Quantifying the effects of climate change on long distance migratory birds: A case study using Hungarian Sand Martins (*Riparia riparia*)

NKFIH/OTKA K 12348, K 120708 Consortia Grant

CLOSING REPORT for the PERIOD 01.12.2020. – 30.11.2021

Our MME/BirdLife Hungary consortium partners provided the necessary field infrastructure and services throughout 2021 and so we were able to adequately perform most of our planned field tasks.

Covid-19 related travel restrictions during the end of summer and autumn of 2021 caused a delay in carrying out important microsatellite analyses with our Austrian partner which finished only in November 2021. We were therefore unable to prepare and submit our planned manuscripts in relation to telomere studies until the end of the project.

Field Investigations in 2021:

- Twice a week between April and August we surveyed all potential breeding sites (30) and colonies (7; 1,141 pairs) at regular intervals within our study area (the river Tisza between Tokaj and Tiszatelek, a 40 km long section), as well as across a 5 km to 10 km wide area along the section) using both cars and a motorboat. We were able to carry out a survey of the river Tisza (Jánd-Szeged, ~600 km) in 2021, surveying 76 potential breeding sites and 15 sand martin colonies (size: 5-854 pairs) where the breeding population was 1,891 pairs.
- In 2021, we investigated 532 burrows with a video endoscope (at seven subcolonies). We were able to measure the start of egg laying, clutch sizes, number of fledged nestlings, prevalence of tick infections, and nest predation in 436 nests (an average seven observation/nest).
- A total of 1,474 individuals (93 juveniles, 1,381 adults) were caught (the number of captures was 2,028) and biometric measurements were recorded between April and July. A total of 178 of these captures were individuals recaptured from previous years. We individually painted and sampled T5 tail feathers from 387 individuals and identified their nests and/or exact ages. We performed blood sampling from 182 individuals.
- We recorded ca. 34 hours of video between April and July (5-10 minutes long at each colony sections where burrows were investigated) in order to identify burrow ownerships of individually painted birds.
- We recorded 40 hours of video during June-July to investigate feeding/foraging activities of individually marked birds and their pairs.
- We were not able to recapture geolocator-tagged individuals during the 2021 field season.
- We were successfully able to deploy low weight (0.45 g) radio transmitters in 2021, LifeTag (CTT), on one of the randomly selected sex of 30 pairs breeding in an early formed section of the colony in order to study the spatiotemporal characteristics of foraging/feeding parents during the intense nestling feeding period and to investigate the usage of the area of the breeding colony area following breeding. We used specific receivers (SensorStation, CTT) with multi-directional antennae systems and stand-alone receivers (CTT Nodes) to record more than eight million transmitter specific signals during the studied period (end of May- October. We measured and blood-sampled parents from 30 nests for detailed genetic investigation. Radio transmitters use solar panels and are able to function for several years; these enabled us to investigate parental presence at the breeding colony after the fledging of nestling, occurrence at expected areas during migration, and dispersal and breeding performance during subsequent years.

Laboratory studies in 2021:

- We computerised all ringing and biometric field measurement data collected in 2021 (2,028 records) alongside nest control data (3,800 records). We also identified the nests of 322 individually painted birds by analysis of video recording.

- We measured and computerised the physical characteristics (length, weight, rachis width) of 307 T5 tail feathers collected in 2021. Throughout the project (2016-2021) we carried out these measurements of 3,470 pairs of T5 feathers sampled in two, or more, consecutive years for longitudinal analysis and for individuals which known age or nest was identified, collected between 1995-2021.

- We repeated this sequence using the FlightR geolocation software package for reconstructing animal paths using data from 14 solar geolocators on recaptured individuals in 2018-2019 considering new independent analysis of high altitude flights, based on temperature sensor of the used geolocator, following recent results of Malmiga et al. (2021). We have found evidence of high altitude long lasting (greater than four hours long) flights during the autumn and spring migration which flights occurred both at night and daylight period and able to explain long distance of movement (over 600 km) within 24 hours considering ~ 30 km/hour speed of the sand martin. On the base of temperature based analysis of movement during the migration raised to use different setup value, which was used before, during the identification of stationary periods. We have finalised the time-consuming setup and analysis and have identified stationary and movement periods for each studied individuals. Thus, combining data from six formerly (2013, 2015) geolocator-tagged individuals with the recent 14 ones, we are now able to identify main migration and wintering sites of 20 individuals who belong to the studied population. Preparation of the manuscript of the investigation with geolocator has a delay because of the reanalysis and submission postponed to 2022.

-We completed genetic analysis (sexing, RTL measurement) of 156 individuals (parents and nestlings of 30 nests) studied in 2020 and carried out the same genetic measurement of parents of 30 nests which foraging/feeding behaviour were studied intensively with radio telemetry in 2021. Following the field season in 2021, we started to carry out the important microsatellite genetic analysis of paternity/maternity at our Austrian partner during autumn, but because of the Covid-19 travel restrictions, only one part of the microsatellite investigation was finished and we need to postpone the preparation and submission of the manuscripts to 2022.

Publications and presentations:

- In cooperation with our Swiss partners, “Spatially different annual cycles but similar haemosporidian infections in distant populations of collared Sand Martins *Riparia riparia*” article accepted and published in the BMC Zoology.

- We have continued to prepare a manuscript “Identification of pre-migratory, migration and wintering areas, timing of its usage and migration speed on the base data of geolocator study for the studied population”.

- We continued preparing the manuscript, “Level of telomere shortening during nestling and adult ages based on longitudinal analysis” as our recently determined high levels of EPP our other prepared manuscript focus on the role of quality of parents in reproductive success.

- The two project leaders of the consortium were editors and authors of several migrating species, including the Sand Martin, in the first Hungarian Breeding Atlas which present the first comprehensive information about spatial and temporal characteristics, including population trend, of bird species in Hungary.

FINAL REPORT

Identifying which areas outside the breeding period (i.e., pre-migratory, migration, wintering) are important to the breeding population of Sand Martins

In the case of the most long-distance migrating passerine species, traditional bird ringing methods provide spatiotemporally limited opportunities to identify areas used by the studied breeding populations in their lifecycle. Therefore, without this information, understanding the decline in these species is very problematic.

This is the case of our Sand Martin study, where we have no any recapture/recovery data from the African wintering area against the 159,500 individuals ringed at breeding colonies between 1982-2021. There are only 142 individuals (0.09% of all ringed individuals) recaptured outside of our study region (Upper Tisza, between Tokaj-Tiszatelek, Fig. 10), from which 55 individuals were recaptured during the breeding season in the Carpathian Bend with an additional two individuals captured from the Czech Republic and Poland. Indeed, of the 85 individuals recaptured outside the breeding season, 45 were found in the post-breeding period between July and August in the Pannonian region (Kopacevo, Osijek, the most southern position, 45.566N) (Fig. 3). A further 40 individuals which found during the spring migration period between middle April and end of May in a wide area including Malta, Corsica, Italy, Greece, Turkey, Israel, Croatia, and Southern Hungary (Fig. 7).

The dominant target of our project was to identify the areas used by the studied population outside the breeding season, to determine the timing of stay in these areas, and to get additional information about the movement during the migration. This information allowed us to use our long-term dataset to understand and explain factors behind the decline of the breeding population.

The use of geolocators also has a key role to solve the large information deficiency. Application of this method for small body weight passerines such as Sand Martin could yield relevant data as first pilot studies on this species in Europe (Szép et al. 2017) and in North America (Imlay et al. 2018) showed.

In the frame of an international cooperation (Hahn et al. 2021) and on the basis of our former geolocator study in 2014-2015, we compared migration and wintering areas as well as the level of haemosporidian parasites in the Hungarian Sand Martin population, with a population breeding in Northern Germany, and with a migratory population in Greece in spring. Our work showed different migration flyways and distant wintering areas for the two investigated breeding populations (Fig. 7). In total, we identified seven Plasmodium and nine Haemoproteus lineages (incl. two and seven new lineages, respectively), the latter presumably typical for swallows (Hirundinae) hosts. 99.5% of infections had a low intensity, typical for chronic infection stages, whereas few individuals (0.5%) showed high parasitaemia typical for acute infections during spring migration and breeding. Our study shows that blood parasite infections are common in several western Palaearctic breeding populations of sand martins who spent the nonbreeding season in West Africa and the lake Chad region. Due to long residency at the nonbreeding grounds blood parasite transmissions may mainly occur at host population-specific residences sites in Europe and Africa; the latter being likely facilitated by unsheltered roosting and thus high vulnerability to hematophagous insects.

Our earlier geolocator studies of Sand Martin in Hungary (Szép et al. 2017, Hahn et al. 2021) led us to investigate data only six (4+2) individuals recaptured after one year of the deployment the geolocator and extending the number of individuals which migration and wintering tracked with geolocator was very important to have proper information about spatial and temporal characteristics of the lifecycle of the population.

In order to identify the migration and wintering areas used by the studied population we used small weight (~0.45g) Intigeo geolocators (Migratech Ltd) with body harness deployed during end of the nestling feeding period in 2017 and 2018 (2017: 98 pc, 2018: 101 pc). Due to field-related difficulties and recently available new methods (usage of temperature data), the time consuming analysis of geolocator data had a delay and needed to repeat in second half of 2021 and not published yet. In our report, we present in details this investigation, because of it importance for the entire project.

In 2017, we deployed geolocators at two colonies, with 23 km distance (Szabolcs: 30 males, 20 females; Tiszatelek: 23 males 25 females) and in 2018, at three colonies situated within ~ 10 km radius (Szabolcs: 37 males, 28 females; Tímár: ten males, 20 females; Tiszabercel: two males, four females).

Out of the 98 individuals deployed with geolocators in 2017, we recaptured eight individuals (5 males, 3 females) at three colonies (Szabolcs: 3, Tiszatelek: 4, Tiszabercel: 1) in 2018, two of these individuals lost the deployed geolocator until the recapture (Tiszatelek: one male, one female). In 2019, we recaptured eight individuals with geolocators (five males, three females) at three colonies, situated within 10 km radius (Szabolcs: 4, Gávavencsellő: 2, Rakamaz: 2).

The recapture rate of individuals deployed with geolocator in the next breeding season (8.2% of 98) was not significantly lower comparing to other adult individuals caught at the same days and colonies in (2017: with geolocators: 8.2%, without geolocators: 15.7% , χ^2= 3.46, df = 1, P = 0.063; 2018: with geolocators: 7.9%, without geolocators: 14.0%, χ^2 = 2.381, df = 1, P = 0.123; Pearson's Chi-Squared test with Yate's correction).

With geolocators deployed in 2017 and 2018 during the breeding period we were able to follow 14 marked and recaptured sand martins (8 males, 6 females) individuals during the entire period between two breeding seasons, except one individual which geolocator stopped the recording from January in 2019.

Our success to recapture individuals with geolocators was largely reduced in 2019 when there was a flood along the river from the end of May to beginning of June by which all early formed burrows and nests disappeared at the river and potentially caused larger rate of emigration from the focal colonies with lower rate of recapture of marked individuals.

Geolocator analyses

We used the FLightR package in R (version 0.4.9; Rakhimberdiev et al. 2017) to generate a spatial probability distribution for each twilight time and retained the median location for subsequent analyses. FLightR uses the curve-fitting method to estimate the positions of birds with a particle filter to optimise the position for each twilight (Lisovski et al. 2020). We used both the period of post geolocator deployment and before recapture in the area of the colonies when the individual was stationary for "in-habitat calibration" of geolocators. We considered model and ageing option of the calibration of FlightR. On the basis of the earlier work of Imlay et al. (2020), the mean distance of Sand Martin flight during a daylight period with foraging could vary between 272-347 km (considering 5.4-6.9 m/s speed) and we considered 300 km daily mean travel distance. We set the algorithm to allow maximum daily flight distances of 1,500 km on a 50 km grid, based on our former investigation (Szép et al. 2017). To estimate locations, we ran the FLightR particle filter with 1 million particles over the spatial grid, checked for outliers, which were subsequently removed and used the median of the posterior probability distribution as the estimates of daily bird locations. The stationary.migration.summary function of FLightR was used with a probability cut off of 0.05 and a minimum stay of 2 twilights to determine whether a bird was stationary or not. We considered the potential arrival and departure dates for each stationary site based on probability cut off of 0.05 values of twilights (arrival at twilight which was not followed by movement, departure at twilight which was followed with movement) and median longitude and latitude values with first and third quartile ranges. Length of stay in stationary site and length of movement movements between stationary sites measured by time (days) between arrival and departure. The great-circle distance measured between median coordinates of the two consecutive stationary periods. All analyses were conducted in R version 4.0.5 (R Core 2020).

Temperature data for identify occurrence of flight in high altitude: A new approach

A drop in the maximum and minimum temperatures, recorded by the geolocator four each four hours long periods, could indicate that flights occurred at high altitudes where air temperature is much lower than at ground level (Malmiga et al. 2021, Sjöberg et al. 2021). This recently published new method using independent data series (temperature) from geolocator information not only allows the investigation of occurrence, length and timing of high altitude flight but at the same time let to test and find proper parameters for FlightR analysis.

In 2021, after detailed analysis of the application of this new method for our existing data, we repeated the entire time consuming FlightR analysis to extract the information from our geolocator data. This caused a large but important delay in the analysis of light/temperature data from geolocators as well as the preparation/submission of manuscript from this important work of the project.

We used temperature data to identify the four hour periods when flight at high altitude could occurred, indicated by the lower temperature comparing to a threshold level based on average values following Malmiga et al. (2021).

The applied six geolocator deployed in 2017 and recaptured in 2018 (Intigeo-W50Z11-DIPv9) recorded the minimum (Tmin) and maximum (Tmax) temperature (C) for each four hours long period, sampled every 5 minutes. At the same time it recorded number of wet/dry events at given point of the geolocator sampled every 30 seconds and maximum conductivity for every four hours period. We calculated separately for each geolocators the average temperature for every 4-h time period Tmin and Tmax separately, considering these values 15 days before the given period. We then calculated Tmin and Tmax threshold values for four hours long period by subtracting 2°C from the minimum value of the average Tmin and Tmax value for each geolocators (Malmiga et al. 2020) (Fig. 1).

We considered that the bird has continuous flight during the entire four hours period when both Tmin and Tmax values were lower than threshold. For measuring the maximum potential length of the continuous flight in high altitude we considered one or more consecutive four hours long periods where flight in high altitude is detected and at least in one period the Tmin and Tmax values were lower than threshold.

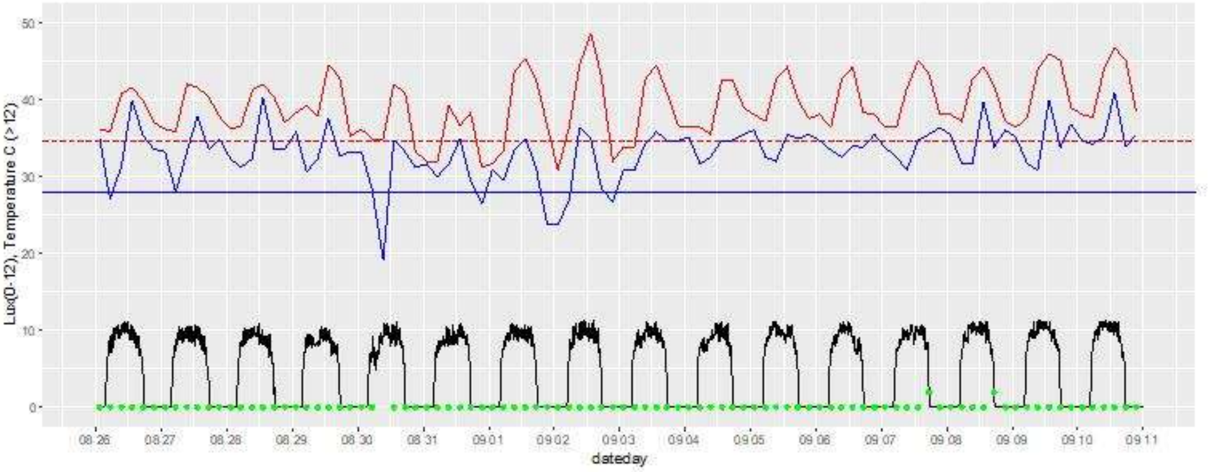

Fig 1. Tmin (blue), Tmax (red) values for each 4 hours period with Tmin (blue horizontal line) and Tmax (red scattered horizontal line) threshold values during autumn migration of the BG263 individuals (started: night of 30th August 2017 and arrived:04th September 2017). Light values (black line) measured in each 5 minutes and number of wet periods (green dot) counted for each four hours period showed.

Indicators of breeding based on light geolocator data

The light data collected maximum light values for every 5 minutes, let us to investigate the end of the breeding, start of using burrow and start of pairing during the study periods.

The individuals used dominantly and frequently burrows in the breeding area both at night (mean=19.9% of nights, SD=11.7%, n=14) and both during daytime (mean=74.7% of days, SD=18.7%, n=14), there were no significant difference between sex ($P > 0.164$, GLM with binomial distribution). There was no sign of usage cavity/burrow at night during the autumn and spring migration periods. In the wintering period four females used for only one night a cavity/burrow. The use of a cavity/burrow in daytime was detected in the case of seven individuals during the spring migration in Europe (four male, three female), where they used it an average 3.4 days (SD = 2.51, range = 1-8 days). Usage of cavity/burrow during the daytime was very rare during the wintering period when only four individuals used it for only for 1-2 days and did not occurred during autumn migration.

The last day/night with usage of burrow in the breeding colony is proper indication of final stage of breeding for individuals which nests were not identified in the year of deployment but light data of geolocators were available.

In the year of deployment, parents finished to use burrows (considered the last day or night with usage the burrow) when nestling was an average 26 days old (SD = 7.931, range = 8-30 days) in the case of seven birds which had known fledged nestlings.

We identified day of start digging/usage of burrow for breeding by considering first day when individual stayed at least 5 minutes continuously in darkness (burrow) between sunrise and sunset which were followed by at least three similar days with maximum one day without darkness.

We identified start of being paired, when individuals stayed at least one hour (twelve times 5 minutes continuously stay) in darkness between sunrise and sunset which were followed by at least five similar days with maximum one day with less dark period.

In the year of the recapture, the start of burrow digging/usage occurred in average 12 days (SD=1.761, range = 9-14 days, n = 6) before the start of egg laying for individuals without sign of lost burrow and in average 7 days (SD = 2.082, range = 5-9 days, n=3) for re-nesting individuals which lost the burrow because of the flood in 2019. The start of pairing occurred in average 7.5 days (SD = 2.258, range = 5-11 days, n = 6) before the egg laying for individuals without sign of lost burrow and in average 5 days (SD = 2.000, range = 3-7 days, n=3) for re-nesting individuals which lost the burrow because of the flood in 2019.

Identification of post-breeding, migration, and wintering periods

After finishing breeding at the colony, the usage of burrow/nest did not indicated trial of second/additional breeding for the studied 14 individuals during 2017-2018. Less than half of the individuals stayed stationary more than two weeks in the breeding area and others stayed an average only 5.9 days. More than half of the individuals used different stationary areas than where they breed, often for several weeks, where the individuals prepared themselves for the autumn migration.

The time between the finish the breeding and arrival to the African wintering region separated to two periods: 1- post-breeding period and 2- autumn migration period. The end of the post-breeding period was measured by the final day of a minimum one week long, last stationary site used in Europe. The start of the autumn migration period was identified when the individuals left the last post-breeding site in Europe.

Start of the wintering season measured by the arrival to the first stationary site in the Sub-Saharan wintering residence region where individuals stayed stationary minimum one week. End of the wintering season measured by the departure from the last stationary site in the Sub-Saharan region where individuals stayed minimum one week.

In the wintering season, all individuals spent long period stationary scattered with some shorter stationary periods, we regarded as the potential moulting period during in which less movement expected. All of this long moulting periods started and finished with usage of a minimum one month long stationary sites. We separated the moulting period during the stay in the wintering region from period before it (pre-wintering) and period after it (post-wintering) when individual after arrival and/or before leaving to/from the wintering region used stationary sites between one and three weeks.

Start of the spring migration period measured by the final day of the last stationary site in the Sub-Saharan wintering residence region where individuals stayed minimum one week. End of the spring migration period measured by the arrival to the final breeding area where individual paired. There were four individuals (1 males and 3 females) which used burrow for at least three consecutive days before arrival to the final breeding site at different area in Europe on the base of light data, but without sign of being paired (Fig. 7).

Post-breeding period

Recaptured individuals deployed with geolocators in 2017 finished not significantly breeding almost one week earlier (2nd July, SD = 4.484, n = 6) comparing to recaptured individuals deployed in 2018 (8th July, SD = 5.529, n = 8; year: $F_{1,12}$ = 3.521, P = 0.085; R^2 = 0.213, GLMln) and left breeding area not significantly earlier in 2017 (average 15th July, SD = 17.57, n = 6) than in 2018 (average 3rd August, SD = 20.336, n = 8) ($F_{1,12}$ = 3.74, P = 0.077; R^2 = 0.223, GLMln).

The individuals stayed an average 20.857 days (SD=20.621, range 2-62 day, n = 14) in the breeding area after finish the breeding. There were only two females which spent the entire post-breeding period in the breeding area.

The average length of the post-breeding period was 55.607 day (SD = 9.063, range 42.8-68.7 day n = 14), from which the individuals stayed in stationary sites in total an average 50.236 day (SD = 9.253, range 36.2-62.7 day n = 14), used an average three stationary areas (range: 1-5) from which they used an average two stationary areas (range: 1-3) at least a week long before start of the autumn migration.

Areas of post-breeding

The distance between breeding area and last post-breeding site, considering positions of used stationary sites during this period, was significantly longer with ~ 500 km in 2017 comparing to 2018 (2017: 859 km, SD = 357, n = 6; 2018: 343 km, SD = 316, n = 8; year: $F_{1,12}$ = 8.19, P = 0.014; R^2 = 0.387, GLM) (Fig. 2). The overall speed of movement, considering total distance and time with movement among stationary sites, was 192 km/day (SD = 106, range 31-388 km/day n = 12, two individuals stayed in the breeding area during the entire post-breeding period).

Fig. 2. Stationary sites and movement among it during post-breeding period, left: 2017, right: 2018. (black: post-breeding sites and movements, red: movement after start of the autumn migration). (Only sites used more than a week showed, median coordinate with first and thirds quarter latitude and longitude intervals)

Existing recapture data from the studied population during July-August, available for the period of 1983-2020, biased toward northern part of the post-breeding areas identified by geolocator study, because there is no any recapture data from the Balkan region which could have similar importance for the studied population in the post-breeding period (Fig. 3).

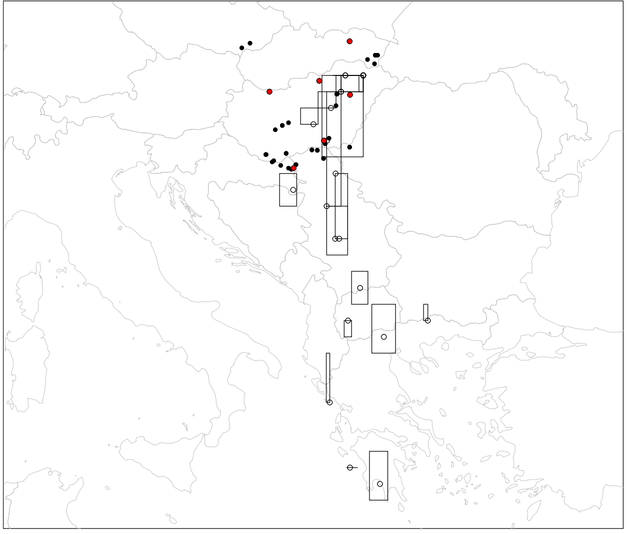

Fig. 3. Identified post-breeding areas during 2017-2018 by geolocators and sites of recaptured individuals between 10th July and 7th September, belong to the studied population. (black circles: post-breeding stationary sites, black dot: recaptured before 2017, red: recaptured during 2017-2021).

Autumn migration

Autumn migration from the last post-breeding site started at an average 29th August (range 17th August – 4th September, n = 14).

Males did not arrive not significantly earlier (average 6th September, range 1st- 20th September) to the wintering region compared to females (average 12th September, range 7th- 18th September, sex: $F_{1,12} = 4.088$, $P = 0.066$; $R^2 = 0.239$, GLMln).

The duration of autumn migration between last post-breeding and first stationary site used for at least one week in the wintering region, was not significantly longer in 2017 comparing to 2018 (2017: 12.25 days, SD = 4.432, n = 6; 2018: 7.35 days, year: $F_{1,12} = 4.51$, $P = 0.055$; $R^2 = 0.258$, GLM).

The total time of individual stayed stationary was average 3.338 day (SD = 2.935, range 0-8.6 days, n =14), individuals used more stationary sites during 2017 comparing to 2018 (2017: 3.0, SD=1.095, 2018: 1.38, SD=1.506; R^2=0.243, P = 0.038, Poisson GLM).

Total distance moved among stationary sites was an average 2979 km (SD = 404, range 2185-3945, n=14).

Total time spent with movement among stationary sites was higher in 2017 comparing to 2018 (2017: 7.761 days, SD = 1.815, 2018: 5.875 days, SD = 1.055; $F_{1,12} = 6.033$, $P = 0.030$; $R^2 = 0.317$, GLM).

The average speed of movement during autumn migration was 470 km/day (SE = 129, range 216-745 km/day), it was significantly higher than during the post-breeding period (Wilcoxon = 6, P < 0.001).

Pre-wintering period

In 2017, nearly all individuals (n = 5) used the first long used stationary sites continuously for more than a month (moulting area) without sign of usage pre-wintering area except one individual which used three pre-migratory sites before reached her moulting area after 32.4 days of arrival to the wintering region (Fig. 4).

In 2018, all individuals (n = 8) used pre-wintering areas before the arrival to their moulting grounds (Fig. 4). Individuals which used versus did not use pre-wintering areas did not differ in the day of finish breeding, start of leaving the breeding, start of autumn migration, and arrival to the wintering region (P > 0.109, Wilcoxon).

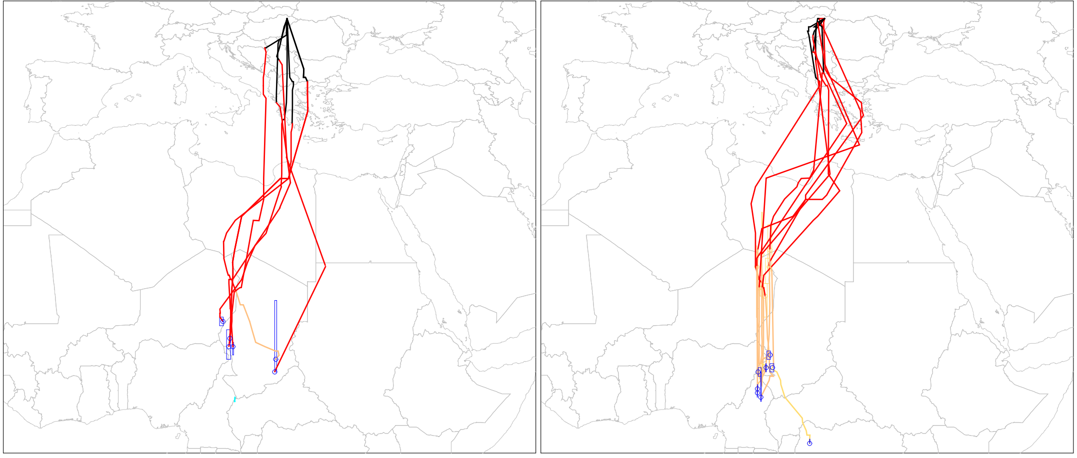

Fig.4. Movement among breeding and first moulting area, left: in 2017, right: in 2018. (black: movement during post-breeding period, red: movement during autumn migration period, yellow: pre-wintering movement until reach the moulting area, blue: area of the first moulting area) (median coordinate with first and thirds quarter latitude and longitude intervals).

The average length of the pre-wintering period was 36.94 day (SD = 17.2, range 20.5-71.4 days, n = 9) with usage of an average 5 stationary sites (range 2-8 days), where they stay in total an average 31.089 days (range 15-59.4 days). The individuals moved an average 1386 km (SD = 428, range 698-2260) with an average 229 km/day speed (SD = 105, range 140-469 km/day, n = 9). The speed of these nine individuals during pre-wintering period was lower comparing to their speed of during autumn migration (Wilcoxon paired = 75, P = 0.003).

During the autumn migration, all individuals used the Balkans to reach the Mediterranean Sea and most of them crossed the Sea between Libya and Greece (Fig. 4). There was one individual which very probably crossed the Mediterranean Sea from Southern Albania to the NW part of Libya. Indeed, from the northern part of Libya most individuals crossed the country using SW direction until they reached ~15 degrees longitude and after moved in a southern direction to reach the Lake Chad region. There was one individual which moved different direction (moved dominantly to South) from the Northern part of Libya.

Moulting period

Data show that arrival to the moulting area was earlier in 2017 (2017: 16th September, SD = 18.747, range 1st- 20th September, 2018: 15th October, SD = 287.38, range 30th September – 19th November; ($F_{1,12}$ = 8.67, R^2 = 0.400, P = 0.012; GLMln). The time interval between start of autumn migration and arrival to the moulting area was shorter in 2017 (2017: 17.65 days, SD = 15.842, 2018: 44.857 days, SD = 19.482; $F_{1,12}$ = 13.293, P = 0.003; R^2 = 0.506, GLMln). The total time of individual stayed stationary during movement from the start of autumn migration was shorter in 2017 (2017: 8.92 days, SD = 11.693, 2018: 34.125 days, SD = 18.575; $F_{1,12}$ = 12.592, P = 0.004; R^2 = 0.482, GLMln) and they used less stationary sites during 2017 (2017: 3.5, SD=3.5, 2018: 6.75, SD=6.75; P = 0.008, R^2=0.379, Poisson GLM). Total distance moved among stationary sites from the start of autumn migration differed between sexes and years (male: 3,538 km, SD=560, female: 4,312 km, SD=931; 2017: 3,220 km, SD = 505, 2018: 4,358 km, SD = 641; sex: $F_{1,12}$ = 7.672, P = 0.018; year: $F_{1,11}$ = 13.42, P = 0.004; R^2 = 0.619, GLM). The average speed during the movement from the start of autumn migration was 387 km/day (SD = 127, range 191-650 km/day, n = 14).

Data show that the time interval between the end of breeding and arrival to the moulting area was shorter in 2017 (2017: 75 days, SD=18.055, 2018: 98.38 days, SD=18.981; $F_{1,12}$ = 6.266, P = 0.028; R^2 = 0.325, GLMln). The total time of individual stayed stationary was shorter in 2017 (2017: 71.506 days, SD = 24.775, 2018: 111.6 days, SD = 20.254; $F_{1,12}$ = 11.134, P = 0.006; R^2 = 0.461, GLM). The birds used an average eight sites (SD=2.542, range 5-12 sites). Total distance moved among stationary sites differed between sexes and years (male: 4,211 km, SD = 366, female: 4,731 km, SD = 530; 2017: 4,079 km, SD = 311, 2018: 4,701 km, SD = 457; sex: $F_{1,12}$ = 7.607, P = 0.019; year: $F_{1,11}$ = 8.32, P = 0.015; R^2 = 0.551, GLM).

Data show that the length of the moulting period took an average of 192.731 days (SD = 25.627, range 147.5-228.5 days, n = 13), similar to field observations (121-141 days, Jenni & Winkler 2020). This range was not significantly longer in 2017/2018 compared to 2018/2019 (2017/2018: 206.583 days, SD = 26.366; 2018: 180.857 days, SD = 19.437; $F_{1,11}$ = 4.096, P = 0.068, R^2 = 0.255, GLM). The individuals stayed stationary on average for 188.731 days (SD =24.477, range 144-226.6 days), used an average 2.46 stationary sites (SD=1.266, range 1-5), moved an average 478 km among stationary sites (SD=529, range 0-1577 km). In the case of individuals used different sites, average speed was 179 km/day (SD=86, range 37-296 km/day, n=9). The speed of movement during the wintering/moulting period was lower comparing to speed of movement during autumn migration (Wilcoxon=78, P=0.001).

Data show that departure from the wintering/moulting area started on average on the 9th April (SD =16.023, range 17th March – 7th May, n = 13).

The studied individuals dominantly used the Lake Chad basin as the main moulting area (Fig. 5), similar to our other two former studies (Szép et al. 2017, Hahn et al. 2021), there were only four individuals (29%) which used different areas in eastern direction (two in SE Chad/Central African Republic) and southern east direction (two in NW Congo).

In 2017, we deployed the same number of geolocators on two colonies situated 23 km km distance (Szabolcs, Tiszatelek) to investigate the similarity in the wintering/moulting areas, from which we recaptured 3-3 individuals in 2018. Against the intense ringing since 1995 at these two colonies, annually only ~ 5-10 % of breeding individuals changed colonies. Two individuals with geolocators from Tiszatelek colony used different moulting area in SE Chad/Central African Republic, 500-600 km distance from the Lake Chad basin which area used by individuals bred in Szabolcs colony. The sample size is small, but we could not exclude that subpopulations breeding over the 10 km distance (dominant percent of individuals return and breed within 10 km radius (Szabó & Szép 2010)) could use distant African wintering/molting areas.

The all studied individuals used the Lake Chad basin before start the spring migration. The studied population showed strong migratory connectivity, especially in the case of area where the spring migration start (Fig. 5).

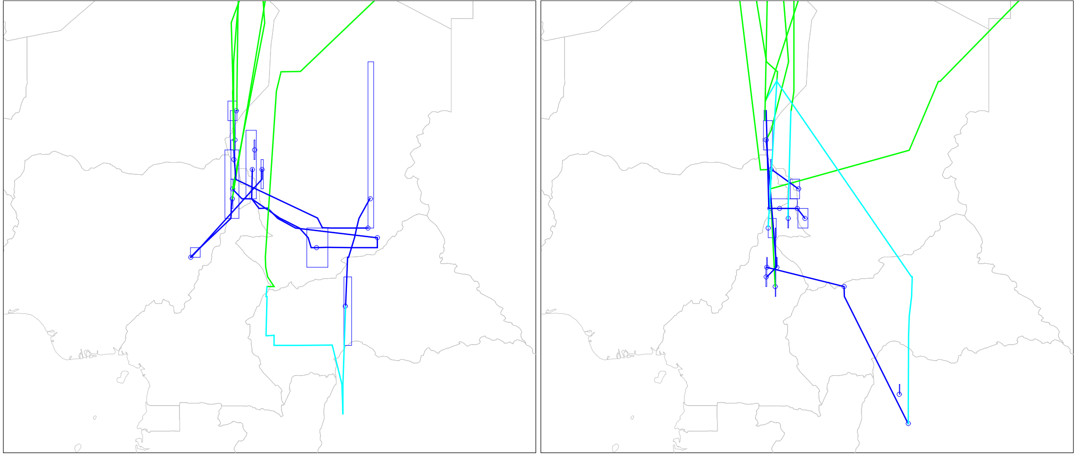

Fig. 5. Moulting areas, left: in 2017/2018, right: in 2018/2019. (blue: stationary sites and movement during the moulting period, light blue: stationary sites and movement between last moulting area and start of spring migration, green: spring migration from the wintering region) (median coordinate with first and thirds quarter latitude and longitude intervals).

Post-wintering period

Around 50% of the marked individuals (2017: one male, one female, 2018: three male, two females) used an average 2.29 stationary sites (SD=1.604, range 1-5 days) in the wintering region after leaving the moulting areas before start the spring migration, where they stayed in total an average 26.557 days (SD=7.993, range 15.5-39.9 days), moved an average 631 km among stationary sites (SD=499, range 50-1515 km) with an average 415 km/day speed (SD=364, range 100-1,102 km/days, n=7), but because some of these movements occurred near the spring equinox and near the equator, distance and speed estimation accuracy could be low (Fig. 5).

Spring migration

Spring migration started at an average 25th April (SD = 11.122, range 6th April-7th May, n = 13) from the wintering region, started not significantly earlier in 2018 (2018: 19th April, SD = 8.796, 2019: 30th April, SD = 10.839, $F_{1,11} = 3.9561$, $P = 0.072$, $R^2 = 0.248$, GLM).

The length of the period until arrival to the final breeding area where the pairing detected was an average 14.3 days (SD = 4.858, range 7.6-23.9 days, n = 13), the birds stayed in stationary sites in total an average 4.731 days (SD=2.623, range 1-9.7 days, n =13), used an average 2.85 stationary sites (SD=1.068, range 2-5) and moved an average 4,136 km among stationary sites (SD = 437, range 3395-4136 km) in this period with an average 484 km/day speed (SD = 182, range 245-763 km/day) during which speed did not differ significantly from the speed of the autumn migration (Wilcoxon = 81, P = 0.878) (Fig. 6).

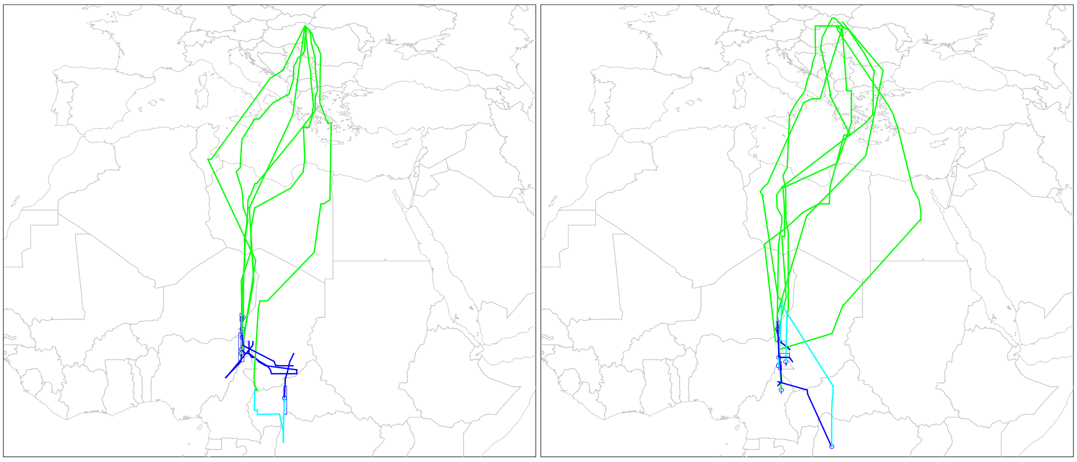

Fig. 6. Movement during the spring migration, left: in 2018, right: in 2019. (blue: movement during moulting period, light blue: movement between last moulting area and start of spring migration, green: spring migration until the breeding area) (median coordinate with first and thirds quarter latitude and longitude intervals).

The existing recapture sites in the spring migration period has a wider West-East distribution than the identified movement path of the individuals based on our geolocator data (Fig. 7). Recapture sites in Corsica, Switzerland, Northern and middle part of Italy very probable indicate usage of more western spring migration flyway which used by population wintering areas situated western direction from the wintering area of the studied population (Hahn et al. 2021). The two most eastern recapture sites (Southern Turkey and Israel) could indicate usage of Eastern flyway of individuals wintering in Eastern Africa, however we could not exclude that individuals wintering in the Lake Chad basin migrate in spring in eastern direction toward river Nile, as one of the studied birds showed in this and another one in one of our former study (Hahn et al. 2021).

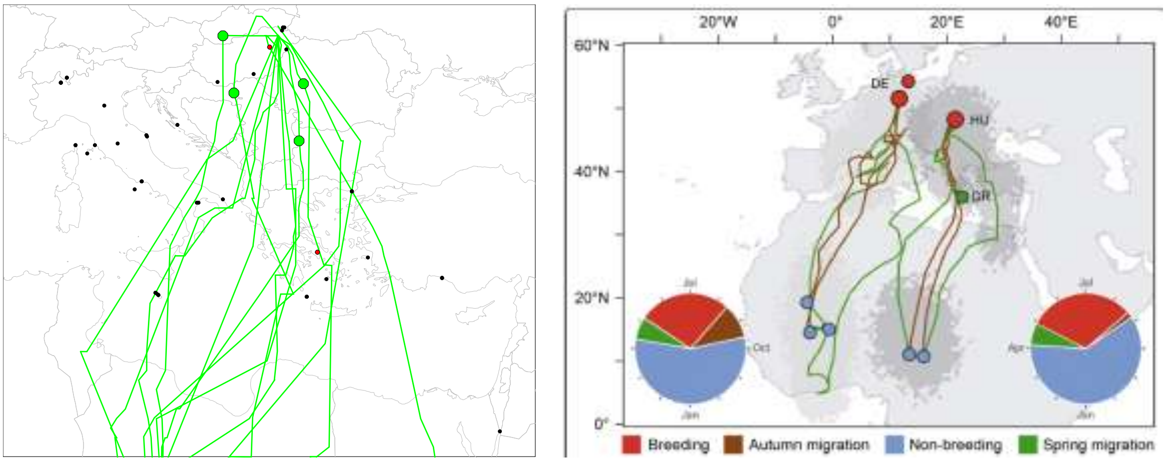

Fig. 7. Movement of individuals with geolocators during the spring migration during 2018-2019 and sites of recaptured individuals between 1st April and 1st of June, belong to the studied population (left) and migration and wintering areas of two populations identified by our former study in 2014/2015 (Hahn et al. 2021) (right). (black dot: recaptured before 2018, red dot: recaptured during 2018-2021, green dot: stationary sites where burrow usage was detected in 2018 and 2019 during spring migration).

Arrival to the breeding area

Marked individuals arrived back to the final breeding area earlier in 2018 comparing to 2019 (2018: 3rd May, SD = 9.333, range 25th April – 18th May, 2019: 18th May, SD = 12.284, range 25th April-22nd May, $F_{1,11} = 5.397$, $P = 0.04$, $R^2 = 0.31$, GLMln).

Four individuals (three females and one male) which potentially tried to breed different area than their final breeding area in Europe before arrival to the final area, on the base usage burrow during daylight, where they stay an average 3.1 days (range 1-4.4 days) but not paired (Fig. 7). In the case of these individuals, the distance between the site of the first and final breeding trial was an average 343 km (SD = 176, range 159-554, n=4).

Individuals started to use burrow earlier in 2018 comparing to 2019 in the final breeding area (2018: 6th May, SD = 7.663, n = 6; 2019: 13rd May, SD=11.086, n=7; $F_{1,11}=9.928$, $P=0.009$, $R^2 = 0.453$, GLM). Usage of burrow was detected an average 5.31 days after arrival to the final breeding area (SD=6.473, range 0-21 days, n = 13). Intense usage of burrow, indication of being paired, started an average 5.2 days following start of burrow usage (SD = 2.741, range 0-9 day, n = 10, data of three individuals which burrows possible collapsed by the flood in 2019 before being paired excluded).

The time interval between day of left the moulting area and day of usage of burrow in the final breeding area was not significantly shorter in 2018 (2018: 26.167 days, SD = 16.618, 2019: 45.143 days, SD = 17.459; $F_{1,11} = 4.115$, $P = 0.067$; $R^2 = 0.255$, GLMln). The total time of individual stayed stationary was an average 24.339 days (SD = 18.925, range 2.6-53.4 days) and they used an average 4.08 sites (SD = 1.891, range 2-8 sites), females used not significantly more stationary sites (male: 3.25, SD = 3.25, female: 5.4, SD = 2.302; P = 0.066, Poisson GLM). Total distance moved among stationary sites was an average 4,476 km (SD = 587, range 3,395-5,389 km, n=13), the average speed was 465 km/day (SD = 177, range 265-763 km/day).

Occurrence and the length of continuous flight at high altitude

We have found the first evidence for migration at night in Sand Martin, a species normally regarded as diurnal alongside many swallow and martin species. Our work indicates that this species uses high altitude during migration, something not known for this bird family (del Hoyo 2004).

In the case of the six individuals with known Tmax and Tmin temperature data, the mean percentage of continuous flight in high altitude among the considered four hours long periods differed among the seasons (F = 4.511, df = 4,25, P = 0.007, ANOVA). Low mean percentages were seen during the wintering and post-breeding seasons and higher levels during the two migration and breeding seasons (Fig. 8).

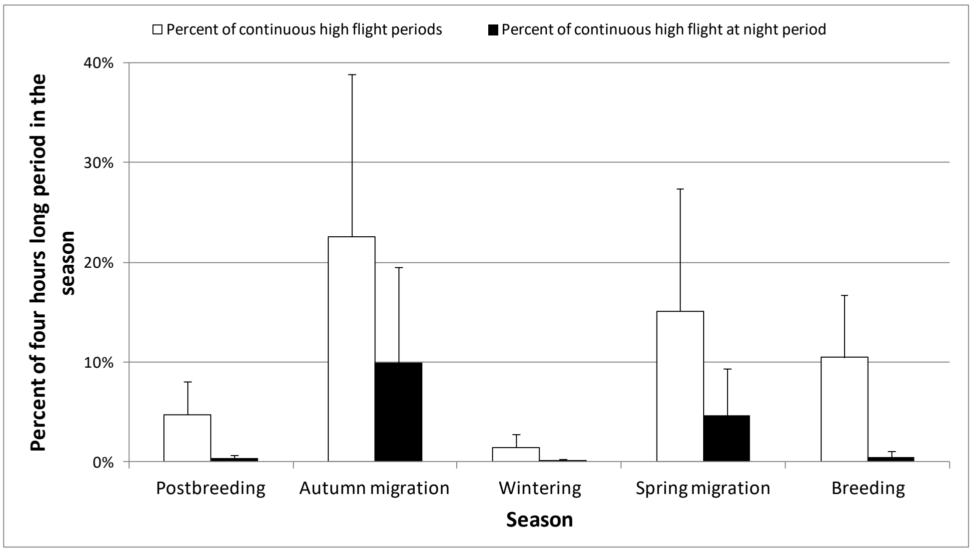

Fig. 8. Mean percentage of continuous flight in high altitude (white: all, black: occurred at night) among the four hours long periods with known Tmax and Tmin values during different seasons in the case of six individuals between 2017-2018.

Mean percentages of continuous flight at night in high altitude differed as well among seasons (F = 4.754, df = 4,25, P = 0.005, ANOVA) with the highest mean percentage during the autumn (10.0%, SD = 9.6%, n = 6) and spring migration (4.7%, SD = 4.7%, n = 6) when 31-44% of the flight in high altitude occurred at night. The level of flight at night in high altitude was lower in other part of the year (post-breeding: 0.3%, SD = 0.4%; wintering: 0.1%, SD = 0.2%; breeding: 0.5%, SD=0.6%; n=6) where only 4.5-9.2% of the flight at high altitude occurred at night (Fig. 8., 9.), the difference was significant comparing to the autumn migration ($P < 0.021$, Bonferroni correction).

The maximum length of continuous flight in high altitude of the six individuals varied between 4 and 20 hours, the longest flights (16-20 hours) occurred only during the autumn and spring migration. The average length of this flight of the individuals varied significantly among the seasons (F=3.205, df=4, 25, P=0.03, ANOVA), it has the highest level during the autumn (10.111 h, SD=5.374, n=6), spring migration (8.825 h, SD=3.274, n=6) and were lower in other seasons (post-breeding: 4.903 h, SD=2.677; wintering: 5.04 h, SD=1.199; breeding: 6.456 h, SD=1.475; n=6).

In the migration periods, continuous flight in high altitude detected frequently during the cross of Sahara (11/12 cases) and less frequently during the cross of the Mediterranean Sea (6/12 cases), all of these flights has parts during night (Fig. 9).

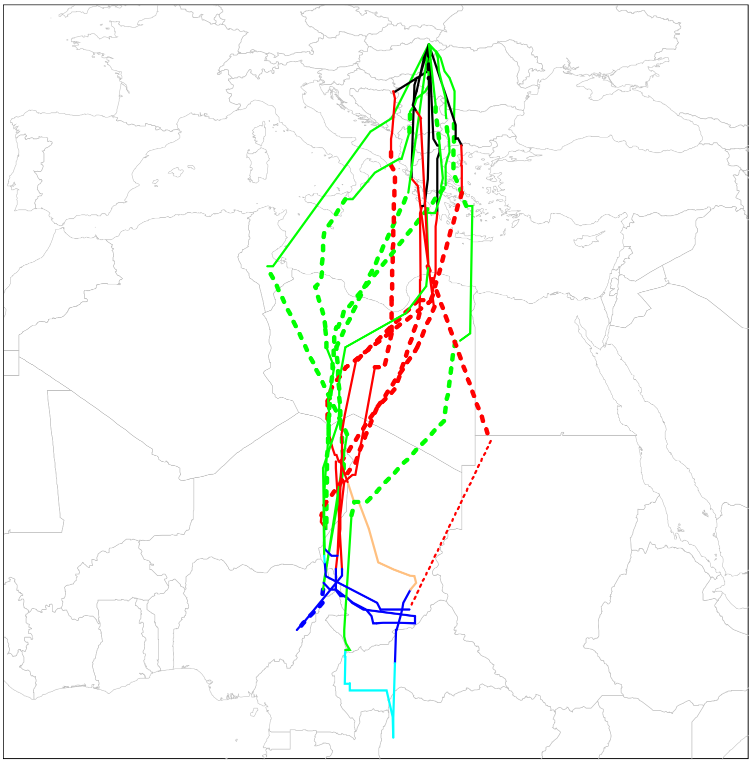

Fig. 9. Movement of six individuals with indication of continuous flight in high altitude, based on available temperature data (scattered thick line: consist night and day time, thick line: consist only day time, thin line: without continuous flight at high altitude), in different seasons (black: post-breeding, red: autumn migration, blue: wintering, green: spring migration). Median latitude, longitude coordinates of stationary sites and movement among stationary sites are considered for drawing lines.

Feather an important indicator of individual quality, condition and distant moulting environment

In the frame of the project we investigated feather quality on the base of our intense ringing and feather sampling work since 1995, resulted sampled feathers from numerous individuals enabling longitudinal and cross-sectional investigation of the role of adaptation to variable environmental conditions on feather morphology (Szép et al. 2019). In our publication, we showed that older individuals tend to possess better quality feathers, measured using bending stiffness, feather length and thickness as proxies. Bending stiffness and feather thickness do not change with individual age, in contrast with increases in feather length and declines in daily feather growth versus age of individual alongside moult duration. Individuals who live to older ages tend to have similar, or higher, feather growth rates and better feather quality than individuals captured at younger ages. Thus, on the basis of strong selection against individuals with slow feather growth, as seen in other species of swallows and martins, which causes a delay in moult completion, the results of this analysis highlight the potential cost of producing better quality feathers when this depends on moult duration.

Feather length also does change during the lifetime of the individual and thus enabled us to further investigate influence of individual and environmental conditions during the moult. The results of this analysis provide important insights on the adaptive significance of these traits, and the potential use of physical characteristics in unravelling the reasons why long distance migratory bird populations are in global decline.

During the project (2016-2021), we continued the collection of the feather (T5, second outermost tail feathers) from each breeding individuals which: - age was known (ringed as pullus/juveniles or ringed as adult more than 3 years before the recapture), - nest were bred was identified (using specific burrow trap, video catching method, individual painting and observation at nest during nestling feeding), - feather was sampled in two consecutive years. In total, we carried out physical characteristics (length, weight, rachis width) measurements of 3,470 pairs of T5 feathers sampled in two or more consecutive years for longitudinal analysis and for individuals which known age or nest, collected between 1995-2021.

The final preparation/submission/publication of the studies where we investigate in details the factors responsible for the change of the feather length moulted in consecutive years in the African wintering area in the level of individuals and population need to finalise the identification of moulting areas by geolocator related studies and it is postponed in 2022.

The use of feather trace elements and stable isotope profiles

On the basis of feathers collected from individuals during geolocator deployment since 2012 as well as one year later (40 pair of T5 tail feathers from 20 individuals), we carried out an analysis of stable isotope composition (d13C, d15N, dD) from these feather samples with cooperation of Finnish researcher (Jyrki Torniainen). Using these feathers we analysed trace element profiles using Energy Dispersive X-Ray Fluorescence Spectrometer (XRF) and also conducted the necessary development and test studies to use this methodology. The available results of analysis enabled us to initiate analysis of both stable isotope and trace element profiles of feather moulted in two consecutive years from the same individuals with known moulting areas in the second year. The final preparation/submission/publication of these studies need to finalise the identification of moulting areas by geolocator related studies and it is postponed in 2022.

Factors influencing the breeding success and condition of the fledged young individuals

We carried out weekly surveys of the size and distribution of the breeding habitat and colonies within our study area (the river Tisza between Tokaj and Tiszatelek, a 40 km section, as well as across a 5 - 10 km wide area along the section) (Fig. 10). We also surveyed annually the length of a 500 km section of the river Tisza (Jánd-Szeged) during July in order to measure the size of all potential breeding sites and colonies of Sand Martin along the section where surveys have been conducted since 1990.

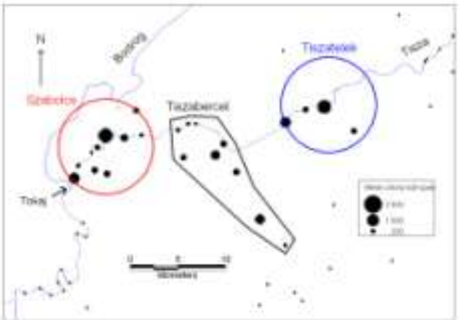

Fig. 10. The intensively studied area with positions of the colonies and regions along the river Tisza between Tokaj and Tiszatelek.

The population size remanded in similar level during 2016-2021, however there was a large decline comparing to the former years (Fig. 11). Behind the large decline, the decreasing size of potential breeding habitat (perpendicular wall) has important role, because of the lower intensity of floods before the breeding seasons during the last decade, however usage of available walls is decreased as well in this period, shortage of breeding habitat alone could not explain the population decrease. We have found the same pattern along the 500 km section of the river as well.

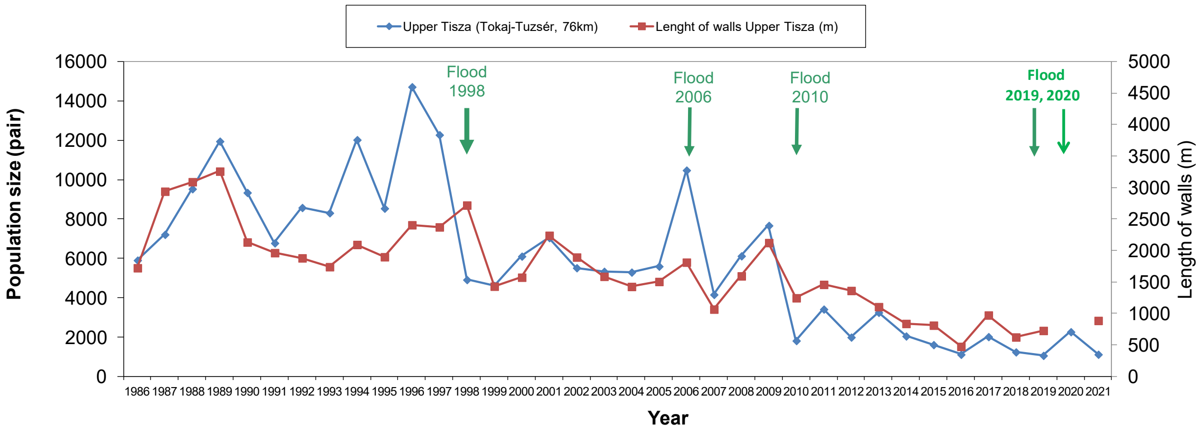

Fig.11. Population size (pair) along the upper section of the river Tisza between Tokaj and Tuzsér (blue) and total length of walls proper for breeding (m) between 1986-2021. Flood during the breeding season indicated with green arrow.

In the frame of the project between 2017-2021 in the studied area, we surveyed 108 subcolonies (within 19 colonies), where 4468 burrows were investigated weekly basin with videoendocopes and start of egg laying, clutch size, fledging success and fledged nestlings with further parameters of reproduction was measured in 2709 burrows. Our work let to extend the former database (1995-2016) related to breeding performance and ready for detailed analysis on population and individual level when studies related to the entire lifecycle of the population finalised.

In population level, the reproductive success during the period between 1995-2021, showed large decrease in years when flood happened in the breeding period, the annual values of the clutch size and number of fledged nestlings did not show obvious tendency. The day of finish the breeding season, measured by the start of egg laying among the second/additional clutches, have earlier values during the last ten years (Fig. 12) and the last 4-5 years the start of the breeding tend to start later by which breeding season tend to be narrower.

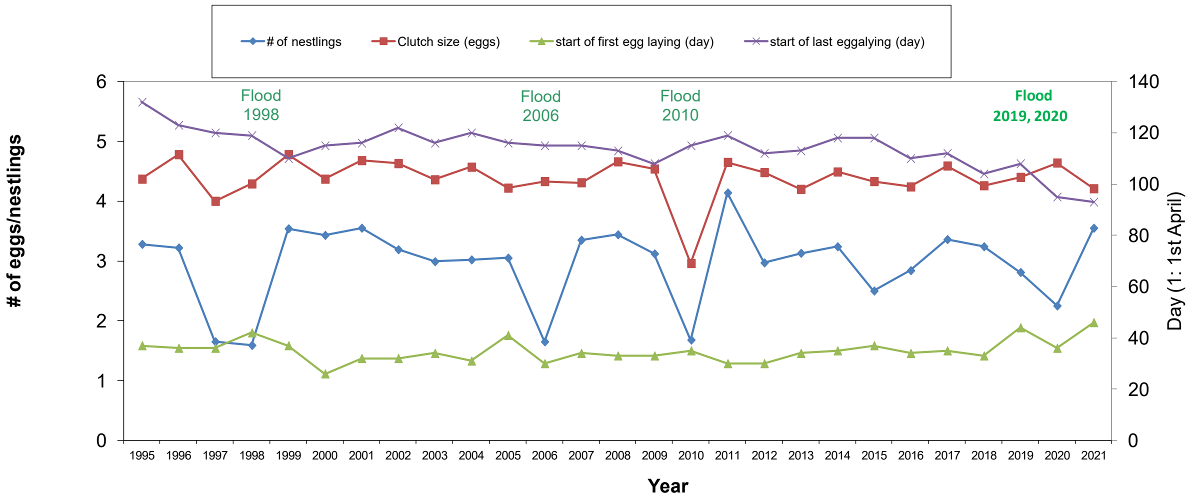

Fig. 12. Annual mean clutch size (eggs) and nestlings (~15 days old) of first clutches in the studied area during 1995-2021 (based on mean values of studied subcolonies, n=17 647 nests) and start of first of egg laying and start of last egg laying (second/additional clutch) in each years.

During the last ten years, the level of tick prevalence (*Ixodes lividus*) in the studied clutches were high in several years without obvious effects on the number of fledged nestlings, but potentially high impact on survival and lifespan following the fledging (Szép and Møller 2000) (Fig. 13).

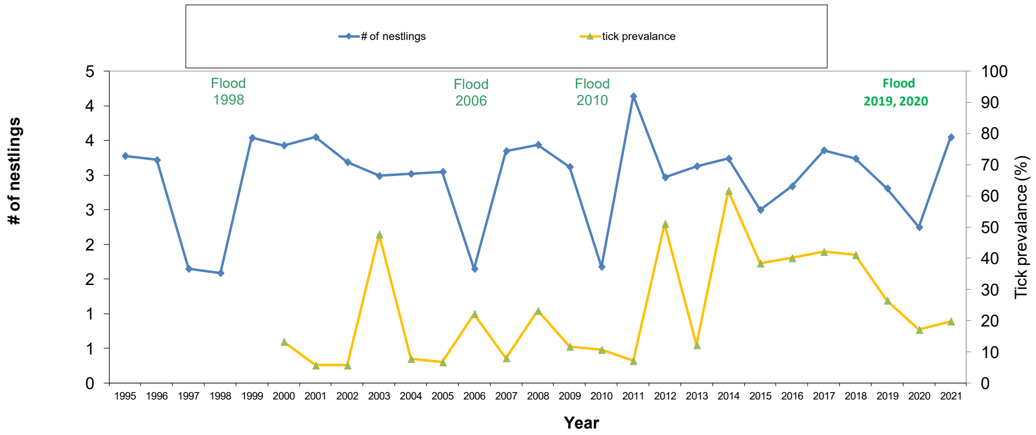

Fig. 13. Annual mean number of fledged nestlings (~15 days old) of first clutches in the studied area during 1995-2021 and percent of clutch where at least one nestling infected with tick (Ixodes lividus) (based on mean values of studied subcolonies where tick was inspected since 2000, n=10 285 nests)

Survival and recruitment modelling

In the project we caught 12 335 individuals (10 260 adults, 1975 juveniles and 96 nestlings) during 2017-2021 at the studied breeding colonies, recaptured 4254 individuals within and between years and carried out biometrical measurements. The intense and frequent ringing let to extend the existing capture-recapture database for modelling population parameters (survival, recruitment, dispersal). With specific methods, video catching (catching with mist-net video recorded and analyses) and individually painted adults (identified their nest by analysing video footage made during nestling feeding), we were able to indentify 2110 nest owners during 2017-2021, which let to investigate individual level the breeding performance.

We modelled population size, survival rate and recruitment in the studied area – on the base of estimation using capture-recapture data of 1995-2019 (Open population model, POPAN, applied best model Phi(s*t) P(s*t) pent(s*t) N(s) (weight=0.991), which showed large fluctuation of the survival rate without obvious tendency (Fig. 14). The estimated population size showed similar large decrease as population size measured in the field in the study area.

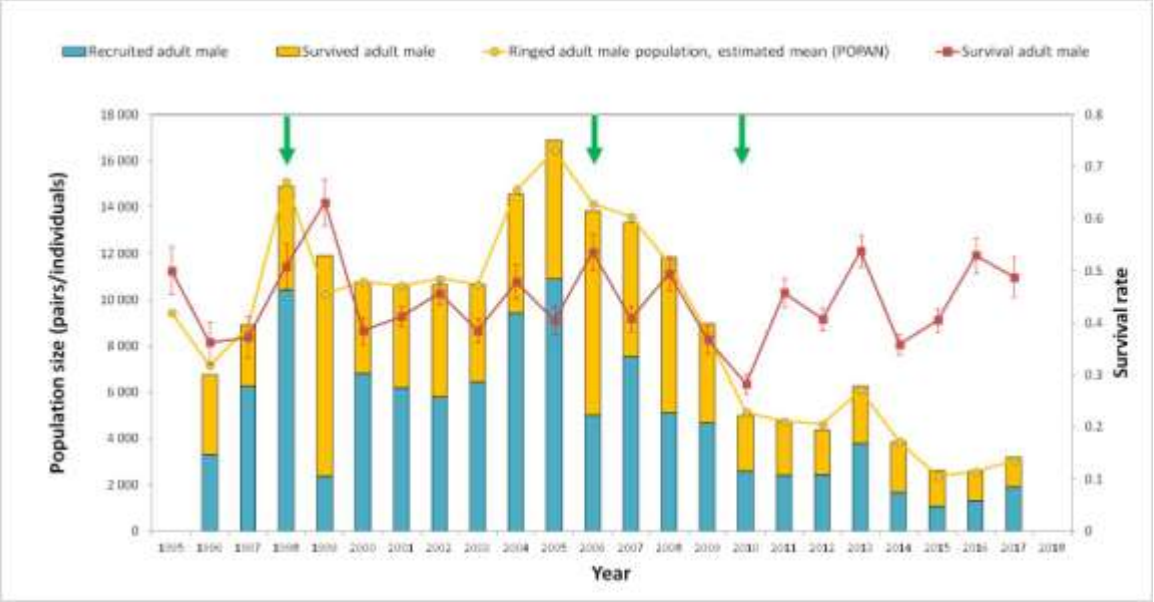

Fig. 14. Estimated population size (pairs), survival rate (adult male), composition of estimated population (number of survived adult from the previous year and recruited adults) based on POPAN analysis of capture-recapture data of 1995-2019. (flood indicated with green arrows)

Considering the number of recruited adults, estimated by the number of nestlings fledged in the studied area in the previous year and multiplied with estimated survival rate of the adult males in the given periods, showed that before the large decrease of the population (~2008-2009) high immigration was happened, because the reproductive success with survival of the studied population was not able to yield that amount of recruitment as modelling indicates (Fig. 15). This results was presented in an oral talk at the EBCC Conference in 2019 (Szép and Halmos 2019). Further modelling of the survival rate and publishing will carry out in 2022, considering identified migration/wintering areas.

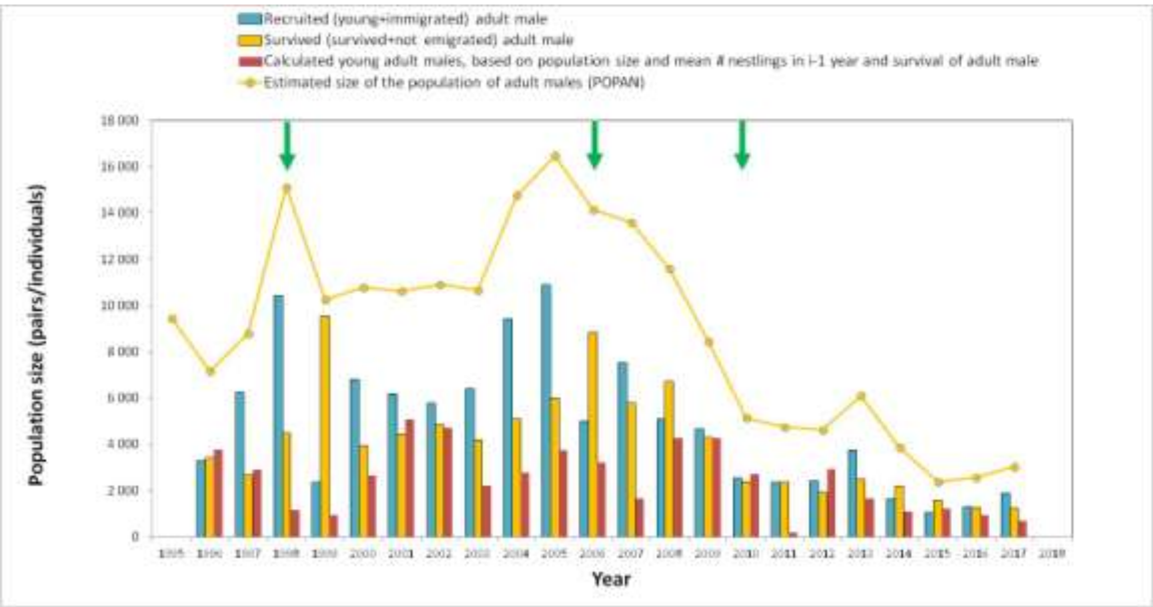

Fig. 15. Estimated population size (pairs), number of survived adult from the previous year, estimated recruited adults based on POPAN analysis of capture-recapture data of 1995-2019 with number of recruited adult estimated on the base of fledged nestlings in the studied area in the previous year and the estimated survival of adult males in the given period. (flood indicated with green arrows).

Genetics of the Sand Martin population

We completed an analysis of paternity and maternity for nestlings from 36 nests using blood samples collected in the same sites and colonies in 2005 when the RTL of parents and their nestlings were measured. Analysis of 304 samples (from nestlings and parents) was finally completed in 2020. We found high levels of extra-pair paternity (EPP) in 47% of clutches. We have found that the sex ratio of EPP offspring was male biased (mean = 65% ±7.8%) but it was unbiased in within-pair paternity (WPP) offspring (47.6% ± 6.7%). The sex ratio among surviving nestlings remained different (EPP: 80%, WPP: 50%) in subsequent years. We were not able to identify the males who were the genetic father of the found EPP offspring but on the base of the applied microsatellite methods, we found that it were 25 different males, which males were an average 1.6 (range 1-4) EPP nestlings in the studied nests. We found that the level of brood parasitism was low (8.3% of nests), there were two nests among it where quasi brood parasitism was found as well.

We found that owners of nest with EPP nestlings caught earlier (both male and female) and egg-laying started earlier than in nest without EPP nestlings (Fig. 16), which indicate that this phenomenon was commoner among early breeders. The nest with EPP nestlings situated in more dense part of the colony than nest without EPP nestlings.

Fig. 16. Start of egg laying (day) in nest without and in nest with EPP nestlings. (day 1: 1st April).

We measured the relative telomere length (RTL) of parents and nestlings and found that telomere length of the nestlings before the fledging (~ 15-18 days old age) were significantly influenced by the telomere length of the social father (positive) and number of ticks (negative), when considered various parameters with potential factors during Linear Mixed Modelling (Fig. 17)

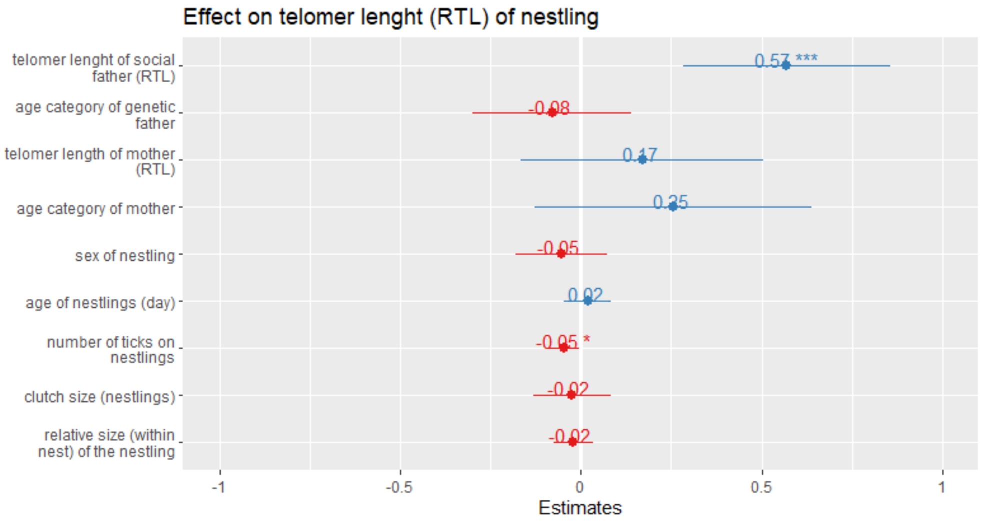

Fig. 17. Influence (slope, CI and significance) of investigated parameters on telomere length (RTL) of nestling.

We were able to recapture 19 individuals in the following year from the studied nestlings and found that their telomere length showed only significant relation (positive) to the telomere length of their social father. Modelling return rate of nestlings showed near significant positive influence of the age of social father and negative influence of clutch size and number of ticks on probability of recapture in the next year (GLM Binomial).

Our investigations showed high level of extra-pair paternity in this socially monogamous species, where EPP level was high among the first formed pairs, which individuals regarded has the best quality. The high positive relationship between telomere length of nestlings and their social father could indicate importance of the good quality of these cuckolded males during the rearing of the nestling, however the EPP in these nests and male biased sex ratio of EPP nestlings raised of other “qualities” of males important for females in the fertilisation period. The found weak positive influence of male age on return rate of nestlings raised the importance of age related factors behind the found high level of EPP.

We modelled the RTL of the adult individuals sampled at two colonies in 2005 (n=75) considered day of sampling relative to the egg laying, breeding colony, day of start of the egg laying, wing length and sex. Model averaging based on the best models (delta AICc <2), showed that only the day of sampling relative to the start of egg laying has significant influence on the RTL of adults (slope= 0.019, SE=0.005, z=3.823, P<0.001), adult sampled later stage of his/her breeding in 2005 has longer RTL. There was difference between RTL of adults at the studied colonies (difference=: 0.261, SE=0.106, z=2.41, P=0.016), but no significant relationship for the other variables (P>0.24) (Fig. 17).

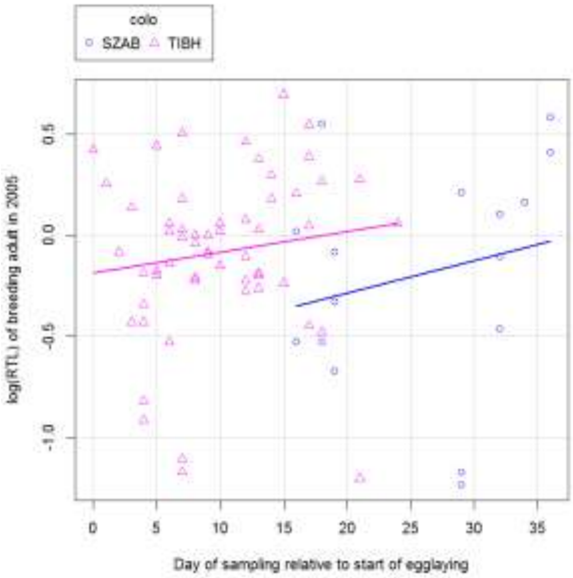

Fig. 17. RTL of adult individuals in 2005 at two colonies (pink: Tiszabercel, blue: Szabolcs) in relation to the day of sampling relative to the start of egg laying (day of sampling – day of start egg laying).

We investigated the change of the telomere length of the breeding adults, blood sampled in 2005 (n=75) and recaptured in the following years in the studied area (n=35). We have found, that adults recaptured during the following years has significantly longer RTL in 2005 than adults which were not recaptured during the following years (recaptured: mean=1.076, SE=0.052, n=38, not recaptured: mean=0.874, SE=0.067, n=37, t=-2.365, df= 68.389, P=0.021, Welch two sample test).

We modelled the change of RTL of 21 adult individuals between 2006 and 2005 with number of nestlings fledged in 2005, tick prevalence in nest in 2005, sex, wing length in 2005 and difference between day of sampling relative to start of egg laying between 2006 and 2005. The model averaging, based on best model (delta AICc <2), showed that difference in days of blood sampling relative to the start of egg laying of the same individuals in two consecutive years have a significant positive influence on the change of RTL (slope=0.047, SE=0.018, z=386, P=0.017) (Fig. 18), which could indicate the ability of the individuals to "repair" the lost of telomere length during the migration (because of the intense movement) after the egg laying, which phenomenon rarely found in the case of short live passerine species (Brown et al 2021).

The change of RTL of adults showed weak non significantly higher decrease for adults in which nest there were ticks on the nestlings in 2005 (difference=-0.621, SE=0.348, z=1.661, P=0.097), change of the RTL has weak non significant positive tendency for birds with longer wing (slope=0.129, SE=0.073, z=1.64, P=0.101). The number of fledged nestlings in 2005 has a very weak negative, no significant effect on the change of RTL (slope=-0.156, SE=0.113, z=1.288, P=0.198), the RTL of females show very weak, a not-significantly higher decrease during two consecutive years (difference= -0.427, SE=0.302, z=1.309, P=0.19).

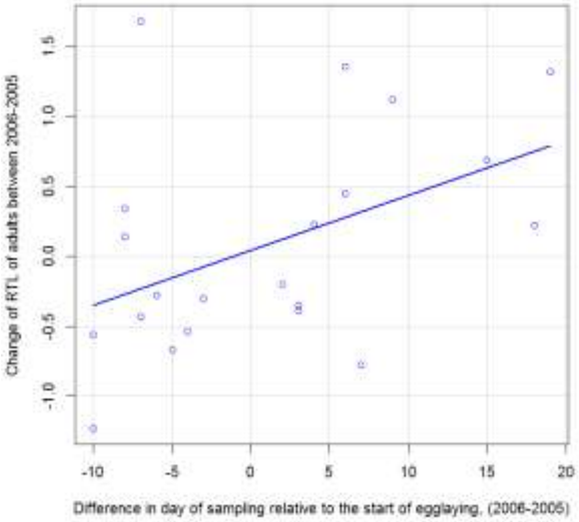

Fig. 18. Change of RTL of adult individuals between 2006 and 2005 in relation to the difference in day of sampling relative to the start of egg laying (day of sampling – day of start egg laying) between 2006-2005.

We extended our study in 2020 and 2021 by collecting detailed behavioural data for the period of pair-formation and foraging/feeding of parents above their genetic data to able to identify male and female behavioural characteristics responsible for the found relationships. We have collected blood sample for telomere measurement in the year of deployment of geolocator and the following year from marked individuals. We have started to carry out genetic analysis (sexing, RTL measurement of 156 individuals in 2020 and further 100 individuals in 2021) and carried out intense and specific radio telemetry and video based field investigations.

However the final microsatellite laboratory investigation finished only in November of 2021, because of the COVID related travelling difficulties both in 2020 and both in 2021. Detailed statistical modelling and analysis, considering the parents feeding/foraging behaviours, will take place in 2022.

Radio telemetry and video investigations

The radio telemetry study with low weight radio transmitter (LifeTag (CTT), Fig. 19) let to investigate the spatial and temporal characteristics of the areas used during the breeding and following period as well because the used LifeTag use solar cell and able to work for several years.

During 2020 and 2021, we followed breeding of each nests (with video endoscope) in an early formed sub colony at Szabolcs village along the river Tisza, in natural habitat, where we caught, individually painted and identified the nest ownerships of adults of ~90% of nests. We randomly selected 30 nests where egg laying started the earliest and deployed 30 pieces a LifeTag (CTT) radio transmitter to randomly selected sex with similar harness as we used for geolocators during the incubation/hatching period of the nests (Fig.19). The used LifeTag has unique digital code and with specific radio receiver stations and antennas which let to follow each movements of marked individuals from/to the subcolony and in ~ 500-1000 m radius of it during the intense nestling feeding period (9th – 14th June) in 2020 and (19th - 30th June) in 2021 and measure the last day of detection in the area of the breeding colony. We recorded daily ~1 hours long videos from the focal subcolonies to investigate visit of nest by individually marked adults.

In 2020, the antennas of the deployed LifeTags were broken by the sand martin after ~ 2 weeks of the deployment, often during the nestling feeding period, by which detection ability of it was zero or decreased dramatically and reduced the number of properly followed individuals (20 individuals, an average 5.35 days, range 3-6 days, an average 25,545 detected signals/individual, range 1,492-69,070 signals/individuals). The flood during the end of June of 2020 which destroyed the entire colony let to investigate the presence of the individuals only in this specific situation. The marked individuals left the area of the colony an average 24th June (SD= 4.64, range 15th June -6th July), there was no additional breeding in the colony, except only in two nests, in 2020.

Because of the antenna failure and at the same time the COVID related travel problems we were not able to investigate occurrence of the marked individuals at different post-breeding areas identified by the geolocator study.

We indicated the found antenna failure problem to the CTT company, who sent freely 30 pieces modified LifeTag in 2021 by which in 2021, we were able to repeat the radio telemetry investigations with much less problem because of the lost of antennas. We were able to follow 22 individuals, an average 8.37 days, (range 2-11 days), an average 33,665 detected signals/individual (range 680-54,834 signals/individuals). The marked individuals left the area of the colony an average 3rd July (SD= 6.191, range 22nd June -11th July) in 2021. On the base of successful application of CTT radio telemetry system on sand martins, we started to initiate the usage of this system along the migration route in Hungary and in the Balkan region to follow the marked individuals during the migration and setup of several radio receiver stations in Albania and Greece are started during 2021.

Fig.19. A LifeTag radio transmitter on a Sand Martin (left), radio receiver stations (CTT SensorStation) with antennas and video recording (Panasonic FZ 2000) from other side of the river at the focal subcolony in 2020.

Along the radio telemetry investigation, we recorded daily 1-1.5 hours long video from large distance (~80-100 m) for measuring feeding rate of individually marked parents when age of nestlings were between 10-18 days (~ 100 hours). Analysis of video recordings let to investigate the feeding rate of parents, influence of number of feeding pairs, radio transmitter/geolocator and “calibrate” the data of radio receiver.

The first detailed modelling of feeding rate/hour of parents of data collected at 39 nests during a week (~1.5 h observation/day, 1410 recorded movement in/out nest) in 2021, considering age of nestlings (quadratic relationship), sex, age category, day, number of nests with feeding and deployment of radio transmitter showed that above significant quadratic influence of the age of nestlings ($P<0.001$, has the maximum feeding rate between 6-16 days old nestlings), female has lower feeding rate comparing to males (difference= -0.143, SE=0.065, P=0.017), there are difference among age categories, one year individuals has lower feeding rate than two years or older individuals (difference=0.289, SE=0.119, P=0.004), feeding rate decreased with day of pairing the pairs (slope=-0.155, SE=0.052, P=0.003), the feeding rate is increasing with the number of pairs feed their 6-16 days old nestlings (slope=0.008, SE=0.004, P=0.024) and individuals with low weight radio transmitter has lower feeding rate (difference=0.215, SE=0.087, P=0.017; GLM Poisson).

Further modelling the time of foraging (measured by time elapsed between two consecutive feeding), showed that foraging time increased with day of pairing of the pairs (slope=89.232, SE=26.564, P=0.001), decreased with the number of pairs feed their 6-16 days old nestlings (slope=-4.591, SE=1.919, P=0.011), there are a non significant difference among age categories, three years old or older individuals has the longest time (P=0.058) and there was no influence of radio transmitter (P=0.886; GLM Gaussian). Modelling of the time of staying in the nest showed, that its length decreased with the age of nestlings (P<0.001), the female stayed longer in the nest than male (difference=78.692, SE=24.728, P=0.001) and individuals with radio transmitter stayed longer than individuals without radio transmitter (difference=82.642, SE=33.981, P=0.003; GLM Gaussian).

On the base of the large and relevant database, collected by our radio telemetry and video observations, we are able to identify groups of individuals within the colony with different foraging/feeding ability, to analyse the influence of the number of feeding individuals on foraging/feeding and reproductive success in the level of individuals and colony and to investigate the influence of the radio transmitter/geolocator on the marked individuals. These investigations at the same time let to test and extend the usage of our geolocators studies.

Because of the field (flood in 2020) and technical problems in 2020 by which we needed to repeat several field work in 2021, we are able to finish the preparation of manuscripts and submit and publish these results only during 2022.

Application of the information and skill provided by the project

On base of the various results of the project, we contributed in organisation, data collection and basic analysis of Hungarian data collection for the second the European Bird Atlas (Keller et al. 2020) and writing chapter of Sand Martin in it (Szép 2020) to present the European level information since the first European Atlas (1990) until the recent data collection (2014-2018) and modelling.

During the project, with strong collaboration with our consortium partner (MME/BirdLife Hungary), we successfully organised the data collection, detailed data analysis with specific spatial modelling for the first Hungarian Bird Atlas (Szép et al. 2021), which is the first national atlas in our region which above the classic presence/absence map of distribution in 10*10 km spatial scale of the breeding species, provide modelled map in 2.5*2-5 km resolution about probability of occurrence, relative density and population trend index with population trend for common breeding and wintering species.

In an wide international cooperation (Morisson et al. 2021), we contributed to investigate the factors behind the decline of migrating species in Europe, based on available data of common bird monitoring in several countries, and found that local productivity could have larger importance behind the decline than survival between breeding season, however various and often accelerated environmental changes in the non-breeding areas (e.g. in Africa) could have strong negative effects as well, which need to understand and to manage.

In these two atlas and the article we did mentioned the project ID because administrative fault, however behind the successful contributions in these publication, the information and skill we had through the project had very important role and we regard as valuable outcome of the project in European and national level.

Difficulties

In our project the detailed investigation of the spatial and temporal characteristics of the migration and wintering areas of the studied population was essential. Following the project plan, we spent large effort to carry out the relevant and important geolocator based minimum three years long field study for this investigation, which lasted in 2020 with several unexpected difficulties by flood in 2019 and 2020. We were able start the time consuming specific analysis of the geolocator data in 2020 but because of a recent, new and very important methods (usage of temperature data recorded by geolocators) we needed to repeat the specific analysis of geolocators in second half of 2021 and able to submit/publish the results only in the beginning of 2022. This delay caused further delay of the most planned investigations for which the geolocator based results are indispensable for publication in high grade scientific journals.

In the case of our planned genetic and related radio telemetry investigations, COVID related restriction both in 2020 and 2021 caused large delay in the planned microsatellite laboratory works with technical problems in 2020 (antenna loss of radio transmitters and flood during the field studies, caused repetition of the planned field study in 2021) by which submission/publishing of results will start in 2022.

Against the above mentioned difficulties, we were able to carry out all planned field and laboratory tasks of the project in cooperation with the consortium partner. Computerised databases and most of the relevant data analysis are ready for preparation of planned manuscripts.

Deviance from the budget plan

In the project there were two kind of deviance from the project plan: 1- more payment for consumables (University of Nyíregyháza consortium partner) in relation to field data collection and laboratory analysis by less payment for equipment, 2- more payment for personal cost (MME/BirdLife Hungary consortium partner) in relation to changed national regulation in relation to salary of the one full-time non-researcher employment (increased level of minimal salary which introduced after the start of project) which carried out by less payment related by the consumables.

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