

Not everyone is shrinking: increases in body mass and wing length in a Sand Martin (*Riparia riparia*) population in northwestern Italy over two decades

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In recent decades, vertebrates, particularly birds, have exhibited notable morphological changes in response to climate change. In birds, these temporal trends usually entail a decrease in body mass and an increase in wing length, sometimes interpreted as a compensatory strategy to maintain migration. This study investigated temporal trends over more than 20 years (2002–23) in wing length and body mass and their relation to environmental conditions, in a Sand Martin *Riparia riparia* population breeding in northwestern Italy. Our findings revealed a significant increase in both traits within the studied population. Although environmental conditions correlated with Sand Martin morphology, they showed no temporal trend. These morphological trends contrast with those exhibited by most long-distance migrants. We suggest that this difference may arise from varying climatic or environmental conditions during early ontogenetic stages, alongside a reduction in pressures selecting for small size associated with the relatively more stable climatic conditions in the wintering region.

Keywords: body size, long-distance migrant, morphology, shape-shifting.

INTRODUCTION

In the past few decades, species have shown a wide range of ecological responses to the changing climate, of which some of the best-known are changes in morphology (Gardner *et al.* 2011, Rydning *et al.* 2021). Body shape and size are fundamental determinants of species ecology and life-history traits due to their essential implications for species movement, thermal biology and ecological interactions (Brown 1995). In birds, changes in morphology and trait size at the population level have been reported in several species of resident and migratory birds captured at bird ringing stations or through examination of museum specimens in North America (Van Buskirk *et al.* 2010, Weeks *et al.* 2020), Amazonia (Jirinec *et al.* 2021), Israel (Yom-Tov 2001, Dubiner & Meiri 2022) and Europe (Yom-Tov *et al.* 2006). The changes observed by these studies usually (but not always) entail a decrease in body mass and bone structure

(e.g. tarsus length) and an increase in wing length. Despite this being the general pattern, some other studies have also found a decrease in wing length (e.g. Van Buskirk *et al.* 2010).

Long-distance migratory birds must adapt to shifting climatic conditions across multiple regions (Jones & Cresswell 2010), and weather conditions at one stage of the annual cycle can significantly influence populations in subsequent seasons (Newton 2004, Mondain-Monval *et al.* 2020). Climate change can, therefore, impact long-distance migrants during breeding, migration and wintering, with repercussions throughout the life cycle. In migratory birds passing through Chicago over the past few decades, both a decrease in body size and an increase in wing length have been observed (Weeks *et al.* 2020). These paired changes have been interpreted as a compensatory strategy to maintain migration in the face of changing weather patterns and wind conditions.

Here, we tested for temporal phenotypic changes in two morphological traits (wing length and body mass) over two decades in a population of Sand Martins *Riparia riparia* breeding in northwestern Italy, to investigate their relationship with

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environmental conditions at different life stages and to determine whether these conditions are also changing. Sand Martins are long-distance migratory birds threatened by changes in habitat and weather conditions (Garrison 1999, del Hoyo *et al.* 2004, Masoero *et al.* 2019). Weather conditions in the wintering grounds are crucial for many Palaearctic migratory birds (Szép 1995, Robinson *et al.* 2008, Norman & Peach 2013), and early studies on Sand Martins revealed a strong effect of severe droughts in the Sahel region on their overwinter survival (e.g. Cowley 1979, Persson 1987).

We aimed to investigate the population-level temporal trends in wing length and body mass of this long-distance migratory bird, the relationship between these morphological traits and weather conditions in the wintering and breeding ranges, and the temporal trends in these weather conditions, which, if present, would indicate climate change. Based on previous studies (e.g. Weeks *et al.* 2020), we expected either a temporal increase in wing length, a reduction in body mass or both during the years of the study. Regarding wing length, Sand Martins undergo a complete moult of their feathers, including wing feathers, in their wintering grounds after the post-reproductive migration. Moult is an energetically demanding process; therefore, we expected weather conditions around the time of the moult to affect wing length. Body mass in aerial insectivores is highly dynamic and influenced by short-term weather conditions (Dumas *et al.* 2024), so we expected weather conditions (i.e. temperature, rainfall) in the breeding area close to the time of weighing to best explain the observed variation in body mass. Furthermore, adverse environmental conditions during migration or wintering can cause selection for individuals of a certain size. For example, Jones (1987) found that a reduction in mean body size occurred over a period of high overwinter mortality, suggesting a selective advantage for smaller body size during drought conditions. We predicted that the environmental conditions in these areas would correlate with body mass or wing length measured during the following breeding season.

METHODS

Study system and general methods

The Sand Martin is an insectivorous bird species present on most continents (except Oceania)

(BirdLife International 2019). Sand Martins breed in colonies of up to 100 pairs on the banks of naturally flowing rivers or, nowadays, in gravel pits. Nests are excavated by the birds using their feet, and tunnels can be up to 1 m long. The populations breeding in Europe are present during the boreal spring and summer (between April and August). These individuals migrate to the overwintering grounds in the Sahel region, an African region south of the Sahara Desert (Mead 1979). Sand Martins start breeding at 1 year and live for an average of 2 years (COSEWIC 2013), with a maximum recorded lifespan of 10 years (Fransson *et al.* 2010).

The study area was located along a c.25-km stretch of the river Po and in the commercially managed quarries surrounding it (between 44.971°N, 7.693°E and 44.832°N, 7.636°E). The study area was located within the River Po Piedmontese Regional Park, to the south of the city of Turin, Italy. The quarries have been active throughout this study, with building materials such as sand and gravel being excavated from the river course. After extraction from the ground, sand and gravel are usually separated into various sizes and stored in stockpiles, creating heaps and banks free of vegetation where the Sand Martins can build their nests (Masoero *et al.* 2019). Throughout the study, staff of the Regional Park were overseeing the work of the quarries under its jurisdiction and the restoration of the excavated banks and surfaces.

This study was part of a long-term monitoring project of the breeding colonies of Sand Martins carried out by A.T. between 2002 and 2023. Sand Martins were caught at breeding colonies using mist-nets, mainly during the morning (Masoero *et al.* 2016, 2019). The capture sessions ranged from one to seven per year (at least one per colony) and occurred during the Sand Martin breeding season (May, June and July). In 2022, the Sand Martins chose to build their colonies in inaccessible sites, making their capture unfeasible. Newly captured individuals were marked with numbered metal rings issued by the Italian Ringing Scheme (Istituto Superiore per la Protezione e la Ricerca Ambientale). If birds were already ringed, then the ring number was recorded. Wing length and body mass were generally measured at each capture as part of the standard processing procedure. Other morphological measures (i.e. tarsus or sternum length) were either not measured at all or

not measured consistently throughout the study. Wing length was measured with a ruler to the nearest 1 mm, and body mass was measured with a digital scale to the nearest 0.1 g (Supplementary material, File S1). We estimated the within-year repeatability of wing length (i.e. the consistency of repeated measurements for the same individual within a year) using linear mixed-effects models with individual-year identity (year_ring) as a random effect. The repeatability was high ($R = 0.949$, standard error = 0.008), indicating that 94.9% of the variance in wing length was explained by differences between individual-year combinations, with low measurement error (narrow confidence interval 0.932–0.965, significant likelihood ratio test $P < 0.0001$).

Individuals were sexed according to the presence or absence of a brood patch and/or shape of the cloaca (Cowley 1999). Ageing was based on plumage; during the breeding season, individuals can only be aged as adults (hatched the previous breeding season or earlier) or, later in the breeding season, as juveniles (just fledged, hatched the same breeding season) (Svensson 1992). In the wintering grounds just after the post-reproductive migration, Sand Martins go through a complete moult, after which adults and juveniles can no longer be distinguished. Due to the location of the breeding colonies (steep walls of sand), it was impossible to investigate nest contents or to capture nestlings; very few just-fledged juveniles were captured, and not consistently every year. For these reasons, we restricted our analyses to adult birds of known sex.

Weather data

We extracted environmental variables encompassing the main geographical areas used by the studied population (Supplementary material, File S2). Local weather conditions in the breeding area were extracted to evaluate the short-term effect of weather on body mass. To evaluate the impact of environmental conditions on the body size of Sand Martins outside the breeding season, we extracted four other indices: Normalized Difference Vegetation Index (NDVI) in two locations within the wintering grounds, the North Atlantic Oscillation (NAO) index and the El Niño–Southern Oscillation (ENSO).

Weather data for the breeding area were extracted from the Arpa Piemonte website (https://www.arpa.piemonte.it/rischi_naturali/snippets_arpa_graphs/

map.meteoweb/) for the weather station located close to the Sand Martin colonies, in the town of Carmagnola (44.886°N, 7.686°E). We extracted data on daily mean temperature and precipitation. Environmental conditions are expected to influence body mass in Sand Martins, as the availability of insect prey is closely linked to weather conditions (Grüebler *et al.* 2008). These variables were extracted in different ways to evaluate temporal trends or to identify the weather window that affects the variation in body mass, as detailed in the Statistical analysis section.

We extracted satellite-derived NDVI values for the overwintering grounds of the Sand Martins. Data were downloaded using the R package MODISTools v.1.1.4 (Tuck *et al.* 2014, Hufkens 2023), which accesses products derived from NASA's MODerate-resolution Imaging Spectroradiometer (MODIS) instruments (Justice *et al.* 1998). We downloaded the band '250m_16_days_NDVI' (NDVI data, with each cell equal to 250×250 m and estimated every 16 days) within the product 'MOD13Q1' (product containing all the terrestrial vegetation indices). We extracted data between 1 September and 31 March (to cover the whole overwintering period of the Sand Martins) and averaged it to obtain one value per overwintering season. Data were downloaded using the function *mt_batch_subset()*, which allows simultaneous downloading of data for multiple locations (i.e. the centroid of the Sahel region, and the location of Lake Chad). As the precise location of the Sand Martins' overwintering grounds of our population is not known, we extracted NDVI values for two 200×200 -km squares, one with the centre 10°N, 10°E, corresponding to the centroid of the Sahel region (main overwintering area for European populations; e.g. Robinson *et al.* 2008, Norman & Peach 2013) and one with the centre 13°N, 14°E, corresponding to Lake Chad (location of an African ringed Sand Martin recovered in Italy; Spina & Volponi 2008). Higher NDVI values correspond to greener vegetation, which is likely to reflect more humid or rainy weather and higher insect abundance (Balbontín *et al.* 2009, Trierweiler *et al.* 2013, Hu *et al.* 2021). These conditions are expected to be beneficial for Sand Martins, as it is for many other insectivorous birds (Ockendon *et al.* 2014).

The NAO index measures the difference in the atmospheric pressure at sea level between the Sub-tropical High (Azores; permanent high-pressure

area) and the Subpolar Low (Iceland; permanent low-pressure area). We used the aggregated station-based NAO index (Schneider *et al.* 2013, Hurrell *et al.* 2023) for winter (December, January, February, March). NAO Index Data were provided by the Climate Analysis Section (NCAR, Boulder, CO, USA; Hurrell *et al.* 2003), downloaded from: <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>. A large difference in the pressure at the two stations (a high index year, denoted NAO+) leads to increased westerlies and, consequently, cool summers and mild and wet winters in Central and Atlantic Europe and dry conditions in central Africa. However, if the index is low (NAO-), then westerlies are suppressed, and winters are cold and dry in northern European areas. Storms track southwards toward the Mediterranean Sea, increasing storm activity and rainfall in southern Europe and Africa. Climate conditions in Africa in relation to NAO are well summarized by Stige *et al.* (2006). During years of negative NAO, the overwintering areas of Sand Martins experience more humid conditions and, therefore, a higher abundance of insects. This index correlates well with apparent survival and spring arrival dates in many trans-Saharan migratory birds (Forchhammer *et al.* 2002, Balbontín *et al.* 2009, Boano *et al.* 2020).

We used the Oceanic Niño Index (ONI) as a measure of the ENSO cycle for the months of December, January and February. The ONI is derived from sea surface temperature anomalies and represents the three-month running mean of sea surface temperature departures in the Niño 3.4 region, based on NOAA ERSST data (National Oceanic and Atmospheric Administration Extended Reconstructed Sea Surface Temperature). An El Niño event is identified when the ONI is equal to or greater than $+0.5^{\circ}\text{C}$, while a La Niña event is indicated by an ONI of less than or equal to -0.5°C . An El Niño or La Niña episode is considered to occur when these thresholds are surpassed for at least five consecutive overlapping 3-month seasons. We obtained the ONI data for the December–January–February trimester from https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php. This index gives an indication of the large weather patterns in the Sand Martin wintering areas (Janicot *et al.* 2001, Rowell 2001), with positive ENSO anomalies bringing drier weather in the western

and central Sahel (Stige *et al.* 2006), and it is used by several studies on trans-Saharan migratory birds and large-scale climate patterns (Robson & Barriocanal 2011, Boano *et al.* 2020, Newton 2023).

Statistical analysis

All analyses were performed using the program R v. 4.4.3 (R Core Team 2025). Linear mixed-effects models (LMMs) were run using the packages lme4 v.1.1–35.1 (Bates *et al.* 2015) and lmerTest v.3.1–3 (Kuznetsova *et al.* 2016). Before fitting the models, continuous response variables were mean-centred ($\mu = 0$) and standardized to a standard deviation of 1. The significance of interactions was tested using the *Anova()* function in the car package v 3.1–3 (Fox & Weisberg 2019), and non-significant ($P > 0.05$) interactions were removed from the model through stepwise deletion. Data, code and results are available at <https://doi.org/10.17605/OSF.IO/5VKB2> (Masoero & Tamietti 2025).

We investigated phenotypic changes in the two morphological traits (wing and body mass as response variables) using LMMs with year of measurement as a fixed effect. In all models, we also included as fixed effects the sex of the individual (two-level factor: male versus female), and the two-way interaction between the sex and year of measurement. As traits were measured several times in the same season (only body mass) and/or in different years (all traits), we included individual identity as a random effect to account for the non-independence of some observations. When analysing variation in body mass, we also included the linear and quadratic effects of hour and day of capture to control for variation in body mass, which often shows daily and seasonal non-linear changes in birds (e.g. Dumas *et al.* 2024). Two-way interactions between the sex of the individual and the hour and day of capture were also included in the model.

Linear mixed-effects models were used to investigate the relationships between morphological traits and weather variables. The models had a structure similar to those for the temporal changes explained above, but included weather variables. For both morphological traits, we included year of measurement as a random effect to account for the non-independence of observations. We tested different weather variables in various models for each trait. In particular, as body mass is highly dynamic in aerial insectivores (Dumas *et al.* 2024), we

tested both for local short-term weather effects (temperature and rainfall using the *climwin* package as explained below) and for long-term effects from environmental condition indices measured during the non-breeding season (i.e. NDVI indices in the Sahel centroid and Lake Chad, NAO index, ENSO index). In contrast, for wing length, we tested only for long-term effects (using the same environmental proxies as for body mass). The variable that best explained variation in the morphological trait was the one for which the model had the lowest Akaike information criterion (AIC) value.

To identify the specific weather periods that best explained variation in body mass, we applied a sliding window approach using the *slidingwin()* function from the R package *climwin* v.1.2.3 (Bailey & van de Pol 2016, van de Pol *et al.* 2016). This method enables simultaneous testing of crucial periods along with descriptive metrics (e.g. mean, sum) and functions (e.g. linear, quadratic) that effectively characterize the relationship between weather and biological data. We used a relative window which opened 20 days before each mass measurement and closed on the day of mass measurement. To identify the best-supported model, *climwin* compares each model's AICc value (the AIC corrected for small sample sizes) relative to the base model (i.e. a model without a weather signal). This base model was fitted using the R package *lme4* v.1.1–35.1 (Bates *et al.* 2015). Our base model included sex, day and hour of capture (linear and quadratic terms) as fixed effects. Hour and day of capture were included to adjust for seasonal and daily fluctuations in body mass, as individuals are not captured at the same time or on the same day. By comparing this base model to those that included the linear and quadratic effects of rainfall and temperature, we were able to select the best-supported model for each environmental variable using ΔAICc , defined as the difference in terms of AICc between the baseline model and a model with a weather signal (Bailey & van de Pol 2016, van de Pol *et al.* 2016). As spurious results can arise from multiple comparisons, we used the function *randwin()* in the package *climwin* to run each model on 1000 randomized datasets and then compared the ΔAICc of the observed versus the randomized data (van de Pol *et al.* 2016). The model was retained only if the probability of the observed signal being due to chance was below 0.01. There was no significant

correlation between mean temperature and rainfall in the selected windows (Pearson's correlation = 0.0055, $t = 0.336$, $df = 3734$, $P = 0.737$).

Temporal changes in the environmental variables were investigated using LMMs with year as a fixed effect. We tested for temporal changes in six response variables: average mean temperature and sum of precipitation in the window identified by the sliding window analyses, NDVI indices in the Sahel centroid and Lake Chad, NAO index, and ENSO index. To estimate temporal trends in local weather conditions, we extracted mean temperature and mean rainfall within two dates (first quartile and third quartile of the distribution of the capture dates, respectively, 27 May and 18 June).

RESULTS

Over the course of the study (2002–23), analyses showed significant increases in wing length and body mass in adults (Table 1 & Fig. 1). In both cases, the interaction between sex and year was not significant ($P > 0.05$) and was therefore removed from the final model. During the 22 years of the study, wing length increased at a similar rate in both sexes (0.32% increase, corresponding to an increase of 0.34 mm), but differed between sexes, with a mean of 105.60 mm (± 2.57 standard deviation (sd)) for females and 105.35 mm (± 2.61 sd) for males. The increase in body mass was 1.4% (corresponding to 0.19 g), and body mass significantly differed between sexes, with a mean of 13.41 g (± 1.04 sd) for females and 12.53 g (± 0.87 sd) for males.

Weather variables that best explained variation in wing length and body mass were, respectively, the NAO index for the winter months and the local conditions of temperature and rain (lowest AICc value, full results for wing length and body mass and all weather variables in Supplementary material, File S3). A higher trans-Saharan winter NAO index was associated with longer wing length (Table 2 & Fig. 2a). For body mass, we obtained two temporal windows using the sliding window methodology, one for temperature with a linear effect between the time of measurement and 1 day before, and one for rainfall with a quadratic effect between 6 and 12 days before the measurement (Table 2). Body mass increased with mean temperature (Fig. 2b) and increased with rainfall initially, then decreased with increasing rainfall (Fig. 2c).

Table 1. Variation of wing length and body mass in relation to sex (male, female) and measurement year in a Sand Martin population in northwestern Italy between 2002 and 2023. As body mass has sometimes been measured multiple times during the breeding season, the variables day and hour of capture were included in this model. Continuous response variables were mean-centred ($\mu = 0$) and standardized to a standard deviation of 1. The random effect for individual identity ('ring') was included in both models. se, standard error.

Predictors	Wing length				Body mass			
	Estimate	se	<i>t</i>	<i>P</i>	Estimate	se	<i>t</i>	<i>P</i>
(Intercept)	105.62	0.063			13.433	0.022		
Year	0.105	0.051	2.05	0.041	0.056	0.020	2.807	0.005
Sex [M]	-0.240	0.086	-2.80	0.005	-0.905	0.031	-29.436	<0.001
Hour of capture					9.341	0.994	9.402	<0.001
Hour of capture ²					-4.757	0.946	-5.029	<0.001
Day of capture					-13.804	1.353	-10.202	<0.001
Day of capture ²					4.970	1.361	3.653	<0.001
Sex [M] × Day of capture					8.664	1.789	4.844	<0.001
Sex [M] × Day of capture ²					0.578	1.804	0.320	0.749
Variance components								
Residuals	1.22				0.44			
Ring	5.50				0.38			
Sample sizes								
Years	21				21			
Rings	3669				3448			
Observations	3917				3695			

Between 2002 and 2023, the winter NAO index did not show any significant temporal trend despite showing strong variations during the course of the study (Fig. 2; slope $\pm$ standard error (se): 0.445 ± 0.448 , $P = 0.332$). Temperature and rainfall also did not show any significant temporal trend during the time of the study (respectively, slope $\pm$ se: 0.116 ± 0.295 , $P = 0.699$; slope $\pm$ se: 5.656 ± 12.443 , $P = 0.654$). We also tested the other weather variables for temporal trends, but only the NDVI values for Lake Chad showed a significant temporal increase during the study (slope $\pm$ se: 0.010 ± 0.004 , $P = 0.012$; Supplementary material, File S4).

DISCUSSION

We found that our population of Sand Martins showed increases in wing length and body mass over the past 20 years. Our study revealed a temporal increase in wing length and body mass; however, the morphological changes reported in the literature are not always consistent. Our result on the temporal increase in wing length is consistent with what is reported in some species of birds (e.g. Goodman *et al.* 2012, Weeks *et al.* 2020,

Dubiner & Meiri 2022, Youngflesh *et al.* 2022, Romano *et al.* 2025), but contrasts with findings from other studies (e.g. Teplitsky *et al.* 2008, Van Buskirk *et al.* 2010). The changes in body mass observed in the studied population contrast with the general decrease observed by several other studies (e.g. Weeks *et al.* 2020, Dubiner & Meiri 2022, Youngflesh *et al.* 2022, Romano *et al.* 2025), but support findings by some other studies (e.g. Goodman *et al.* 2012). This inconsistency in morphological changes among birds emphasizes the need to examine temporal trends across an ever-expanding range of species.

Many avian species exhibit morphological adaptations in response to environmental pressures (Weeks *et al.* 2020, Dubiner & Meiri 2022, Youngflesh *et al.* 2022), but these changes usually entail a decrease in body mass and/or an increase in wing length or body length. For instance, studies of museum specimens and mist-netting data have documented population-level changes in traits such as body mass, wing length and tarsus length, reflecting the impact of varying climatic conditions on these birds (Yom-Tov 2001, Yom-Tov *et al.* 2006, Weeks *et al.* 2020, Jirinec *et al.* 2021, Dubiner & Meiri 2022). These studies highlight

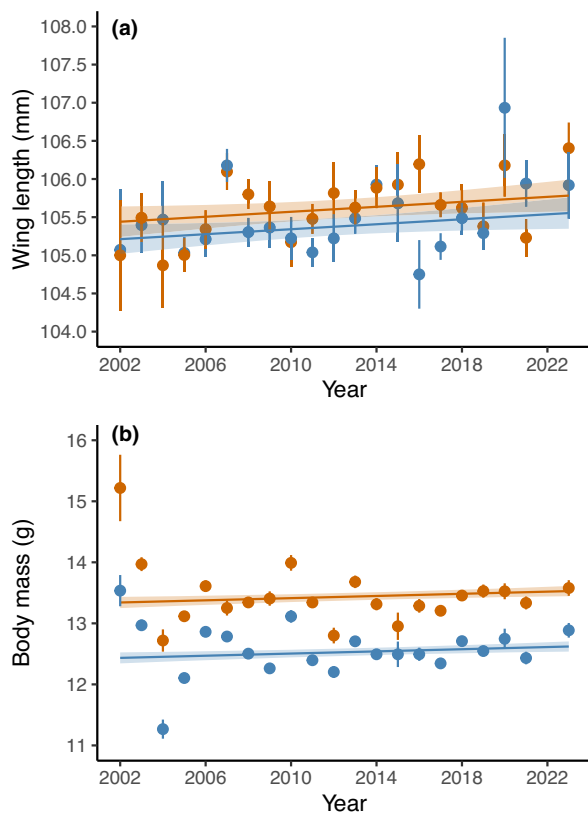


Figure 1. Predicted values (and 95% CI) of the variation of wing length (a) and body mass (b) in female (orange) and male (blue) Sand Martins between 2002 and 2023 in north-western Italy. Predicted lines are obtained using average values of the other continuous variables, if present. Annual mean ($\pm$ standard error of the mean) variation is represented with dots and bars.

the importance of understanding how morphological traits can shift in response to environmental changes, as they are critical for survival and reproductive success in migratory species. Hence, the concurrent increase in wing length and body mass in our Sand Martin population raises intriguing questions about the specific ecological and evolutionary factors giving rise to them.

We found correlations between morphological traits and weather conditions, although no temporal trends were observed in these environmental variables, in contrast to the directional changes in morphological traits. Generally, a positive NAO phase leads to higher Mediterranean sea surface temperatures, which enhances moisture transport to the Sahel and increases rainfall (Mohino *et al.* 2024). Therefore, a positive NAO is generally associated with increased rainfall in the Sahel,

while a negative phase can lead to drier conditions. We were surprised that neither of the NDVI indices showed a better performance than the NAO index. However, as we are unaware of the precise location of the wintering grounds of the studied Sand Martins, we are probably not using the correct locality to extract NDVI values. It is also possible that the wintering destinations change annually depending on local conditions in the Sahel region. Indeed, the Sahel region has become wetter since the 1990s, with increased rainfall attributed to the intensification of the West African monsoon (Biasutti 2019). Although the region experienced severe droughts in the 1970s and 1980s, leading to a significant decline in rainfall, the last two decades have seen a recovery in precipitation levels, approaching the long-term averages observed over the 20th century. Currently, the area is experiencing a different precipitation pattern, characterized by more frequent but lighter rainfall. This shift reduces the likelihood of both flooding and droughts (Bichet & Diedhiou 2018), which has beneficial consequences for humans and possibly also for avian species wintering in the region. These milder conditions have been linked to the absence of consistent temporal trends in average apparent survival of Sand Martins in the studied population (Masoero *et al.* 2016). In contrast, the extreme droughts of the 1970s and 1980s caused dramatic population declines in Sand Martins and selection against larger body size (Jones 1987, Bryant & Jones 1995). In contrast with our findings, in other swallow species, including the trans-Saharan migratory Barn Swallow *Hirundo rustica* and the North American Tree Swallow *Tachycineta bicolor*, adults have undergone a decrease in body size traits, such as body mass, keel length and wing length (Shipley *et al.* 2022, Romano *et al.* 2025). The drivers of these changes are likely to be different, despite the species being closely related. For example, climate change could have an effect during the nestling stage, which is not possible to investigate in the current study. Indeed, developmental phenotypic plasticity, influenced by varying environmental conditions during early life stages (Andrew *et al.* 2017, Corregidor-Castro *et al.* 2023, Tabh & Nord 2023, Major *et al.* 2024), may explain these phenotypic changes over time.

Another proposed explanation for the observed morphological changes in Sand Martins is that the strength and/or the direction of selection on

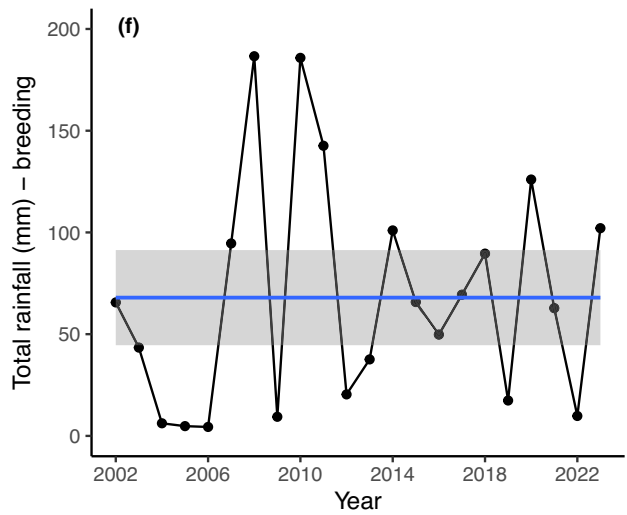
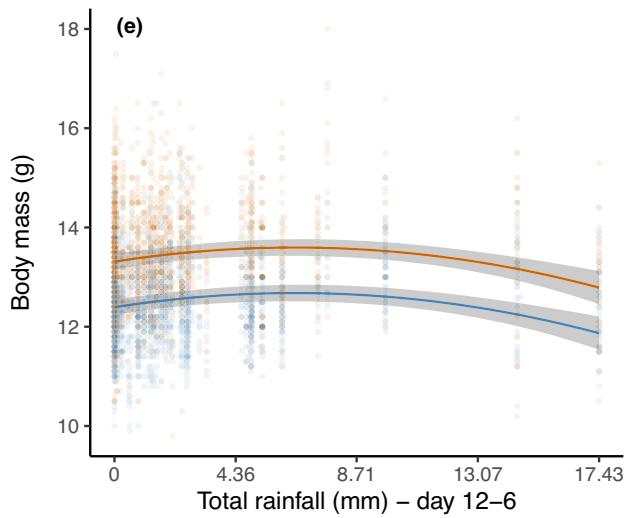
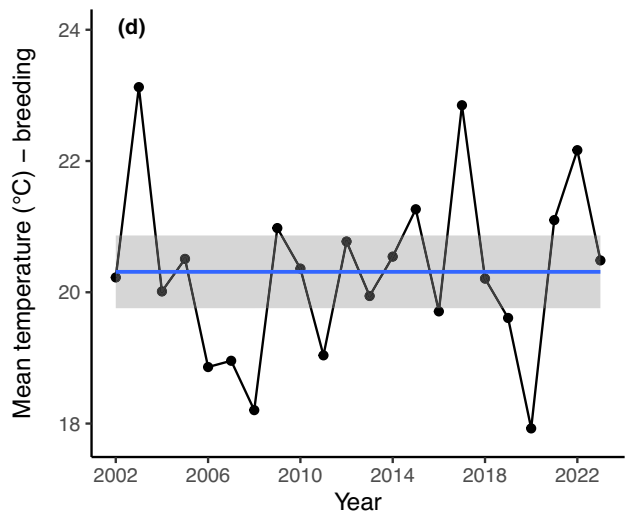
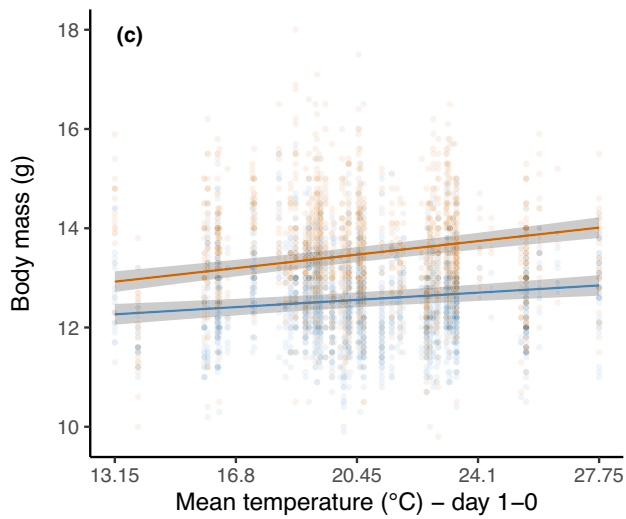
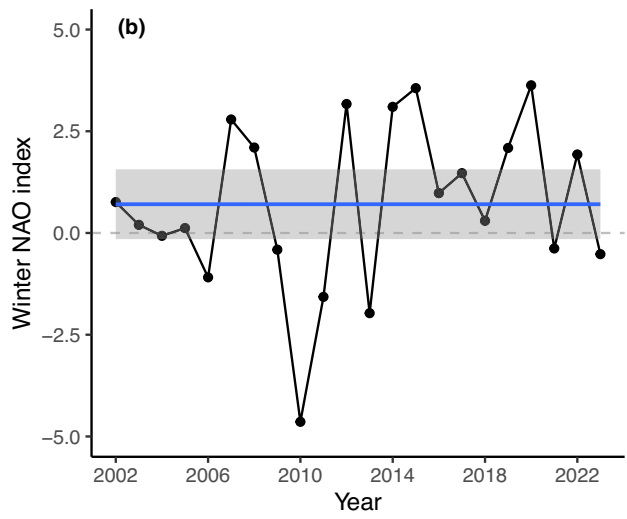
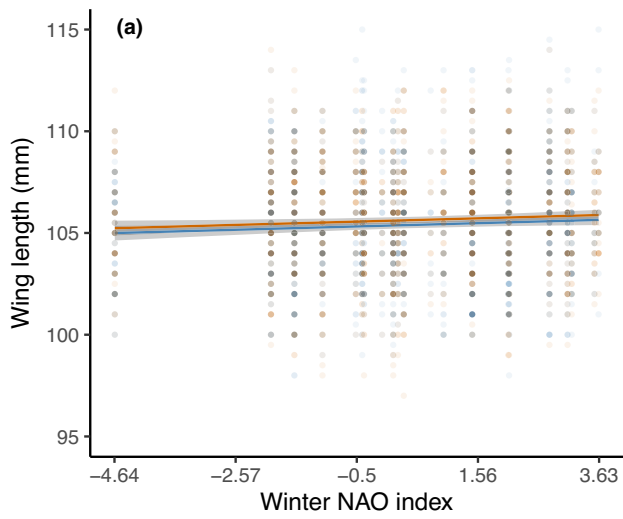
Table 2. Variation of wing length and body mass in relation to sex (F: females, M: males) and, respectively, the North Atlantic Oscillation (NAO) index for the winter months (December, January, February, March) and the local mean temperature (between 1 and 0 day from measurement) and total rainfall (between 12 and 6 days before the measurement) in a Sand Martin population in north-western Italy between 2002 and 2023. As body mass has sometimes been measured multiple times during the breeding season, the variables day and hour of capture were included in this model. Continuous response variables were mean-centred ($\mu = 0$) and standardized to a standard deviation of 1. The random effects for individual identity ('ring') and for 'year' of measurement were included in both models. se, standard error.

Predictors	Wing length				Body mass			
	Estimate	se	<i>t</i>	<i>P</i>	Estimate	se	<i>t</i>	<i>P</i>
(Intercept)	105.663	0.084			11.876	0.220		
Winter NAO index	0.155	0.069	2.25	0.025				
Sex [M]	−0.251	0.086	−2.93	0.003	−0.192	0.263	−0.729	0.466
Rainfall					−1.034	1.217	−0.85	0.396
Rainfall ²					−8.223	1.447	−5.681	<0.001
Temperature					0.075	0.01	7.382	<0.001
Temperature × Sex [M]					−0.035	0.013	−2.729	0.006
Hour of capture					−20.985	1.863	−11.267	<0.001
Hour of capture ²					4.185	1.568	2.669	0.008
Day of capture					7.633	1.145	6.664	<0.001
Day of capture ²					−3.022	1.066	−2.835	0.005
Sex [M] × Day of capture					13.034	2.2	5.925	<0.001
Sex [M] × Day of capture ²					1.495	1.756	0.851	0.395
Variance components								
Residuals	1.15				0.37			
Ring	5.51				0.40			
Year	0.06				0.10			
Sample sizes								
Years	21				21			
Rings	3648				3448			
Observations	3917				3695			

body size varies in response to variations in weather patterns along their migratory route. Hahn *et al.* (2015) found that wing length in migratory birds is correlated with the spring phenology of reproduction, suggesting that longer wings enable optimal arrival times by allowing for higher migration speeds. This adaptation is crucial for ensuring that birds reach their breeding grounds in synchrony with the availability of resources, such as food and nesting sites, which

are often influenced by climatic conditions. Additionally, an increase in both wing length and body mass contributes to maintaining the wing load, enhancing manoeuvrability and decreasing overall flight costs in migratory birds (Bowlin & Wikelski 2008). These aerodynamic advantages are significant for navigating through varying weather conditions, as they allow birds to respond more effectively to changes in wind patterns and thermal updrafts during migration.

Figure 2. Relationship between two morphological traits (wing length (a) and body mass (c, e)) in female (orange) and male (blue) Sand Martins and, respectively, the North Atlantic Oscillation (NAO) index for the winter months (December, January, February, March) (a), local mean temperature (between 1 and 0 day from measurement) (c) and total rainfall (between 12 and 6 days before the measurement) (e) in the breeding area. Each dot is one observation (darker dots represent a higher number of observations). The temporal variation of the NAO index (b), of local mean temperature (d) and total rainfall (f) between the first and third quartiles of the measurement dates. Fitted lines show 95% confidence intervals (shaded areas).



CONCLUSIONS

Our findings demonstrate that Sand Martins in the studied population have exhibited increases in wing length and body mass over the past two decades. These changes occurred despite the absence of clear temporal trends in local temperature, rainfall or the winter NAO index – suggesting climatic stability during the study period. Previous research indicates that droughts in the Sahel during the late 20th century imposed strong negative selection on larger individuals, favouring a decrease in body size during winter (Bryant & Jones 1995). Consistent with this, we observed no continued body size reduction coinciding with a stabilized Sahel climate. Instead, less intense winter selection – combined with persistent positive selection for larger body size during the breeding season (as linked to higher reproductive success and survival (e.g. Shipley *et al.* 2022)) – may have enabled a gradual rebound toward the historical body size equilibrium. This delayed response highlights how shifts in environmental selection pressures can produce time-lagged evolutionary responses in migratory birds (Radchuk *et al.* 2019), particularly as Sahel ecosystems themselves may recover gradually after prolonged droughts.

Finally, it is essential to recognize that, alongside natural selection, developmental phenotypic plasticity could also shape these morphological outcomes, as conditions during early development are likely to influence adult traits in Sand Martins and related species. Future research that integrates perspectives on both genetic adaptation and plastic responses will be valuable for a comprehensive understanding of avian morphological change under fluctuating environmental regimens.

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AUTHOR CONTRIBUTIONS

Giulia Masoero: Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; validation; methodology; formal analysis; project administration; data curation; supervision; resources; software. **Alberto Tamiatti:** Project administration; data curation; supervision; resources; writing – review and editing; funding acquisition; investigation.

ETHICAL NOTE

None.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code used for statistical analysis and plots are available via the Open Science Framework at <https://doi.org/10.17605/OSF.IO/5VKB2>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

File S1. Temporal size changes.

File S2. Weather data.

File S3. Weather conditions and morphology.

File S4. Temporal changes in weather.