ORIGINAL ARTICLE

Revealing different migration strategies in a Baltic Common Tern (*Sterna hirundo*) population with light-level geolocators

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Abstract

The Common Tern (*Sterna hirundo*) is one of Germany's farthest migrating bird species. Ringing studies have shown the use of the East Atlantic flyway, and according to their main wintering areas at the western and southern African coasts, German and European Common Tern populations have been divided into two allohiemic groups. However, first ring recoveries of German Common Terns in Israel indicated that some of the birds breeding in eastern Germany cross central Europe and migrate along the eastern African coast. To investigate the migratory behavior of Common Terns from East Germany, we fitted 40 Common Terns breeding in a colony at the German Baltic coast with light-level geolocators. Twenty-four loggers with analyzable datasets could be retrieved, revealing two different migratory strategies within one population. Seventeen individuals (70.83%) used the eastern Atlantic flyway and spent the winter at the western African coast, the Gulf of Guinea and the southern African coast, while the other individuals ($n = 7$; 29.17%) crossed central Europe, migrated along the eastern African coast and overwintered in the Mozambique Channel and South African coast. We, therefore, suggest to add a third allohiemic group to complement the picture of European Common Tern migration. Moreover, our results provide new knowledge and open new questions, which can be used for future studies regarding the evolution of different migratory strategies and its consequences in relation to climate change.

Keywords Migration · Tracking · Light-level geolocation · Common Tern · *Sterna hirundo*

Zusammenfassung

Licht-Dunkel-Geolokation zeigt verschiedene Zugstrategien an der Ostsee brütender Flussseeschwalben (Sterna hirundo). Flussseeschwalben (*Sterna hirundo*) gehören zu den am weitesten ziehenden Vogelarten in Deutschland. Beringungsstudien haben gezeigt, dass sie den Ostatlantischen Zugweg nutzen, und entsprechend ihrer Winterquartiere an den west- und südafrikanischen Küsten wurden deutsche und europäische Brutpopulationen in zwei allohiemische Gruppen eingeteilt. Erste Wiederfunde beringter Flussseeschwalben in Israel weisen allerdings darauf hin, dass offenbar einige im Osten Deutschlands brütende Flussseeschwalben Mitteleuropa überqueren und einen Zugweg entlang der ostafrikanischen Küste nutzen. Um das Zugverhalten an der deutschen Ostseeküste brütender Flussseeschwalben zu dokumentieren haben wir 40 Individuen mit Hell-Dunkel-Geolokatoren ausgestatt Vierundzwanzig auswertbare Datensätze konnten analysiert werden, die die Nutzung zweier unterschiedlicher Zugstrategien zeigten. Siebzehn (70.83%) der Vögel nutzten den ostatlantischen Zugweg und verbrachten den Winter an der westafrikanischen Küste, im Golf von Guinea und an der südafrikanischen Küste, während die übrigen ($n = 7$, 29.17%) Mitteleuropa überflogen, entlang der ostafrikanischen Küste zogen und in der Straße von Mosambik und an der Küste Südafrikas überwinterten. Anhand dieser Ergebnisse schlagen wir vor eine dritte allohiemische Gruppe zu der bisherigen Einteilung hinzuzufügen um das Bild der Migration europäischer Flussseeschwalben

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zu vervollständigen. Unsere Ergebnisse liefern neue Grundlagen und öffnen neuen Fragen für die weitere Erforschung der Entstehung der verschiedenen Migrationsstrategien sowie der daraus entstehenden Folgen im Angesicht des Klimawandels.

Introduction

Humans always had been fascinated by the mysteries of annual bird migration. During the last 120 years, many of them have been solved thanks to bird ringing, however, many questions are still open. In many cases migration is primarily an adaptation for exploiting seasonal peaks of resource abundance and avoiding seasonal resource depression (Alerstam et al. 2003), which enable migratory species to breed in regions which are not suitable for year-round use. It comes, however, with the drawback of a dependency on a linked chain of sites essential for completing their annual cycles (Myers et al. 1987). As threats to sites within these chains may drive rapid population declines of migrant species (Runge et al. 2015), a better understanding of migration strategies (e.g. routes, stopover sites, and wintering areas) is fundamental for the protection of threatened migratory bird species, especially in the context of climate change and human induced habitat loss.

One of Germany's farthest migrating bird species is the Common Tern (*Sterna hirundo*), considered as critically endangered in the German red list (Ryslavy et al. 2020). Most of the German Common Terns breed in the Wadden Sea and at the Baltic coast, but smaller numbers are also found in inland colonies at rivers and lakes (Gedeon et al. 2014). Ring recoveries have shown that the wintering areas of German Common Terns are up to the southernmost parts of Africa (Bairlein et al. 2014). Several analyses of ring recoveries have shown that they use the East Atlantic Flyway, migrating in south-western direction, following the European and African Atlantic coasts (Nebelsiek 1966; Neubauer 1982; Bairlein et al. 2014; Heinicke et al. 2016). Based on their main wintering areas, German breeding populations have been divided into two main groups (Neubauer 1982): the birds breeding at the North Sea as well as in western and southern German inland, which mainly overwinter at the western African coasts between Western Sahara and Nigeria (Nebelsiek 1966; Neubauer 1982; Bairlein et al. 2014), and the birds breeding at the Baltic coast and in eastern German inland, which migrate further and spend the winter at the southern African coasts (Neubauer 1982; Bairlein et al. 2014; Heinicke et al. 2016).

In 2011, a Common Tern ringed at Böhmke Island (northeast Germany, Fig. 1), which had been recaptured in Israel (Fiedler et al. 2013), was the first evidence of a German Common Tern using a migration route in south-eastern direction. One year later, a bird ringed in Israel was found breeding in an inland colony at Lake Trauerwiesen in Saxony (eastern German inland, Fig. 1, Fiedler et al. 2013).

So far, migration between eastern Germany and Israel has been documented for twelve individuals (database Hiddensee bird ringing center), raising suspicion that the proportion of German Common Terns using an eastern migration route might be larger than expected when the first bird was caught. Beside the birds ringed or recaptured in Israel, there are only four other recoveries of German Common Terns which might be assigned to the eastern route. They concern individuals ringed in eastern Germany which were recently found in southern Poland, Czech Republic, and Hungary (Fiedler et al. 2020). Until now, there are no ring recoveries of German Common Terns from eastern Africa, but it has been presumed that birds using the eastern migration route follow the red sea and eastern African coast to wintering areas in southern Africa (Heinicke et al.2016).

In the last decades, tracking devices such as global positioning systems (GPS) and light-level geolocators became smaller and more lightweight, hence could be used to reveal the secret year-round migratory behavior of an increasing number of species (McKinnon et al. 2013; Alarcón and Lambertucci 2018). Light-level geolocators record ambient light intensity and the geographic information can be estimated from the reconstructed times of dawn and dusk (Fiedler 2009; Bridge et al. 2013). They have been used successfully before on Common Terns, revealing the migration routes and wintering areas of individuals breeding in northern America (Nisbet et al. 2011; Bracey et al. 2018) and the Azores (Neves et al. 2015). Becker et al. (2016) and Kralj et al. (2020) were the first to use light-level geolocators on Common Terns in continental Europe. The terns fitted with geolocators in Wilhelmshaven confirmed the main wintering areas of north-western German Common Terns in western Africa (Becker et al. 2016, see also Kürten et al. 2022), whereas Kralj et al. (2020) revealed the eastern flyway, used by Hungarian and Croatian Common Terns, for the first time.

Baltic Common Terns, however, have not been tracked yet, and knowledge about their migratory behavior is based only on ring recoveries. To fill this gap and get a more detailed insight into their migratory behavior we fitted 40 breeding individuals from a colony at the German Baltic coast with light-level geolocators. Our aim was to get detailed information about their migration routes, stopover sites, and wintering areas, especially for birds using the eastern route, where recoveries of ringed birds are extremely rare. An identification of migration routes, stopover sites and wintering areas is important, as it may help to adjust and/or develop new knowledge-based conservation management that may not only help to conserve Common Terns, but also
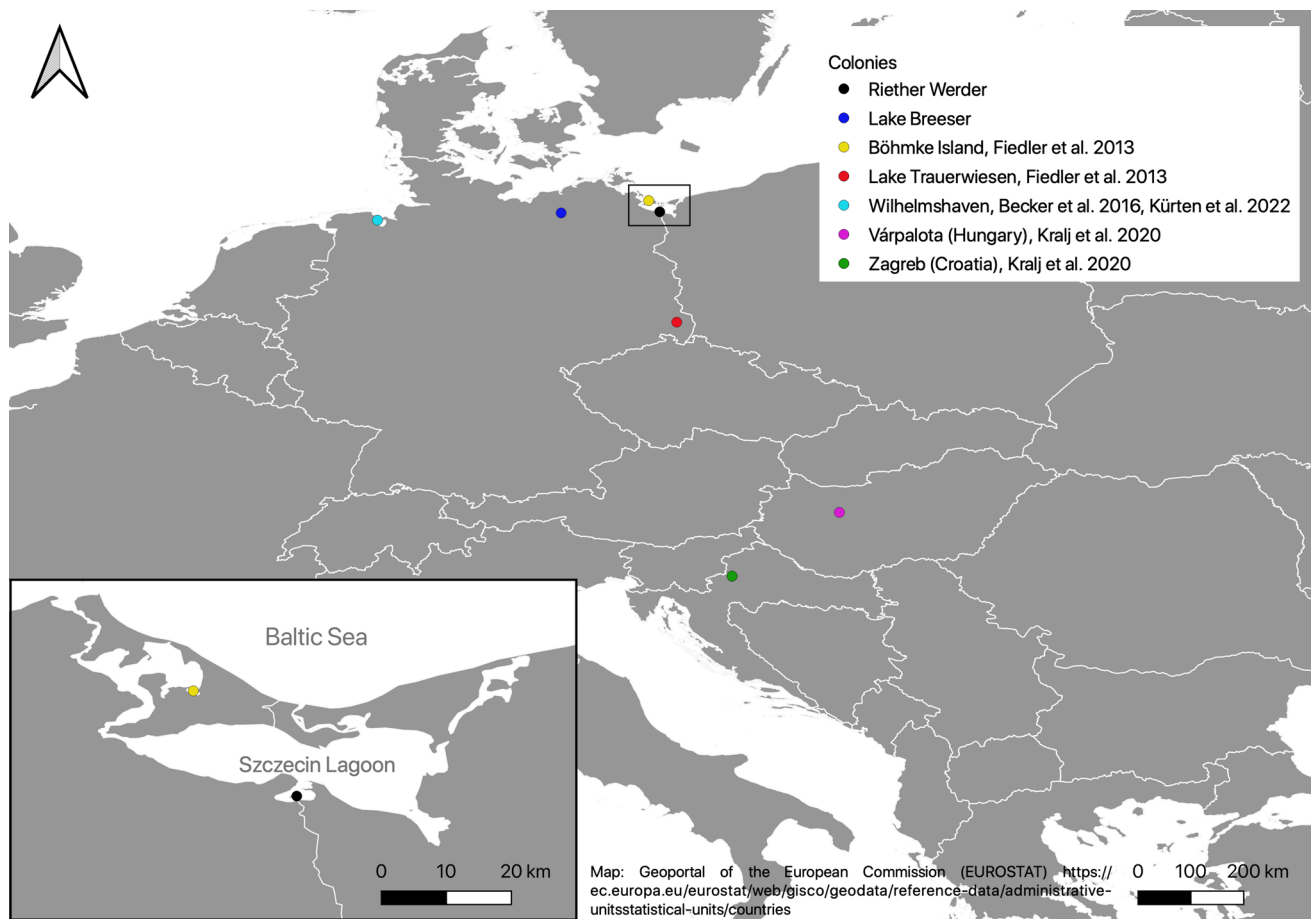
Fig.1 Locations of all European Common Tern colonies mentioned in this article

other migratory species suffering from climate change and human induced habitat alterations.

Methods

Study site and study birds

Common Terns are long-distance migratory seabirds (Becker and Ludwigs 2004), which show a high degree of breeding philopatry (Szostek and Becker 2012; Zhang et al. 2015). They are relatively easy to catch during the incubation, and as they are large enough to carry loggers without detectable negative effects on their reproductive success and survival (Kürten et al. 2019) are well suited for geolocator studies.

In Mecklenburg-Western Pomerania, Common Terns breed in several colonies at the Baltic coast, as well as in inland colonies at lakes (Köhler and Neubauer 2015). Currently, the largest colony with about 150 pairs is found on Riether Werder (53°42′ N 014°16′ E, Fig. 1), a protected island in the German part of the Szczecin Lagoon. Although

the degree of interconnectedness is unknown, Common Terns breeding on Riether Werder seem to be part of a larger population in the western Baltic Sea, since natal and breeding dispersal is shown regularly between birds from Mecklenburg—Western Pomerania, eastern German Inland, Poland and the Baltic coast of Denmark, whereas exchange with the North Sea population is extremely rare (Heinicke et al. 2016).

Since 2013, breeding birds and nestlings have been ringed annually in the colony on Riether Werder, so the birds are used to the presence of ringers during the whole breeding season. To prevent egg damage while catching the breeding adults with walk-in cage traps placed on the nest, the real eggs were temporally exchanged with fake eggs, and stored in polystyrene boxes to prevent cooling.

Programming, deployment and recovery of geolocators

A total of 40 individuals were fitted with light-level geolocators (Intigeo-W65A9-SEA, Migrate Technology Ltd) during the breeding season in 2019. To enhance the chance of

recapture, only birds which have been recorded breeding at least once before in the colony on Riether Werder were chosen. Thirty-nine of them had been ringed in the colony on Riether Werder, either as breeding adults or nestlings, and one had been ringed as nestling in a colony at Lake Breeser (Fig. 1) in 2003, but it was breeding on Riether Werder since 2013. The loggers were programmed to sample light intensity and wet/dry data. Light intensity was sampled every minute and the maximum light intensity was recorded every 5 min. Wet/dry conditions were sampled every 30 s, for "wet" counts conductivity was set to only record contact with saltwater to identify periods when a bird was exposed to seawater.

To attach the geolocators to the bird's leg, they were wrapped in a thin layer of self-annealing tape and mounted to a plastic leg ring with an UV-resistant cable tie. The plastic rings were glued to prevent ring loss. The total weight of the ring, geolocator, tape, tie, and glue was 0.95 g ($\pm$ 0.02 g), representing 0.7% of the mean body mass of an adult Common Tern (around 130 g according to Wendeln and Becker 1996), which conforms with the international standards of maximum 3–5% of an animal`s body weight (Bridge et al. 2011), and can be used without having detectable negative effects on their survival (Kürten et al. 2019). The average handling time per bird was about five minutes.

In the following breeding season, a total of 29 (72.5%) of the individuals fitted with a logger could be recaptured in the colony on Riether Werder. One other bird was seen twice and identified by its coded leg ring but could not be recaptured. Another individual was photographed with its logger still present at a post-breeding roosting assembly in Świnoujście (24 km north from Riether Werder) in August 2020, but its breeding place remained unknown. After recapturing a bird, the logger and cable tie were removed. As four of the recaptured birds had lost their loggers, a total of 25 (62.5%) of the loggers could be retrieved. Of the 25 retrieved loggers, 23 (92%) had worked properly for the entire year, while the other two stopped working after 8 and 2 months, respectively. The latter one was excluded from all analyses, as the bird had not left the breeding area when the logger failed.

Data analysis

After extracting the data, light-level analyses were conducted in R Studio (v4.0.2, RStudio Team 2020) according to the online supplementary manual of Lisovski et al. (2020), using the packages BAStag (Wotherspoon et al. 2016) for twilight determination, FLightR (v0.5.1 Rakhimberdiev et al. 2015) for the analyses and maps (Becker et al. 2018) for the visualizations.

Twilight determination was done with a light-level threshold of 1.5 lx, extreme outliers (wrongly identified

sunrises or sunsets caused by periods of strong shading at day or artificial lighting at night) were removed manually. Data recorded during the breeding time, identified by the long shading periods when birds covered the logger during incubation, were excluded from the analyses. Two 5–20-day calibration periods at the breeding site were set individually for each bird (first after the incubation period and prior to migration, second after returning to the colony and prior to incubation). A second calibration period was not possible for the loggers which stopped working during the year ($n = 2$). Based on a preliminary and unconstrained analysis of the geolocation data using the software Intiproc, (v1.03, provided by Migrate Technology), we spatially constrained the final model between 35° W, 40° S, 25° E and 60° N for birds using the western migration route, and 5° W, 40° S, 70° E and 60° N for birds using the eastern migration route, using the make.grid function. We run the model with the $1e^6$ particle filter recommended by Lisovski et al. (2020).

The stopover analyses were conducted with a cut-off probability (minimal threshold probability of moving, Lisovski et al. 2020) of 0.4. Stopovers were defined as stationary periods where an individual had spent at least 10 twilights (5 days) in a given area, as Common Terns are thought to use stopover sites for more than 5 days (Becker et al. 2016; Kralj et al. 2020). The full R code is shown in online resource 1.

As post-breeding dispersal and start of autumn migration was not always easy to differentiate, only movements resulting in stopovers of ≥ 20 days which were still $\geq 50°$N were considered as post-breeding dispersal. Stopovers estimated < 200 km from Riether Werder were neglected due to the general imprecision of light-level geolocation. As not all individuals remained stationary during winter, wintering areas were defined as those where the birds stayed between November and January. Consequently, they could be large or consist of two or more smaller regions, spatially separated.

Duration of migration was defined as the time between departure from the Szczecin Lagoon or, in birds showing post-breeding dispersal, from the area to which they dispersed and arrival at the wintering area and vice versa. Wet/dry data were plotted as minutes per day in which a logger had contact to saltwater. The low salinity of the Szczecin-lagoon (ranging between 0.5 and 2 PSU, Radziejewska and Schernewski 2008), which basically resembles freshwater, allowed us to identify first and last contact to saltwater after and before the breeding season, which could be used to confirm the dates of departure from or arrival at the breeding area, respectively. Arrival and departure dates were defined as the date when the bird arrived at or departed from the region where it spent the winter.

According to their migration route and wintering areas the birds where divided into three groups:

Group A: used western migration route, wintered in western Africa and the Gulf of Guinea;

Group B: used western migration route, wintered in Namibia and South Africa;

Group C: used eastern migration route, wintered in Mozambique and South Africa.

For statistical comparison of autumn and spring migration all individuals with full datasets ($n = 23$) were used. Paired t tests or, if data were not normally distributed, Wilcoxon signed-rank tests were used to compare duration of autumn and spring migration and the number of days spent at stopover sites during each migration phase.

Birds wintering in western Africa were excluded for the statistical comparisons between birds using the eastern and birds using the western migration route, to have a direct comparison between birds wintering at the same latitude. Welch's two-sample *t* tests or, for not normally distributed data Mann–Whitney *U* tests, were used to compare the duration of migration phases as well as the number of days spent at stopover sites during both migration phases

between the birds of groups B and C. To compare the dates of start of spring migration and arrival in the breeding area between birds of groups B and C, dates were converted into day of the year and analyzed for differences using Welch's two-sample t tests.

Visualization

Two maps were generated using QGIS (v3.8, QGIS Development Team 2021), one showing the locations of all Common Tern colonies mentioned in this Article (Fig. 1), the other one showing all individual tracks and the wintering areas of the Common Terns tagged at Riether Werder (Fig. 2). Wintering areas were visualized separately for birds of groups A, B, and C using the *heatmap* function (quartic kernel estimation with a radius of 2° and an output grid size of 0,1°) for locations estimated for daily twilight events in FlightR between the individually estimated days of arrival at and departure from the wintering area.

Fig. 2 Migration routes and wintering areas of 24 Common Terns from Riether Werder tracked with light-level geolocators. Three groups are represented: A: western migration route, wintering in western Africa and Gulf of Guinea; B: western migration route, wintering in Namibia and South Africa; and C: eastern migration route, wintering in Mozambique and South Africa. Wintering areas for group A, B, and C are visualized as *heatmaps* based on the individually estimated location for each twilight event between arrival at and departure from the wintering area

Map: Geoportal of the European Commission (EUROSTAT): https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-unitsstatistical-units/countries
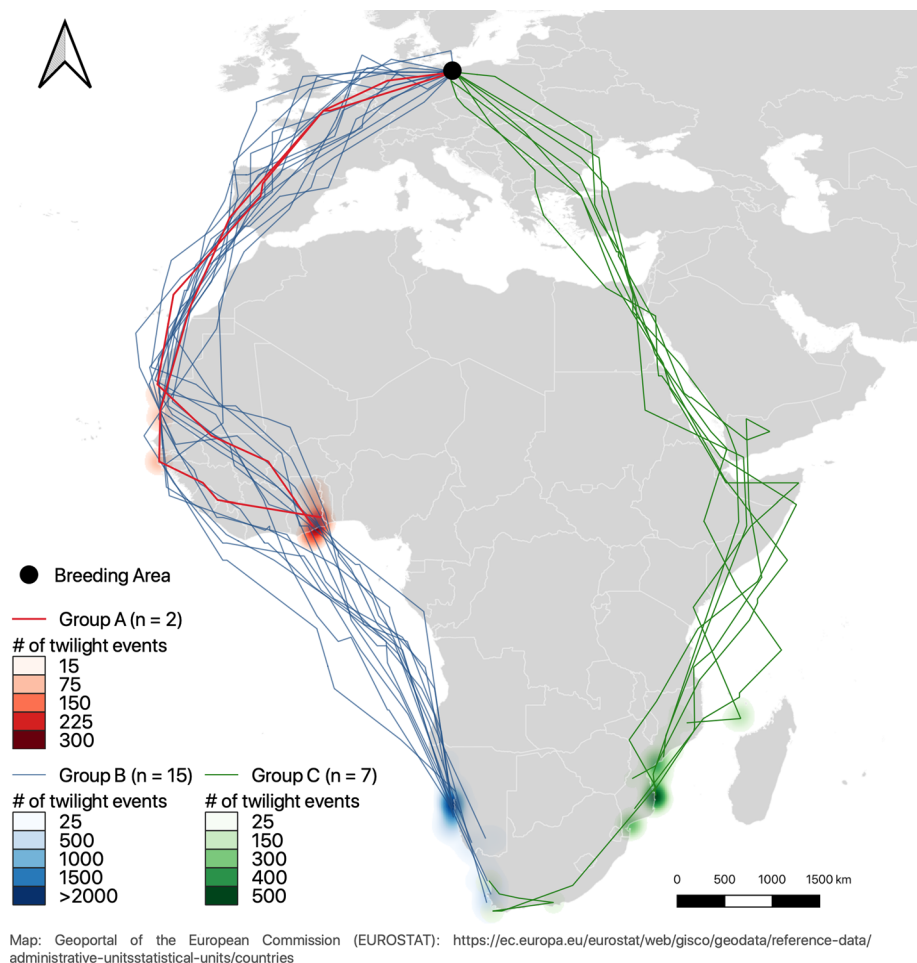
Results

Summary of immersion data

The Szczecin-lagoon was not recognized as saltwater by the loggers. In all birds, first saltwater contacts were registered after the breeding season, although in eight individuals first saltwater contact was recorded before the estimated departure from the breeding area (online resource 2). During migration and in the wintering areas, all birds had contact to saltwater nearly every day, ranging between several minutes and several hours. First saltwater contact after the breeding season and last saltwater contact before returning to the breeding area are shown in Online resource 2, individual plots of saltwater contact during the year in minutes per day are shown in Online Resource 3.

Migration data analyses

Of the 24 birds with analyzable data, 17 (70.83%) took the western migration route, and seven (29.17%) the eastern route. Tracked migration routes and wintering areas of all individuals are shown in Fig. 2. A table summarizing arrival and departure dates, duration of migration phases, and the number of days spent at stopover sites can be found in Online Resource 2. Individual plots showing the migration routes, stopover sites, and wintering areas are shown in Online Resource 4.

After breeding, most individuals stayed around the Szczecin-lagoon, while one individual dispersed west to the Netherlands (BS676) and stayed at the Wadden Sea for 43 days until it started autumn migration.

Mean start of autumn migration was August 13th ± 18.9 days (July 5th–September 20th). Birds using the western migration route followed the Eastern Atlantic Flyway (Fig. 2). Their stopover behavior was highly variable. Three birds reached their wintering areas at the western (BS667 & BS694) and southern (BS685) African coasts, without making any stopovers at all, while the others made one or several stopovers, which in some cases lasted up to several weeks. Birds using the western migration route stopped in three main areas (Fig. 2): The North Sea ($n=8$), western African coast ($n=8$), and the Gulf of Guinea ($n=11$). In the Gulf of Guinea, especially the coastal areas of south-eastern Ghana were often used as stopover sites. Two individuals even spent the entire winter in western Africa. One (BS667) spent the time between end of August and beginning of December at the coasts of Mauritania and Senegal before moving to the coast of Ghana, where it joined the other one (BS694), which spent the entire winter in this region. The remaining

15 individuals migrated further south to wintering areas at the coasts of Namibia and South Africa and made further stopovers at the coasts of Gabon, Congo or Angola. At the southern African coast, the area around Walvis Bay (Namibia) was the most frequented wintering area ($n=10$).

Spring migration started on average on March 18th ± 8.0 days (March 5th–March 30th). The birds did not stop in the Gulf of Guinea during spring migration, but all birds rested some time at the western African coast ($n=17$) before flying back to Europe. Eight of the birds stopped at Bay of Biscay, a stopover site that was not used during autumn migration, and six individuals stopped at the North Sea before they returned to the breeding area. Mean arrival date was on April 23rd ± 6.6 days (April 10th–May 9th).

Birds using the eastern migration route either directly crossed central Europe to reach the Mediterranean coast in Greece or Turkey ($n=3$) or first flew to the western coast of the Black Sea and then turned south to the Mediterranean Sea ($n=4$). After crossing the Mediterranean Sea, they all followed the Red Sea, crossed the Horn of Africa and followed the eastern African coast south. The most frequented stopover sites were at the southern Red Sea and Gulf of Aden, where five of the seven birds spent between 30 and 68 days. Further stopovers were scattered over the coasts of Somalia, Kenia, and Tanzania. The wintering areas of six of the seven birds on the eastern flyway were at the Mozambique Channel. Five of them wintered at the Mozambican coast, and one (BS666) stayed for 84 days around the Comoro Islands and Madagascar, before it moved to the Mozambican coast, where the logger stopped working. The seventh bird (BS695) rested for 36 days in southern Mozambique, and then flew to South Africa, where it moved back and forth twice between the areas around Port Elizabeth and Cape Town.

Mean start of spring migration of birds using the eastern migration route was on March 2nd ± 6.1 days (February 24th–March 13th). They did not make stopovers at the southern Red Sea and Gulf of Aden during spring migration, but short stopovers were scattered over the northern Red Sea, Suez Canal and the Nile delta. All of them made stopovers at the Mediterranean coast of Turkey or Greece, or the western coast of the Black Sea before crossing central Europe and returning to the breeding area. Mean arrival day of birds using the eastern migration route was on April 20th ± 1.5 days (April 18th–22nd).

Although autumn migration lasted longer in some individuals, no significant differences between the duration of autumn and spring migration were found, neither for all birds (Wilcoxon signed-rank test: $V=146$, $p=0.820$, $n=23$), nor when only considering birds using the western migration route (paired-sample t test: $t(16)=-0.832$, $p=0.418$, $n=17$)

or birds using the eastern migration route (paired-sample *t* test: $t(5) = 1.072$, $p = 0.333$, $n = 6$).

Even though some of the birds, especially those using the eastern flyway, made long stopovers during autumn migration, in general there were no significant differences between the number of days spent at stopover sites during autumn and spring migration (Wilcoxon signed-rank test for all individuals: $V = 112$, $p = 0.649$, $n = 23$; paired-sample t test for birds using the western route: $t(16) = -1.823$, $p = 0.087$ $n = 17$; paired-sample t test for birds using the eastern route: $t(5) = 1.089$, $p = 0.326$, $n = 6$).

However, both migration phases lasted significantly longer in birds using the eastern migration route than in birds using the western migration route (Welch two-sample *t* test for autumn migration: $t(6.390) = 2.452$, $p = 0.047$, $n = 22$; Welch two-sample *t* test for spring migration: $t(9.412) = 3.269$, $p = 0.009$, $n = 21$). Similarly, during both migration phases birds using the eastern migration route spent significantly more time at stopover sites than birds using the western migration route (Welch two-sample *t* test for autumn migration: $t(6.349) = 2.965$, $p = 0.023$, $n = 22$; Wilcoxon signed-rank test for spring migration: $V = 80$, $p = 0.007$, $n = 21$).

Start of spring migration was significant earlier in birds using the eastern migration route than in birds using the western migration route (Welch two-sample *t* test: $t(11.995) = -4.527$, $p < 0.001$, $n = 21$), but arrival date in the breeding area showed no significant difference (Welch two-sample *t* test: $t(17.284) = -1.555$, $p = 0.138$ $n = 21$), although it was scattered over a larger time period by birds using the western route.

Discussion

Despite the indications of German Common Terns using a migration route in south-eastern direction since the first individual was recaptured in Israel (Fiedler et al. 2013), the large proportion of birds using the eastern migration route in this study, and the diversity of wintering areas exceeded our expectations. Based on ringing studies by Neubauer (1982), Bairlein et al. (2014), and Heinicke et al. (2016) it had been expected that the vast majority of the tagged birds would use the western migration route and spend the winter in Namibia and South Africa. Compared to ring recoveries, geolocation data, however, provide a much more detailed view of migratory behaviour, as shown for several other European tern species (e.g. *Chlidonias niger*, Van der Winden et al. 2014, *Sterna dougalli,* Redfern et. al. 2021, *Sterna paradisaea*, Egevang et al. 2010; McKnight et al. 2013).

Most of the birds from Riether Werder stayed around the Szczecin-lagoon until the start of autumn migration, confirming the importance of the lagoon as roosting area

(Heinicke et al. 2016). According to the immersion data, some individuals also stayed at the open Baltic Sea, as the loggers registered contact to saltwater before the bird left the breeding area. Some of the birds indeed have been seen roosting in Świnoujście at the outer coast of Usedom and Wollin, in August 2020 (database Hiddensee bird ringing central). As the distance between Riether Werder and the open Baltic Sea, where salinity ranges between 5 and 10 PSU (Zettler et al. 2007), is less than 30 km (the Szczecin Lagoon and open Baltic Sea are only separated by a small spit of land, see Fig. 1), such movements were not recognized by geolocation data. In agreement with Neubauer (1982) and Heinicke et al. (2016), first individuals started autumn migration in July, while the departure of the last individual on September 20th coincide with latest observations of Common Terns in Mecklenburg-Western Pomerania at the end of September and beginning of October (Köhler and Neubauer 2015).

Western migration route

Birds on the western route followed the East Atlantic Flyway, confirming the routes indicated by ringing studies (Neubauer 1982; Glutz von Blotzheim and Bauer 1999; Bairlein et al. 2014; Heinicke et al. 2016). The behavior of tagged birds was highly variable with regards to the number of stopovers as well as the time spent at stopover sites. Many of the birds using the western migration route had stopped at the North Sea. Most of these stopovers only lasted a few days, but some birds stayed there for longer periods, suggesting that the North Sea is an important stopover site for Common terns.

Nearly all of the birds using the western migration route stopped at least once in western Africa, most made several stopovers in the region between Western Sahara and Liberia, and/or in the Gulf of Guinea. The coastal region of western Africa is a highly productive upwelling area (Helmke et al. 2005), which is a very attractive region for wintering for many seabirds (Grecian et al. 2016), including different tern species (e.g. Becker et al. 2016; Heinicke et al. 2016; Redfern et al. 2021). In the Gulf of Guinea, the coastal areas of Ghana seem to be the most important stopover sites. Due to a high food abundance in brackish and saltwater wetlands, Common Terns are found in large numbers in this area (Ahulu et al. 2006). Especially the Ramsar sites around the capital Accra, such as Densu Delta, Songor Lagoon and Keta Lagoon are important roosting and wintering areas as they provide roosting and feeding sites for tens of thousands of waterbirds (Ntiamoa-Baidu et al 1998; Ahulu et al. 2006; Lamptey and Ofori-Danson 2014; Holbech et al. 2018). The wintering areas at the coasts of Mauretania, Senegal and Ghana used by two birds from Riether Werder, were also

found as main wintering areas for Common Terns tagged in Wilhelmshaven (Becker et al. 2016, Kürten et al. 2022).

Wintering areas further south were found in Namibia and South Africa, as expected for Baltic birds according to ringing studies (Neubauer 1982; Bairlein et al. 2014; Heinicke et al. 2016). Most important stopover and wintering areas here seem to be around Walvis Bay, a Ramsar site of international importance, which according to Wearne and Underhill (2005) hosts up to 15% of the flyway population of Common Terns. In South Africa, the area between St. Helena Bay and Cape Town, was used as wintering area by our birds, which agrees with ringing studies, although German Common Terns have been found at the southern and eastern coast of South Africa as well (Elliott 1971; Bairlein et al. 2014). The wintering areas at the coasts of Namibia and western South Africa lay at the Benguela current upwelling system, one of the world's most productive marine ecosystems (Shannon and Field 1985), providing food for many endemic and wintering seabird species (Makhado et al. 2021).

While Gulf of Guinea did not play a role as resting area during spring migration, the Bay of Biscay was found to be a highly frequented stopover site, although not used during autumn migration. Although not clear, this pattern might be correlated with a strong increase of primary production in the Bay of Biscay in March and April (Garcia-Soto and Pingree 2009) and the recruitment of Anchovies (*Engraulis encrasicolus)* which spawn there in spring (Borja et al. 1996) and are a favorite prey of Common Terns (Mauco et al. 2001).

Eastern migration route

For the birds using the eastern migration route, two general strategies to cross central Europe can be derived from the geolocation data, although not all individuals used the same strategy during both migration phases. The birds either migrated directly to the eastern Mediterranean coast or made a detour to the Black Sea. The most important stopover sites for birds using this route were in the southern Red Sea and Gulf of Aden. This area was also identified as an important stopover site by Kralj et al. (2020), as all four of their Common Terns tagged in Croatia and Hungary stopped there as well, three of them for more than 2 months. The southern Red Sea is a highly productive marine ecosystem, especially during winter when cold and nutrient rich water from the Indian Ocean is pressed through the Gulf of Aden into the Red Sea by winter monsoons (Raitsos et al. 2015). However, similar to Croatian and Hungarian Common Terns (Kralj et al. 2020), the birds from Riether Werder did not stay there during the high productive phase in winter. They moved further south and their main wintering area was in the Mozambique Channel, where five of them spent the winter at the Mozambican coast, while one stayed around the

Comoro Islands until it also moved to the continental coast in January.

The Mozambique Channel is a very productive region (José et al. 2016), which has been identified as wintering area for Croatian Common Terns (Kralj et al. 2020), as well as a hotspot for foraging tropical seabirds (Le Corre et al. 2012) and wintering sub-Antarctic seabirds (Jaquemet et al. 2014). However, the productivity in the Mozambique Channel depends on strong eddy activity, bringing nutrient rich water to surface layers (José et al. 2016). Annually, four to seven eddies transit from north to south through the Mozambique Channel (Tew Kai and Marsac 2010), leading to an unequal distribution of productivity through the year. This might be an explanation for birds on the eastern route, in contrast to many on the western migration route, to move between different sites during winter. One of the individuals moved further south and to the South African coast, even rounding the Cape of Good Hope.

Similar to Croatian and Hungarian Common Terns (Kralj et al. 2020), the birds tagged at Riether Werder made no stopovers in the southern Red Sea during spring migration, but before they crossed Europe to return to their breeding area, they all made stopovers, either at the Mediterranean coast of Turkey or Greece, or at the western coast of the Black Sea.

Spring and autumn migration

Although autumn migration lasted up to 3 months for some individuals, we could not confirm the results of Kralj et al. (2020), which indicate that autumn migration lasted four times longer than spring migration, as we found no significant difference between the duration of the migration phases. Faster spring migration is a common pattern in birds (Nilsson et al. 2013), although the opposite was found for the Common Terns tagged in Wilhelmshaven (Becker et al. 2016; Kürten et al. 2022). This contrasting pattern may be caused by differences in the migration behavior between the different populations under study, or by variances in weather and wind conditions between different study years and migration routes, but also could be the result of low sample sizes, especially in the study by Kralj et al. (2020; $n = 2$) and high individual variation. In our study, on both flyways some birds were faster during spring migration while others were faster during autumn migration, indicating that there is indeed strong individual variation.

However, our results confirmed indications made by Kralj et al. (2020) when comparing to Becker et al. (2016), that birds using the eastern route spent significantly more time at stopover sites than those on the western route, which resulted in a significantly longer duration of migration phases. Although not clear, this difference may be caused by differences in weather and wind conditions, or differences

in the food abundance along the different migration routes. Birds using the eastern route started spring migration significantly earlier than birds using the western route, perhaps to compensate for the longer duration of migration and to arrive at the same time at the breeding colony than birds using the western route, since there was no significant difference between the arrival dates of both groups. This makes sense considering that late arrival could have negative fitness effects as individuals have to compete with their conspecifics for high-quality nest sites and mates (Kokko 1999).

Allohiemic groups

Variations in wintering areas between different European Common Tern groups have been noticed earlier (Radford 1961). Elliott (1971) applied the idea of splitting western European and Scandinavian terns into two allohiemic groups according to their main wintering areas (after Salomonsen 1955). Neubauer (1982) showed that the separation line between these groups go through Germany, and assigned the populations of the North Sea as well as western and southern German inland to the western European group, which mainly winters in western Africa, and the Baltic population as well as eastern German inland populations to the group with the Scandinavian terns, which mainly winter in southern Africa.

When the first German ringed Common Tern was recaptured in Israel in 2011, Fiedler et al. (2013) suggested it was a rare exception. That nearly a third of the birds tagged on Riether Werder used the eastern migration route may not be generalizable to all eastern German populations. However, since the colony on Riether Werder is currently the largest in Mecklenburg—Western Pomerania, it seems like the number of individuals using the eastern flyway has been severely underestimated. Furthermore, recent logger (Kralj et al. 2020) and ringing studies (for example in Israel, Kiat 2020) indicate that the eastern African flyway is used far more often than expected. First results of the ringing study in Israel show that the breeding areas of Common Terns ringed or recaptured in Israel are distributed over eastern Germany, Poland, Lithuania, Latvia, southern Finland, Belarus, Ukraine, Romania, Bulgaria, Slovakia, Croatia, and Hungary (Heinicke et al. 2016; Fiedler et al. 2018). Therefore, we suggest to add a third group of eastern European Common Terns, those with a breeding area between eastern Germany, southern Finland, and the Black Sea, and wintering areas at the south-eastern African coast to the grouping by Elliot (1971) and Neubauer (1982) to complement the picture of European Common Tern migration behavior.

Two hypotheses might explain the current lack of ring recoveries of German Common Terns on the eastern African flyway. The population of eastern European Common Terns may be expanding in western direction. If birds using the eastern African migration route started breeding in eastern Germany only a decade or two ago, this would explain why the recoveries in eastern Europe and Israel accumulate since 2011 (Fiedler et al. 2013, 2018, 2020). However, as the tern project in Israel started in 2010 (Heinicke et al. 2016), the lack of recoveries may also be a result of low ringing and reporting activities along the flyway before the project started. As recoveries from eastern African countries such as Egypt, Sudan, Eritrea, Djibouti, Somalia, Kenia, and Tanzania are lacking for Croatian and Hungarian birds as well (Kralj et al. 2020), this might be a hint that reporting rates of ringed terns are indeed low in these countries.

A long-term use of the eastern flyway by eastern German Common Terns may also explain some of the ring recoveries at the eastern coast of South Africa. Ringing studies (Elliott 1971; Neubauer 1982; Bairlein et al. 2014; Heinicke et al. 2016) show recoveries of Common Terns ringed in Germany at the eastern coast of South Africa, for example around Port Elizabeth and Durban. Not knowing about the eastern African flyway, such recoveries of ringed Common Terns had been assigned to birds using the western migration route without questioning. But the fact that one of our tagged birds reached the area around Cape Town using the eastern migration route, and also stayed around Port Elizabeth, might indicate that recoveries of German ringed Common Terns in eastern South Africa may have been assigned falsely to birds using the western route. Unfortunately, the possibility of some of these birds reaching South Africa on the eastern flyway cannot be validated retrospectively.

Important stopover and wintering locations and their conservation

Although stopover sites may be occupied only for a short period of time, even small amounts of habitat loss could have dramatic negative effects if it concerns crucial stopover sites (Runge et al. 2014). Based on the frequency and duration of use, we identified the following stopover sites and wintering areas as being potentially crucial for German and European Common Tern populations. For birds on the western route, the upwelling areas of the Canary current at the north-western African coast, and the Benguela current at the south-western African coast as well as the productive brackish and saltwater wetlands in the Gulf of Guinea (especially in Ghana) seem to be of particular importance. However, terns have to face direct and indirect threats in these regions. Hunting and trapping of terns for food or sport seem to have long tradition in western Africa (Meininger 1988; Stienen et al. 1998), and according to Heinicke et al. (2016), annually around 2% of all fledged Common Terns are reported as being caught and killed in western Africa, and reporting rates are very low in the local communities (Meininger 1988, Stienem et al. 1998). At both upwelling areas, seabirds in

general are also threatened by overfishing (Crawford 2007; Grémillet et al. 2015, 2016), which in Namibia and South Africa already leads to rapid declines of endemic seabirds (Crawford 2007).

For birds on the eastern route, the southern Red Sea and Gulf of Aden have been identified as the most important stopover site, while the Mozambique Channel seems to be their main wintering area. Both, the southern Red Sea (Gladstone et al. 1999) and the Mozambique Channel (Le Corre et al. 2012) face a high risk of pollution due to oil industry and highly frequented maritime routes. Biodiversity in the southern Red Sea in particular is threatened by habitat alteration due to strong increase of human populations (Gajdzik et al. 2021). Ambitious conservation plans for the Red Sea and Gulf of Aden have been made already in the 1990s, but only a fraction of them has been implemented until today (Gajdzik et al. 2021).

Additionally, the effects of climate change are likely to be the largest threats for terns in the future (Palestis 2014). Culp et al. (2017) showed Common Terns and other tern species having a high vulnerability to climate change as well. As migratory species depend upon the availability of suitable habitat in multiple locations, all of which may be affected by climate change in different ways, they face an increased potential for deleterious impacts at some point in their annual cycle (Robinson et al. 2009). Climate change already contributed to strong range shifts of prey species in the Benguela current upwelling system (Crawford et al. 2015; Grémillet et al. 2016), and the western tropical Indian Ocean is warming faster than any other tropical ocean, altering monsoon circulation and marine food webs (Roxy et al. 2014). These changes may affect weather and wind conditions as well as the productivity of stopover sites and wintering areas crucial for terns migrating along the African coasts. At this point, we are not able to conclude if the terns face a higher risk along the eastern or the western route, or how their fitness might be affected depending on the migration route. But the colony on Riether Werder seems to be the perfect place for further studies on differences in migration behavior of Common Terns using different migration strategies, as the colony comprises birds using both routes and different wintering areas. Future studies at the colony of Riether Werder should also consider tracking individuals for subsequent migration cycles to determine the consistency of migratory behavior and the potential consequences of consistent behavior. Tracking of partners and offspring as well as genetic analyses may also help us to understand the species population dynamic and the establishment and evolution of different migration strategies.

Conclusions

This study was the first one tagging Common Terns at the Baltic Sea. Our results gave a new insight into the diverse migration behavior of Common Terns breeding in Germany. We confirmed that the eastern flyway is frequented far more often by Common Terns than expected. Moreover, a larger proportion than expected (nearly one third) of birds taking the eastern over the western flyway, enabled us to determine important stopover sites and wintering areas on both migration routes. We, therefore, suggest, that the northeastern and eastern European Common Terns that use the eastern flyway should be considered as a third allohiemic group, complementing the grouping made by Elliot (1971) and Neubauer (1982).

Common Terns as well as other birds relaying on the identified stopover sites and wintering areas are threatened by human activities ranging from trapping and killing, to overfishing, pollution, habitat loss, and unpredictable alterations of habitats as consequence of global warming. These are the typical threats many migratory species are facing today, and as all countries along the flyways of migratory species share a responsibility, international efforts and cooperation will be necessary to conserve these birds and their natural habitats.

Declarations

References

Ahulu AM, Nunoo FKE, Owusu EH (2006) Food preferences of the common tern, *Sterna hirundo* (Linnaeus, 1758) at the Densu floodplains, Accra. West Afr J Appl Ecol 9:141–148. https://doi.org/10.4314/wajae.v9i1.45678

Alarcón PAE, Lambertucci SA (2018) A three-decade review of telemetry studies on vultures and condors. Mov Ecol 6:13. https://doi.org/10.1186/s40462-018-0133-5

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103:247–260

Bairlein F, Dierschke J, Dierschke V, Salewski V, Geiter O, Hüppop K, Köppen U, Fiedler W (2014) Atlas des Vogelzugs. AULA Verlag, Wiebelsheim

Becker PH, Ludwigs J-D (2004) *Sterna hirundo* common tern. In: Parkin D (ed) BWP Update, vol 6. Oxford University Press, New York, pp 93–139 (**Nos 1 and 2**)

Becker PH, Schmaljohann H, Riechert J, Wagenknecht G, Zajková Z, Gonzáles-Solís J (2016) Common Terns on the East Atlantic Flyway: temporal-spatial distribution during the non-breeding period. J Ornithol 157:927–940. https://doi.org/10.1007/s10336-016-1346-2

Becker RA, Wilks AR, Brownrigg R, Minka TP, Deckmyn A. (2018) Maps: draw geo- graphical maps. version 3.3.0. https://CRAN.R-project.org/package=maps. Accessed 01 June 2020

Borja Á, Uriate A, Valencia V, Motos L, Uirate A (1996) Relationship between anchovy (*Engraulis encrasicolus* L.) recruitment and the environment in the Bay of Biscay. Sci Mar 60:179–192

Bracey A, Lisovski S, Moore D, McKellar A, Craig E, Matteson S, Strand F, Costa J, Pekarik C, Curtis P, Niemi G, Cuthbert F (2018) Migratory routes and wintering locations of declining inland North American Common Terns. Auk 135:385–399. https://doi.org/10.1642/AUK-17-210.1

Bridge ES, Kelly JF, Contina A, Gabirelson RM, MacCurdy RB, Winler DW (2013) Advances in tracking small migratory birds: a technical review of light-level geolocation. J Field Ornithol 84:121–137. https://doi.org/10.1111/jofo.12011

Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fléron RW, Hartl P, Kays R, Kelly JF, Robinson WD, Wikelski M (2011) Technology on the move: recent and forthcoming innovations for tracking migratory birds. Bioscience 61:689–698. https://doi.org/10.1525/bio.2011.61.9.7

Crawford RJ (2007) Food, fishing and seabirds in the Benguela upwelling system. J Ornithol 148:253–260. https://doi.org/10.1007/s10336-007-0228-z

Crawford RJ, Makhado AB, Whittington PA, Randall RM, Oosthuizen WH, Waller LJ (2015) A changing distribution of seabirds in South Africa—the possible impact of climate and its consequences. Front Ecol Evol 3:10. https://doi.org/10.3389/fevo.2015.00010

Culp LA, Cohen EB, Scarpignato AL, Thogmartin WE, Marra PP (2017) Full annual cycle climate change vulnerability assessment for migratory birds. Ecosphere. https://doi.org/10.1002/ecs2.1565

Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. PNAS 107:2078–2208. https://doi.org/10.1073/pnas.0909493107

Elliott CCH (1971) Analysis of the ringing and recoveries of three migrant terns. Ostrich 42:71–82. https://doi.org/10.1080/00306525.1971.9633398

Fiedler W (2009) New technologies for monitoring bird migration and behaviour. Ring Migr 24:175–179. https://doi.org/10.1080/03078698.2009.9674389

Fiedler W, Geiter O, Köppen U (2013) Ringfunde—herausgepickt. Vogelwarte 51:131–136

Fiedler W, Geiter O, Hermann C (2018) Ringfunde—herausgepickt. Vogelwarte 56:281–284

Fiedler W, Geiter O, Herrmann C (2020) Ringfunde—herausgepickt. Vogelwarte 58:423–427

Gajdzik L, Green AL, Cochran JEM, Hardenstine RS, Tanabe LK, Berumen ML (2021) Using species connectivity to achieve coordinated large-scale marine conservation efforts in the Red sea. Mar Poll Bull 122:112244. https://doi.org/10.1016/j.marpolbul.2021.112244

Garcia-Soto C, Pingree RD (2009) Spring and summer blooms of phytoplankton (SeaWiFS/MODIS) along a ferry line in the Bay of Biscay and western English channel. Cont Shelf Res 29:1111–1122. https://doi.org/10.1016/j.csr.2008.12.012

Gedeon K, Grüneberg C, Mitschke A, Sudfeldt C, Eikhorst W, Fischer S, Flade M, Frick S, Geiersberger I, Koop B, Kramer M, Krüger T, Roth N, Ryslavy T, Stübing S, Sudmann SR, Steffens R, Völker F, Witt K (2014) Atlas deutscher Brutvogelarten. Dachverband Deutscher Avifaunisten, Münster

Gladstone W, Tawfig N, Nasr D, Andersen I, Cheung C, Drammeh H, Krupp F, Lintner S (1999) Sustainable use of renewable resources and conservation in the Red Sea and Gulf of Aden: issues, needs and strategic actions. Ocean Coastal Man 42:671–697

Glutz von Blotzheim UN, Bauer KM (1999) Handbuch der Vögel Mitteleuropas. Band 8/1, 2nd edn. AULA Verlag, Wiebelsheim

Grecian WJ, Witt MJ, Atrill MJ, Baerhop S, Becker PH, Egevang C, Furness RW, Godley BJ, Gonzáles-Solís J, Grémillet D, Kopp M, Lescroël A, Matthiopoulous J, Patrick SC, Peter HU, Phillips RA, Stenhouse IJ, Votier SC (2016) Seabird diversity hotspot linked to ocean productivity in the Canary current large marine ecosystem. Biol Lett 12:20160024. https://doi.org/10.1098/rsbl.2016.0024

Grémillet D, Peron C, Provost P, Kato A, Amèlineau F, Ropert-Coudert Y, Ryan PG, Pichgeru L (2016) Starving seabirds: unprofitable foraging and its fitness consequences in Cape gannets competing

with fisheries in the Benguela upwelling ecosystem. Mar Biol 163:35. https://doi.org/10.1007/s00227-015-2798-2

Grémillet D, Peron C, Provost P, Lescroël A (2015) Adult and juvenile European seabirds at risk from marine plundering off West Africa. Biol Cons 182:143–147. https://doi.org/10.1016/j.biocon.2014.12.001

Heinicke T, Herrmann C, Köppen U (2016) Migration und Ansiedlungsverhalten ausgewählter Küstenvogelarten (Charadriidae, Laridae, Sternidae) in Mecklenburg-Vorpommern. Eine Auswertung von Ringfunden. Natur Naturschutz Mecklenbg Vorpomm. 44(3):190

Helmke P, Romero O, Fischer G (2005) Northwest African upwelling and its effect on offshore organic carbon export to the deep sea. Global Biochem Cycles. https://doi.org/10.1029/2004GB002265

Holbech LH, Gbogbo F, Aikins TK (2018) Abundance and prey capture success of Common Terns (*Sterna hirundo*) and Pied Kingfischers (*Ceryle rudis*) in relation to water clarity in southeast coastal Ghana. Avian Res 9:25. https://doi.org/10.1186/s40657-018-0116-7

Jaquemet S, Ternon JF, Kaehler S, Thiebot JB, Dyer B, Bemanaja E, Marteau C, Le Corre M (2014) Contrasted structuring effects of mesoscale features on the seabird community in the Mozambique channel. Deep sea res. Part II Top. Stud Oceanogr 100:200–211. https://doi.org/10.1016/j.dsr2.2013.10.027

José YS, Penven P, Aumont O, Machu E, Moloney CL, Shillington F, Maury O (2016) Suppressing and enhancing effects of mesoscale dynamics on biological production in the Mozambique channel. J Mar Syst 158:129–139. https://doi.org/10.1016/j.jmarsys.2016.02.003

Kiat Y (2020): Warsaw, Minsk, Cape Town and a few terns. Updates from the Israeli Tern project. BirdLife Israel. https://www.birds.org.il/en/article/article-yosef-kiat-terns-project-updates-july-2020. Accessed: 21 November 2020

Köhler J, Neubauer W (2015) Flussseeschwalbe (*Sterna Hirundo*). Beiträge Zur Avifauna Mecklenburg-Vorpommerns 2:53–68

Kokko H (1999) Competition for early arrival in migratory birds. J Anim Ecol 68:940–950. https://doi.org/10.1046/j.1365-2656.1999.00343.x

Kralj J, Martinović M, Jurinović L, Szinai P, Sütő S, Preiszner B (2020) Geolocator study reveals east African migration route of Central European Common Terns. Avian Res 11:6. https://doi.org/10.1186/s40657-020-00191-z

Kürten N, Schmaljohann H, Bichet C, Haest B, Vedder O, Gonzáles-Solís J, Bouwhuis, (2022) Highly individual repeatability of the migratory behaviour of a long-distance migratory seabird. Mov Ecol 10:5. https://doi.org/10.1186/s40462-022-00303-y

Kürten N, Vedder O, González-Solís J, Schmaljohann H, Bouwhuis S (2019) No detectable effect of light-level geolocators on the behaviour and fitness of a long-distance migratory seabird. J Ornithol 160:1087–1095. https://doi.org/10.1007/s10336-019-01686-3

Lamptey AM, Ofori-Danson PK (2014) Review of the distribution of waterbirds in two tropical coastal Ramsar Lagoons in Ghana, West Africa. J Appl Ecol 22:77–91

Le Corre M, Jaeger A, Pinet P, Kappes A, Weimerskirch H, Catry T, Ramos JA, Russel JC, Shah N, Jaquemet S (2012) Tracking seabirds to identify potential marine protected areas in the tropical western Indian Ocean. Biol Conserv 156:83–93. https://doi.org/10.1016/j.biocon.2011.11.015

Lisovski S, Bauer S, Briedis M, Davidson SC, Dhanjal-Adams KL, Hallworth MT, Karagicheva J, Meier CM, Merkel B, Ouwehand J, Pedersen L, Rakhimberdiev E, Roberto-Charron A, Seavy NE, Summer MD, Taylor CM, Wotherspoon SJ, Bridge ES (2020) Light-level geolocator analyses: A user's guide. Journal of Animal Ecology 89:221–36. https://doi.org/10.1111/1365-2656.13036.

Online Supplementary: https://geolocationmanual.vogelwarte.ch/. Accessed 01June 2020

Makhado AB, Braby R, Dyer BM, Kemper J, McInnes AM, Tom D, Crawford RJM (2021) In: Mikkola H (ed) Birds—challenges and opportunities for buisness, conservation and research. IntechOpen, London

Mauco L, Favero M, Bó MS (2001) Food and feeding biology of the common tern during the nonbreeding season in Samborombon Bay, Buenos Aires, Argentina. Waterbirds 24:89–96. https://doi.org/10.2307/1522247

McKinnon EA, Fraser KC, Stuchbury BJM (2013) New discoveries in landbird migration using geolocators, and a flight plan for the future. Auk 130:211–222. https://doi.org/10.1525/auk.2013.12226

McKnight A, Allyn AJ, Duffy DC, Irons DB (2013) 'Stepping stone' pattern in Pacific Arctic tern migration reveals the importance of upwelling areas. Mar Ecol Prog Ser 491:253–264. https://doi.org/10.3354/meps10469

Meininger PL (1988) A preliminary investigation of tern catching in Senegal, winter 1987/88. ICBP. https://doi.org/10.13140/RG.2.2.29727.46243

Myers JP, Morrison RIG, Antas PZ, Harrington BA, Lovejoy TE, Sallaberry M, Senner SE, Tarak A (1987) Conservation strategy for migratory species. Am Sci 75:19–26

Nebelsiek U (1966) Das Schicksal der Flußseeschwalbe (*Sterna hirundo*) und der Lachsseeschwalbe (*Gelochelidon nilotica*) als Brutvögel Bayerns. Ornithol Anz 7:823–846

Neubauer W (1982) Der Zug mitteleuropaeischer Flusseeschwalben (*Sterna hirundo*) nach Ringfunden. Ber Vogelwarte Hiddensee 2:59–82

Neves VC, Nava CP, Cormons M, Bremer E, Castresana G, Lima P, Azevedojun SM, Phillips RA, Magalhaes MC, Santos RS (2015) Migration routes and non-breeding areas of common terns (*Sterna hirundo*) from the Azores. Emu 115:158–167. https://doi.org/10.1071/MU13112

Nilsson C, Klaassen RHG, Alerstam T (2013) Differences in speed and duration of bird migration between spring and autumn. Am Nat 181:837–845. https://doi.org/10.1086/670335

Nisbet ICT, Mostello CS, Veit RR, Fox JW, Afanasyev V (2011) Migrations and winter quarters of five common terns tracked using geolocators. Waterbirds 34:32–39. https://doi.org/10.1675/063.034.0104

Ntiamoa-Baidu Y, Piersma T, Wiersma P, Poot M, Battley P, Gordon C (1998) Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. Ibis 140:89–103. https://doi.org/10.1111/j.1474-919X.1998.tb04545.x

Palestis BG (2014) The role of behavior in tern conservation. Curr Zool 60(500):514. https://doi.org/10.1093/czoolo/60.4.500

QGIS Development Team (2021) QGIS Geographic Information System, QGIS Association. Available from: https://www.qgis.org/

Radford MC (1961) A study of the British ringing records of the common tern and arctic tern and comparison with some foreign records. Bird Study 8:174–184. https://doi.org/10.1080/00063656109476003

Radziejewska T, Schernewski G (2008) The Sczcecin (Oder-) Lagoon. Schiewer U (2008) Ecology of Baltic coastal waters, ecological studies 197. Springer, Berlin-Heidelberg, pp 115–129

Raitsos DE, Yi X, Platt T, Racault MF, Brewin RJW, Pradhan Y, Papadopoulos VP, Sathyendranath S, Hoteit I (2015) Monsoon oscillations regulate fertility of the Red sea. Geophys Res Lett 42:855–862. https://doi.org/10.1002/2014GL062882

Rakhimberdiev E, Winkler DW, Bridge ES, Seavy NE, Sheldon D, Piersma T, Saveliev A (2015) A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. Mov Ecol 3:25. https://doi.org/10.1186/s40462-015-0062-5

Redfern CPF, Kinchin-Smith D, Newton S, Morrison P, Bolton M, Piec D (2021) Upwelling systems in the migration ecology of European Roseate Terns *Sterna dougallii*. Ibis 163:549–565. https://doi.org/10.1111/ibi.12915

Robinson AR, Crick HQP, Learmonth JA, Maclean IMD, Thomas CD, Bairlein F, Forchhammer MC, Francis CM, Gill JA, Godley BJ, Harwood J, Hays GC, Huntley B, Hutson AM, Pierce GJ, Rehfisch MM, Sims DW, Santos MB, Sparks TH, Stroud D, Visser ME (2009) Travelling through a warming world: climate change and migratory species. Endang Species Res 7:87–99

Roxy MK, Ritika K, Terray P, Masson S (2014) The curious case of Indian ocean Warming. J Clim 27:8501–8509. https://doi.org/10.1175/JCLI-D-14-00471.1

RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston. http://www.rstudio.com/. Accessed 01 Nov 2020

Runge CA, Martin TG, Possingham PH, Willis SG, Fuller RA (2014) Conserving mobile species. Front Ecol Environ 12:395–402. https://doi.org/10.1890/130237

Runge CA, Watson JEM, Butchart SHM, Hanson JO, Possingham HP, Fuller RA (2015) Protected areas and global conservation of migratory birds. Science 350:1255–1258. https://doi.org/10.1126/science.aac9180

Ryslavy T, Bauer HG, Gerlach B, Hüppop O, Stahmer J, Südbeck P, Sudfeld C (2020) Rote Liste der Brutvögel Deutschlands. 6. Fassung, 30.Sept. 2020. Berichte Zum Vogelschutz 57:13–122

Salomonsen F (1955) The evolutionary significance of bird-migration. Dan Biol Medd 22:6

Shannon LV, Field JG (1985) Are fish stocks food-limited in the southern Benguela pelagic ecosystem? Mar Ecol Prog Ser 22:7–19

Stienen EWM, Jonard A, Brenninkmeijer A (1998) Tern trapping along the Senegalese coast. Sula 12:19–26

Szostek KL, Becker PH (2012) Terns in trouble: demographic consequences of low breeding success and recruitment on a common tern population in the German Wadden Sea. J Ornithol 153:313–326. https://doi.org/10.1007/s10336-011-0745-7

Tew Kai E, Marsac F (2010) Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique channel. Prog Oceanogr 86:214–223. https://doi.org/10.1016/j.pocean.2010.04.010

Van der Winden J, Fijn RC, Van Horssen PW, Gerritsen-Davidse D, Piersma T (2014) Idiosyncratic migrations of Black Terns (*Chlidonias niger*): diversity in routes and stopovers. Waterbirds 37:162–174. https://doi.org/10.1675/063.037.0205

Wearne K, Underhill LG (2005) Walvis Bay: a key wetland for waders and other coastal birds in southern Africa. Wader Study Group Bul 107:24–30

Wendeln H, Becker PH (1996) Body mass change in breeding Common Terns *Sterna hirundo*. Bird Study 43:85–95. https://doi.org/10.1080/00063659609460998

Wotherspoon S, Sumner M, Lisovski S (2016) R Package BAStag: Basic data processing for light based geolocation archival tags. GitHub Repository. https://github.com/SWotherspoon/BAStag. Accessed 01. June 2020

Zettler ML, Schiedek D, Bobertz B (2007) Benthic biodiversity indices versus salinity gradient in the southern Baltic sea. Mar Pollut Bull 55:258–270. https://doi.org/10.1016/j.marpolbul.2006.08.024

Zhang H, Rebke M, Becker PH, Bouwhuis S (2015) Fitness prospects: effects of age, sex and recruitment age on reproductive value in a long-lived seabird. J Anim Ecol 84:199–207. https://doi.org/10.1111/1365-2656.12259