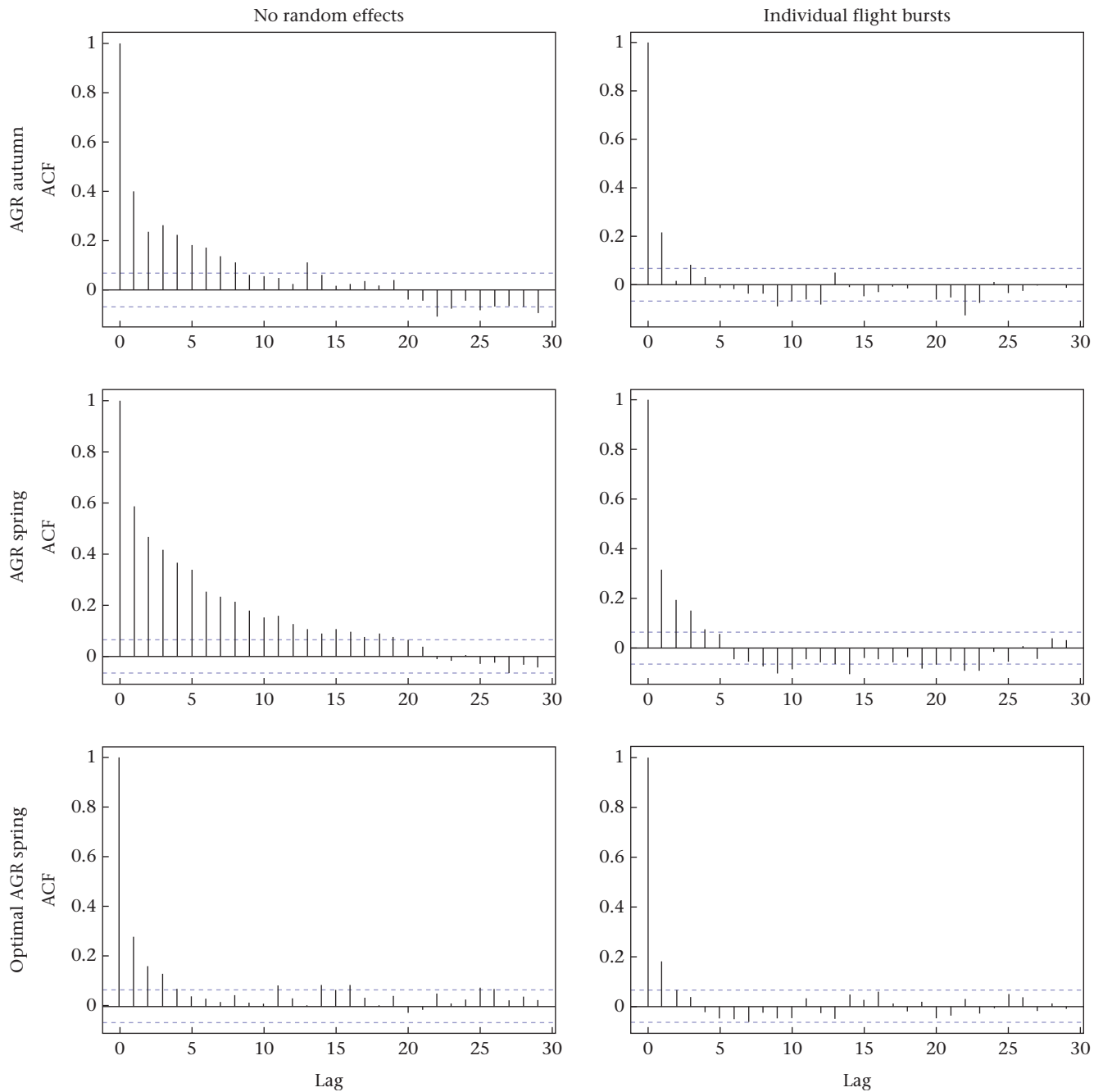
Figure A4. Autocorrelation of residuals of models with no random effects and with individual flight bursts as random effects for air-to-groundspeed ratios (AGR) in autumn and spring and the deviation from optimal AGR altitude in spring. ACF is the estimated autocorrelation function. Horizontal dashed lines represent the ACF value that would be expected if there were autocorrelation given the sample size (ACF $= \pm 1.96/\sqrt{N}$). Note that lag $= 0$ is a comparison with itself so by definition should always have the highest correlation.
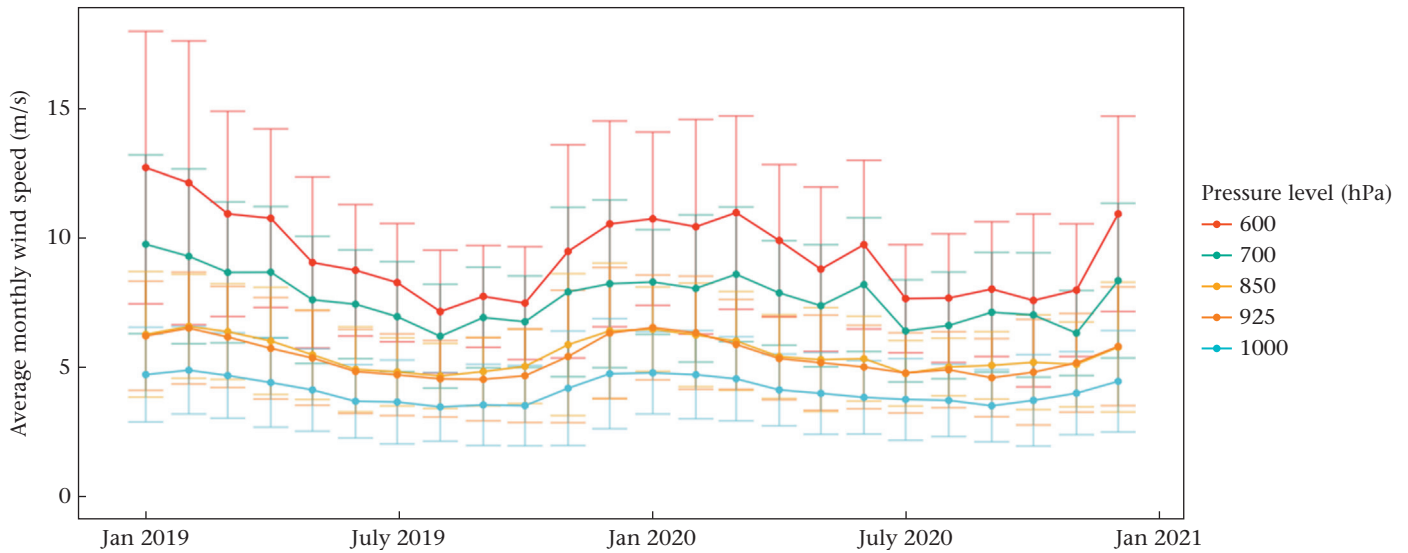
Figure A5. Average monthly wind speed (m/s) over the study area (between −18 and 39° longitude and 3 and 43° latitude) during 2019 and 2020. Wind speed is presented at five atmospheric pressure levels: 1000 hPa is close to the surface and 600 hPa is around 4200 m above sea level. Error bars show the standard deviation around the mean for the geographical region. Data on daily wind speed were downloaded from the NCEP Reanalysis I data set provided by NOAA/OAR/ESRL PSD, Boulder, CO, U.S.A. (http://www.esrl.noaa.gov/psd/).
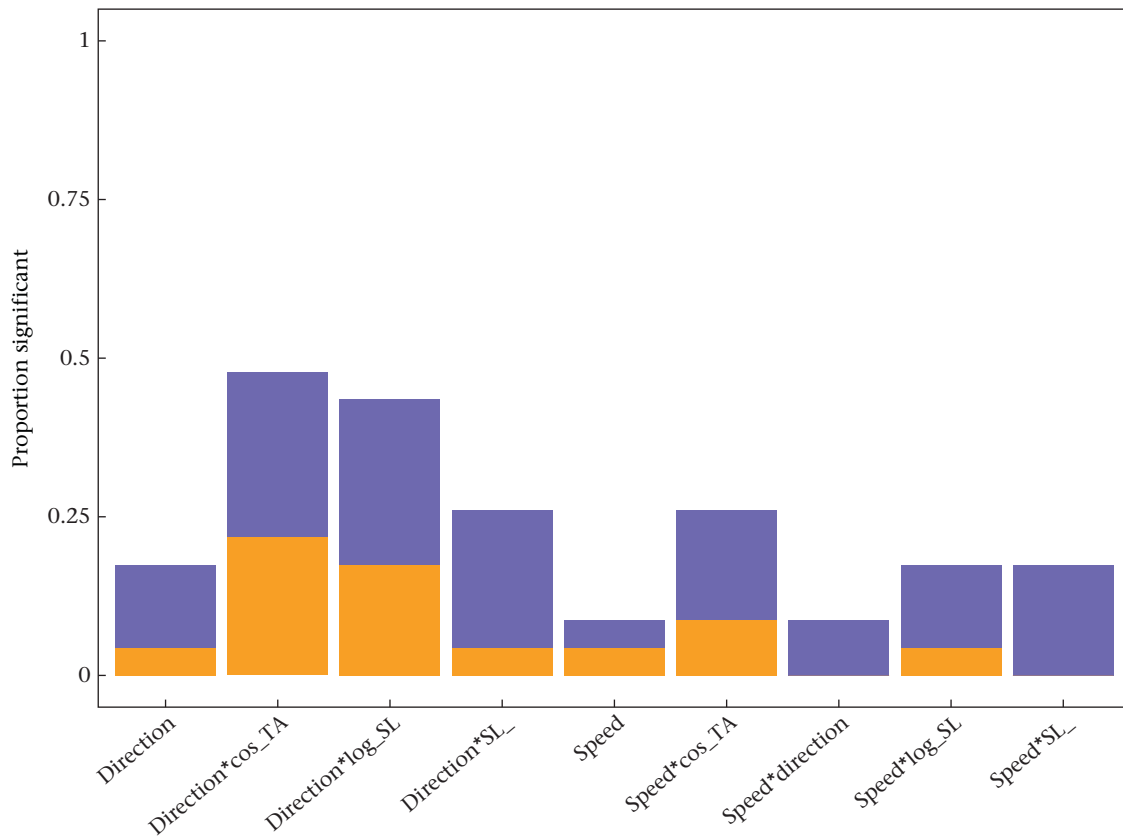

Figure A6. Proportion of individual models for which environmental covariates (wind speed and direction) and movement variables were significant fixed effects in integrated step selection functions fitted for 13 adult (purple) and 10 subadult (orange) Caspian terns during Sahara−Mediterranean crossings. Cos_TA = cosine of turning angles, direction = wind direction, SL_ = step length, log _SL = natural logarithm of step length, speed = wind speed.