DIFFERENCES IN HEAD-BILL LENGTH AMONG COMMON TERNS *STERNA HIRUNDO* FROM SEVEN BREEDING AREAS AROUND THE NORTH ATLANTIC OCEAN AND INLAND IN NORTH AMERICA

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ABSTRACT

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We investigated geographical variation in size of Common Terns *Sterna hirundo* by measuring head-bill lengths (HBLs) in birds from five breeding areas around the North Atlantic Ocean and two breeding sites inland in North America. HBLs were slightly larger (by about 1%) in Europe than in North America and much larger (by about 3.9%) in Bermuda than in either continental area. HBL measurements were highly repeatable, and we recommend their use as an index of body size in terns.

Key words: Bermuda, Common Tern, geographic variation, head-bill length, North Atlantic Ocean, *Sterna hirundo*

INTRODUCTION

In three previous papers, we reported on genetic differences among populations of Common Terns *Sterna hirundo* breeding in Europe and at sites around the North Atlantic Ocean (Szczys et al., 2012) and on freshwater sites across eastern North America (Arnold et al., 2022; Szczys et al., 2017). Here, we investigate possible morphological differences among Common Terns breeding in these same areas. No consistent differences in plumage patterns or coloration are known (Arnold et al., 2020; Cramp & Simmons, 1983; Malling Olsen & Larsson, 2010; Voous, 1957), so we focused on possible differences in body size. Measurements of body dimensions reported in recent compilations do not permit rigorous statistical comparisons (Arnold et al., 2020; Becker & Ludwigs, 2004; Malling Olsen & Larsson, 2010), so we present new or recent measurements from three breeding areas in northern and western Europe, one in Bermuda, and three in eastern North America, including two inland in the Great Lakes region. The only body dimension that has been measured in the same way at all seven locations is head-bill length (the distance from the back of the skull to the tip of the bill; hereinafter, *HBL*). Because bill dimensions can have a strong genetic component (Knief et al., 2012) and HBL may be heritable (Larsson et al., 1997), geographic comparisons of HBL among populations may provide a phenotype-level test of population divergence. We, therefore, tested whether HBL differs among the seven populations in our study and, further, whether the strongest divergence occurs in the isolated Bermuda population. The latter has experienced severe bottlenecks, some of which were driven by hurricanes (Nisbet et al., 2010; Szczys et al., 2012; Wingate & Nisbet, 2020; Wingate et al., 2020).

METHODS

Study Sites

We obtained measurements of HBL in Common Terns (hereinafter, *terns*) from seven breeding areas around the North Atlantic Ocean and inland in eastern North America (Fig. 1).

Group 1: North-Central Europe

More than 600 terns were killed by highly pathogenic avian influenza virus at an intensively monitored breeding colony at the Banter See, in Wilhelmshaven, Germany (53°31′N, 008°06′E) in 2022 and 2023 (Ewing & Bouwhuis, 2025; Pohlmann et al., 2023). After being frozen at −20 °C within hours of death, 104 of these birds were thawed and measured by SB in March 2024.

Groups 2, 3: Other European Breeding Areas

Terns were trapped while on spring migration along the coast of Senegal in 2021, 2022, and 2023 (Monticelli et al., 2025). A total

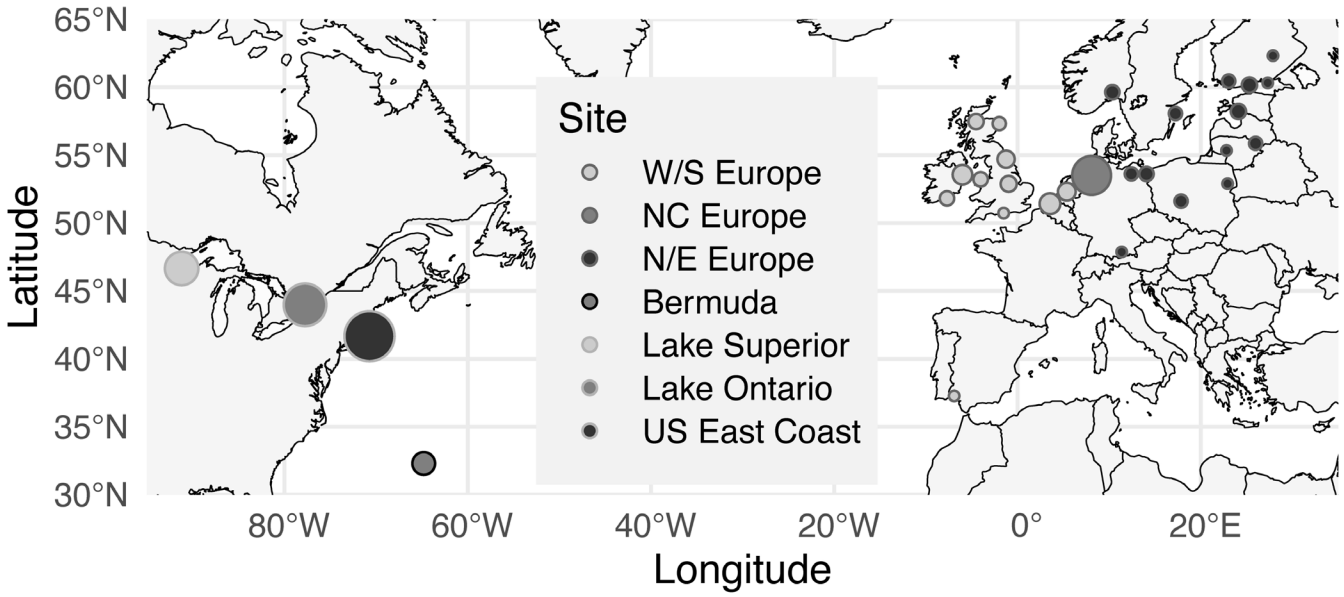

Fig. 1. Breeding areas of Common Terns *Sterna hirundo* from which samples were obtained. Diameters of circles are proportional to the number of birds sampled from each location. N/E Europe: sites to the north, northeast, or east of the Banter See in Germany; NC Europe: North-Central Europe; W/S Europe: sites to the west or southwest of the Banter See; see Methods section for more details.

of 104 birds had been banded previously, and 99 of these could be assigned to breeding sites in Europe, either because they had been banded as chicks or because they were color-banded in Senegal and subsequently resighted at breeding sites. The breeding areas of these birds were divided into three categories (Fig. 1): (1) three birds banded at the Banter See colony and two banded in the eastern Netherlands are included in the sample for North-Central Europe (see previous paragraph, Group 1); (2) 32 birds were assigned to breeding areas to the north, northeast, or east of the Banter See, ranging from southern Germany to Norway and Finland (sites labeled N/E Europe in Fig. 1); (3) 62 birds were assigned to breeding areas to the west and southwest of the Banter See, ranging from the Netherlands to Scotland, Ireland, and Spain (sites labeled W/S Europe in Fig. 1). In addition, three birds had been banded in southern Africa (Namibia and South Africa) and were assigned to Group 2 (total $n = 35$) on the basis of banding recoveries and light-level trackers indicating that most terns that winter in southern Africa breed either in northern or eastern Europe or in western Asia (Becker & Ludwigs, 2004; Piro & Schmitz Ornés, 2022). All birds trapped in Senegal were measured by HD.

Group 4: Bermuda

Terns ($n = 21$) were trapped on nests at seven locations in the Bermuda archipelago (about 32°N, 065°W) in 2006–2010 (Nisbet et al., 2010; Szczys et al., 2012). All HBLs were measured by ICTN.

Group 5: US East Coast

Terns were caught on nests at Bird Island, Massachusetts, USA (41°40′N, 070°43′W), in 1988–2004 (Breton et al., 2014; Nisbet et al., 2020). Because of extensive natal and breeding dispersal between this site and other breeding sites along the Atlantic coast (Arnold et al., 2020; Breton et al., 2014; Tims et al., 2004; and authors' unpublished data), we treat this site as representative of the US East Coast. All HBLs ($n = 212$) were measured by ESB in 2002 (Nisbet et al., 2007) and by ICTN in other years.

Group 6: Lake Ontario

Terns ($n = 140$) were trapped on nests at Presqu'ile Provincial Park, Ontario, Canada (43°59′N, 077°45′W) in 2011–2015. All HBLs were measured by JMA or SAO.

Group 7: Lake Superior

Terns ($n = 72$) were trapped on nests at two breeding sites in Lake Superior, USA—Interstate Island (46°45′N, 092°07′W) and Ashland Island (46°37′N, 090°52′W)—in 2025. There is substantial dispersal of terns between these two sites (A. Bracey, unpublished data), so we treat them as comprising a single breeding area. All HBLs were measured by AB.

Sexing

HBL is consistently larger in male Common Terns than in females (Monticelli et al., 2025; Nisbet et al., 2007). All terns included in this study were sexed genetically from blood or feather samples. Birds from Europe (including those trapped in Senegal) were sexed by SB as described in Monticelli et al. (2025). Birds from all other areas were sexed by PS as described in Nisbet et al. (2010) and Szczys et al. (2012).

Statistical Analysis

We selected the HBL in the year when sex was determined as a single measure of HBL for each bird. We then applied a nested analysis of variance (ANOVA) to test the dependence of HBL on sex and breeding area. Birds from the three North American sites and from the three European breeding areas were grouped as two regional populations; the Bermuda birds remained separate as a

third regional population. The analysis included sex as a factor as well as breeding area nested within regional population. We used Tukey's tests for comparisons among populations.

To estimate repeatability of measurements, we compiled all cases in which an individual bird had been measured more than once: these included the birds from Bermuda and the three North American sites. We then used the "rptR" package in R (R Core Team, 2025) to calculate repeatability, defined as the ratio of group-level variance to the sum of group-level variance and data-level variance (Stoffel et al., 2025). We calculated repeatability within each site and for the entire pooled data set. For all analyses, we specified a Gaussian data distribution and ran 5,000 bootstraps with no permutation. In addition, we calculated the differences between all possible pairs of same-bird measurements, deriving a mean pairwise difference and standard error for each site and for all sites combined.

Ethics Statement

Field work by ESB in 2002 was approved by the University of Minnesota Institutional Animal Care and Use Committee (IACUC) and was carried out under US Federal Fish and Wildlife Permit No. MB778956-1 and Massachusetts Division of Fisheries and Wildlife Permit No. 086.02SCB, issued to ICTN. Field work by ICTN at Bird Island in other years was carried out under renewals of the same permits. Field work by ICTN in Bermuda was carried out under a permit issued by J. Ward, Bermuda's Director of Conservation Services, to D. B. Wingate. Field work by AB was conducted under USGS Bird Banding Laboratory permit no. 05322, Wisconsin state migratory bird master permit no. MB99414A-0, and Wisconsin Department of Natural Resources IACUC permit no. 2016-AB-01. Field work by HD and DM was conducted under partnership agreements with Senegal's Direction des Parcs Nationaux and Direction des Aires Marines Communautaires Protégées. Field work by JMA and SAO was conducted under approved Pennsylvania State University IACUC protocols 36295 and 45332, Canadian Wildlife Service Scientific Permits CA0267 and CA0308, Bird Banding Permits 10431V and 10431W, and annual Letters of Authorization to Conduct Research in a Provincial Park. Field work at all locations conformed to ethical guidelines for the use of wild birds in research (Fair et al., 2010).

TABLE 1
Mean head-bill lengths (mm) of female and male Common Terns *Sterna hirundo* in seven areas of the North Atlantic and North America[a]

Location(s)	Females	Males
N Central Europe	77.07 ± 0.30 (47)	80.26 ± 0.29 (62)
N/E Europe[b]	77.26 ± 0.51 (20)	80.13 ± 0.59 (12)
W/S Europe[b]	76.95 ± 0.36 (27)	80.46 ± 0.30 (35)
Bermuda	80.06 ± 0.35 (16)	82.65 ± 0.52 (5)
US East Coast	76.24 ± 0.18 (102)	79.45 ± 0.18 (110)
Lake Ontario	77.07 ± 0.20 (75)	79.28 ± 0.23 (65)
Lake Superior	76.42 ± 0.26 (42)	79.31 ± 0.37 (30)

[a] Entries are in the form mean ± standard error (*n*). See Methods section for delineation of the breeding areas and the specific locations where samples were collected.

[b] N/E Europe: sites to the north, northeast, or east of the Banter See in Germany; W/S Europe: sites to the west or southwest of the Banter See.

RESULTS

HBLs were longer in males than in females in all seven samples, by an average of about 3.0 mm (approximate mean over all seven comparisons; about 3.8% of the grand mean of the 14 data sets; all $p < .001$; Table 1). Neither sex showed a significant difference in HBL among the three breeding areas in Europe or among the three breeding areas in North America (Tukey's tests, all $p > .05$). Pooling data to yield one composite sample for Europe and one for North America, HBLs were larger in Europe than in North America by about 0.8 mm (about 1%; $p < .001$; Fig. 2). After controlling for sex, HBLs were much larger (by an average of about 3.1 mm, or about 3.9%) in the Bermuda sample than in any of the other six samples (Tukey's tests, all $p < .001$; Table 1, Fig. 2).

For the four sites for which multiple measurements of HBL were available for some or all birds, repeatability ranged from 0.89 at Lake Ontario to 0.96 at the US East Coast, with a value of 0.93 for all sites combined (Table 2). Mean pairwise differences for all same-bird measurements ranged from 0.48 ± 0.07 mm in Bermuda to 0.76 ± 0.08 mm at Lake Superior, with an overall mean of 0.66 ± 0.01 mm (Table 2).

DISCUSSION

HBL is difficult to measure accurately on dried museum skins and is rarely reported in sources that rely on museum material (e.g., Becker & Ludwigs, 2004; Malling Olsen & Larsson, 2010). However, HBL is easy to measure precisely and accurately in live birds and is increasingly reported in monographs that rely on field data (e.g., Arnold et al., 2020). It is primarily a structural measurement (the length of the skull plus the maxillary bones) but also includes the rhamphotheca (the keratinized integument that covers the bill), which may fluctuate slightly in length due to wear and growth. However, HBL is less likely to be affected by postmortem shrinkage or in-life feather wear than other reported measurements. The high values for repeatability reported in this study (Table 2) support the reliability and precision of HBL measurements, even though the measurements from one site (US East Coast) were obtained by different observers in different years.

Tarsus length is also a structural measurement but is more difficult to measure precisely and accurately on live birds: reported ranges for Common Terns vary widely, probably because of different methods of measurement (Arnold et al., 2020). Nisbet et al. (2007) used a multivariate index of body size in Common Terns: the first principal component (PC1) of a principal component analysis (PCA) on six variables. PC1 included HBL, bill depth, and tarsus length, with HBL contributing the highest loading. We recommend that HBL or PC1 should be adopted more widely as indices of body size in field studies.

This study has two main findings. First, Common Terns from a wide range of locations in Europe have significantly longer HBLs than those from three widely spaced sites in North America, but the difference is only slight (averaging about 1%). The small size of this difference is noteworthy given the lack of evidence for interchange of individuals between the two continental breeding populations (Nisbet & Safina, 1996).

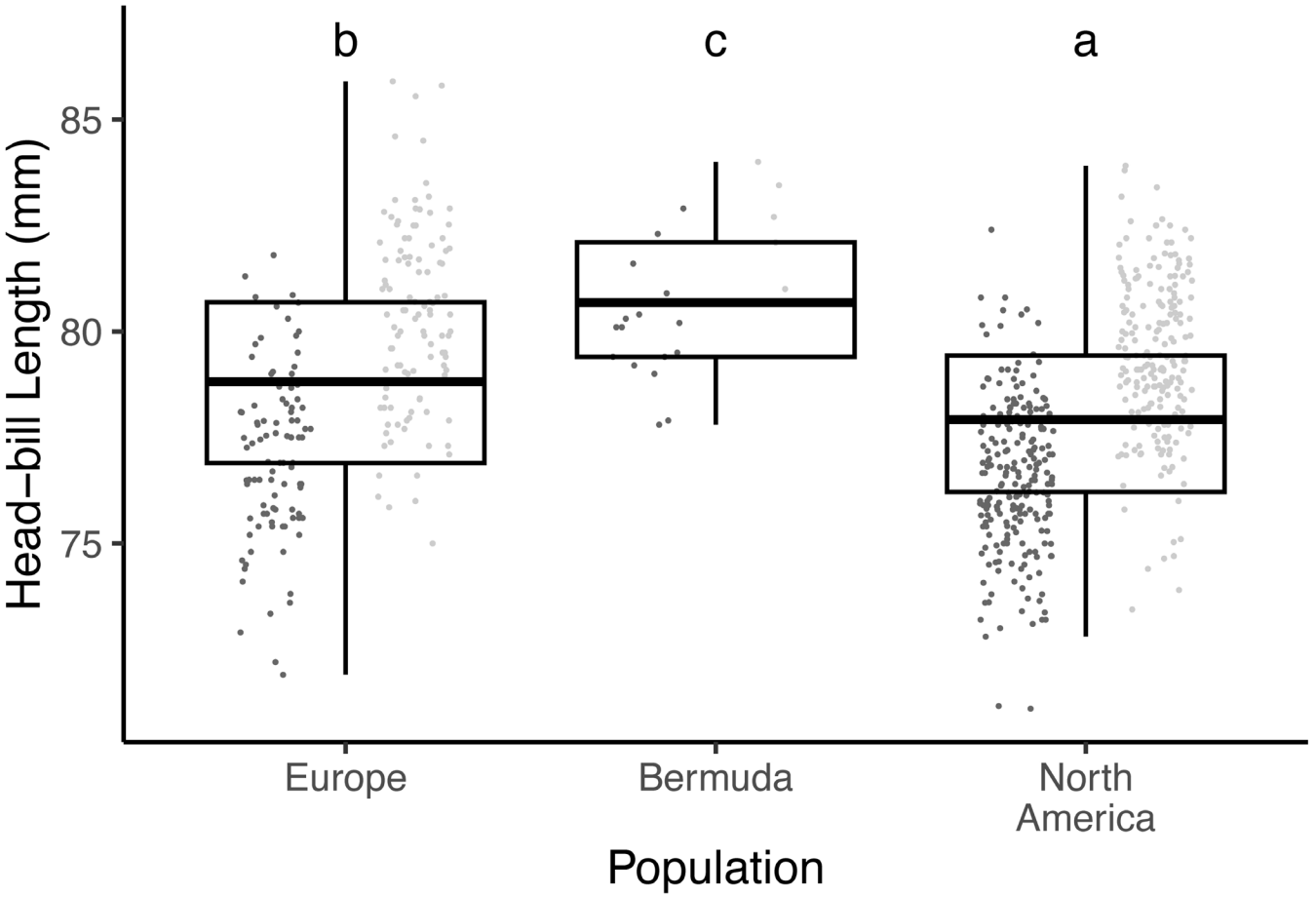

Fig. 2. Means and variation for head-bill measurements across three regional populations of Common Terns *Sterna hirundo*. Boxes indicate 25% to 75% quantiles, with midlines indicating mean values. Individual measurements are shown with jittered data points separated by sex within each site, with females on the left (dark gray points) and males on the right (light gray points). Significant differences ($p < .001$) among regions are indicated by letters at the top of the graph.

Second, Common Terns from Bermuda had much longer HBLs than those from either continental Europe or North America; the mean difference is about 3.9% (Table 1; Fig. 2). This finding is based on a small sample (Table 1), but that sample included almost all the terns breeding in Bermuda in 2006–2010 (Nisbet et al., 2010). Numbers have dwindled since 2010, and the population is now close to extirpation (M. Mejías, personal communication, 22 December 2025). Our finding of a morphological difference adds to previous findings that the Bermuda terns also differed genetically (Szczys et al., 2012) and ecologically (Wingate et al., 2020) from continental terns.

TABLE 2
Repeatability for head-bill length measurements of Common Terns *Sterna hirundo* across four study locations and for all study locations combined[a]

Location	Birds	Measurements	Repeatability	Mean difference ± SE[b] (mm)
Bermuda	10	21	0.95	0.48 ± 0.07
US East Coast	136	450	0.96	0.54 ± 0.02
Lake Ontario	101	411	0.89	0.75 ± 0.02
Lake Superior	72	144	0.91	0.76 ± 0.08
All	319	1,026	0.93	0.66 ± 0.01

[a] Columns for "Birds" and "Measurements" indicate the number of birds measured two or more times and the total number of measurements, respectively.
[b] Standard error

Hypothetically, these differences might have arisen by genetic drift following population "bottlenecks" (Sendell-Price et al., 2020). The Bermuda terns are known to have passed through bottlenecks in the 1840s (Wingate & Nisbet, 2020) and in 2003 (Nisbet et al., 2010). However, almost all the birds sampled in this study had been alive prior to the 2003 bottleneck (Nisbet et al., 2010). Unfortunately, there is virtually no information on this population between the 1840s and the 1940s (Wingate & Nisbet, 2020). It is possible that the breeding population survived throughout this period, perhaps passing through multiple bottlenecks. However, it is also possible that it was extirpated in the 1840s and that Bermuda was recolonized at some later date by terns from a population that already had high values of HBL.

The only isolated population that might have served as a source for recolonization of Bermuda and might plausibly have been

morphologically different from the population of mainland North America is that in the southern Caribbean (Aruba to islands off Venezuela). This population is currently thriving (Bradley & Norton, 2009), but we have found only one small set of measurements of Common Terns. Voous (1957) reported measurements of wing length and "bill" for nine birds: the wing measurements were much shorter than those reported for European birds by Becker and Ludwigs (2004) and by Malling Olsen and Larsson (2010)—means of 256 mm vs. 271–273 mm—while the bill measurements were much longer—means of 43 mm vs. 36–39 mm; these large differences probably reflect differences in methods of measurement. We suggest that acquisition of further data (both mensural and genetic) from south Caribbean breeders should be a priority for future studies.

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AUTHOR CONTRIBUTIONS

Conceptualization: ICTN, DM. Field work: ICTN, ESB, JMA, SAO, HD, AB, DM. Laboratory work: PS, SB. Writing—original draft: ICTN, ESB, DM. Writing—review & editing: all coauthors.

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