Diet Composition and Reproductive Performance in Central Europe's Last Gull-Billed Tern Population – a Long-Term Study

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Diet composition and reproductive performance in Central Europe's last Gull-billed Tern population – a long-term study

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As more and more species are in decline, understanding the various aspects underlying their population dynamics is crucial to optimise conservation efforts. Hereto, we studied the diet composition and reproductive performance of Gull-billed Terns forming the last breeding population in Central Europe by analysing population-level data collected between 2011 and 2022 as part of a conservation program. We show that the main prey types vary among breeding stages and across years. When observed foraging for themselves, Gull-billed Terns were mainly found to eat insects, whereas crabs and worms were the main prey items used for courtship feeding and chick provisioning. The proportion of prey of terrestrial origin used for courtship feeding increased over the study period, whereas no such change was observed in prey used for self-feeding or chick provisioning. Clutch and egg size also increased over the study period but were not correlated with the proportion of terrestrial prey used in courtship. Fledging success did not change over time and was not correlated with variation in chick diet. These results confirm that the Gull-billed Terns in this population are generalist feeders and suggest that their breeding success is not currently threatened by a lack of, or changes in, specific prey types. The shift towards more terrestrial prey in part of their diet may, however, indicate changes in the aquatic ecosystem, which should be further assessed, together with other potential risks for these threatened birds, such as inbreeding and pollution.

Key words: *Gelochelidon nilotica*, feeding ecology, foraging behaviour, courtship feeding, provisioning behaviour, feeding observations, conservation project

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Breeding success relies on the availability of suitable breeding habitat (Séchaud *et al.* 2022), favourable environmental conditions, such as adequate temperature, no heavy wind or rain (Schreiber 2002), as well as sufficient quantity and quality of food (Stienen *et al.* 2000, Oro *et al.* 2004, Paillisson *et al.* 2007). As the impact of anthropogenic factors on the environment increases, pollution of foraging habitats, altered environmental conditions, changes in food availability and dietary shifts occur (Hoegh-Guldberg & Bruno 2010, Burger & Gochfeld 2002, Church *et al.* 2019, Howells *et al.* 2017). Marine ecosystems and estuaries seem especially strongly affected, showing severe changes in the distribution and productivity of species and the structure of food chains (Scanes *et al.* 2020, Sydeman *et al.* 2021).

As top predators, various sea- and other waterbirds are optimal indicators for ecosystem health (Velarde *et al.* 2019) and environmental changes associated with climatic and anthropogenic factors (Burger 2002, Moreno *et al.* 2016). To understand the threats faced by these birds, and hopefully develop or optimise knowledge-based conservation programmes, it is necessary to understand the various aspects of breeding success that underlie their population dynamics. In terms of foraging, sea-and waterbirds such as gulls and terns do not solely rely on marine environments but can also exploit terrestrial habitats (Paillisson *et al.* 2007, Bécares *et al.* 2015). Given that these birds are particularly susceptible to fluctuations in food abundance (Bécares *et al.* 2015, Cury *et al.* 2011, Isaksson *et al.* 2016, Paillisson *et al.* 2007), with declines in body condition, clutch and egg size, and overall breeding success when food is limited (e.g. Albano *et al.* 2011, Dahdul & Horn 2003, Vedder *et al.* 2019, Wendeln *et al.* 2000), studying changes in diets and their effects on breeding success is a logical first step.

Where reductions in single food resources may be especially important for specialists, such as piscivorous species (e.g. Vedder *et al.* 2017), they may also influence the diet of generalists, potentially leading to a diversification or switch of the diet (MacArthur & Pianka, 1966, Schwemmer & Garthe 2008). The Gull-billed Tern *Gelochelidon nilotica* is such a species, in contrast to most other tern species. Its foraging habitats may consist of coastal areas (Erwin *et al.* 1998), rice fields (Antón-Tello *et al.* 2021), freshwater habitats (Fasola *et al.* 1989), grassland and agricultural lands (Scridel *et al.* 2023). As a consequence, Gull-billed Terns are known to feed on a variety of aquatic and terrestrial prey items (Dies *et al.* 2005), which may differ in type and proportion depending on the specific foraging habitats surrounding the breeding area, as well as their availability during the different breeding stages (Bogliani *et al.* 1990, Goutner, 1991, Isaksson *et al.* 2016, Scridel *et al.* 2023).

In Central Europe, Gull-billed Terns are highly endangered after a pronounced population decline in the mid of the last century (Rasmussen & Fischer 1997). To protect the remaining breeding pairs (c. 40), it is crucial to gather information on different aspects underlying their population dynamics. As such, we analysed 12 years of diet data collected in the last breeding colony of Gull-billed Terns in Central Europe as part of a conservation program. Based on previous studies showing the generalist diet of Gull-billed Terns and their use of different foraging habitats (Goutner 1991, Dies *et al.* 2005, Scridel *et al.* 2023), we expected their prey to reflect habitat availability surrounding the breeding area and to show annual variability reflecting changes in availability of different prey, as for example shown by Goutner (1991). Therefore, we (1) identified the main prey items and tested for variation among years, and (2) tested for diet differences between

A colour-ringed Gull-billed Tern from the Neufelderkoog colony catching a crab (photo Fred Visscher, 27 June 2023).

adults and chicks. Most importantly, we then (3) tested whether diet composition during different phases of the reproductive cycle explained variation in reproductive parameters, such as clutch and egg size and the average number of chicks produced. With respect to the latter, we expected high quality prey items in the self-feeding and courtship feeding diet to translate to larger clutches containing heavier and larger eggs (as for example shown in Common Terns *Sterna hirundo* (Nisbet 1973) and Audouin's Gulls *Ichthyaetus audouinii* (Oro *et al.* 1996)) and high-quality prey items in the chick diet to translate to higher fledgling success (Nisbet 1978).

METHODS

Study species

Gull-billed Terns are medium-sized terns (c. 170–200 g) in the family of Laridae. They have a worldwide distribution, but very fragmented breeding areas (BirdLife International 2019). In Central Europe, Gull-billed Terns return from their wintering areas in mid-April and usually start breeding mid-May. Foraging adults usually fly over terrestrial and aquatic habitats, facing the ground or surface in order to locate potential prey. After localisation, and regardless of the habitat, the birds then dive down, pluck the prey item and either eat it directly in flight or transport it to the breeding area. During courtship and incubation, males provide prey for the females (Sears 1981). Clutch size averages two to three eggs, whereas the number of fledglings per breeding pair averages one to two chicks (Møller 1975, Sears 1981). Most of the adults leave the breeding areas, with their chicks, by mid-August to migrate to their wintering areas.

Study area

Due to human-induced modifications of breeding habitats, most Gull-billed Tern populations in Central Europe decreased in the second half of the 20th century, leaving only a small isolated population consisting of c. 40 breeding pairs at Neufelderkoog (53°53'44"N, 8°58'49"E) in the transition zone from the river Elbe to the German North Sea (Nebelsiek 1966, Sánchez *et al.* 2004, Berndt 2018, Risch *et al.* 2018), an important area for coastal birds, providing suitable habitats for breeding and resting (Koffijberg *et al.* 2017). Because of the dramatic population decline, a conservation project was started in 2011 to protect the last Central European population of Gull-billed Terns at Neufelderkoog (https://gelochelidon.de/).

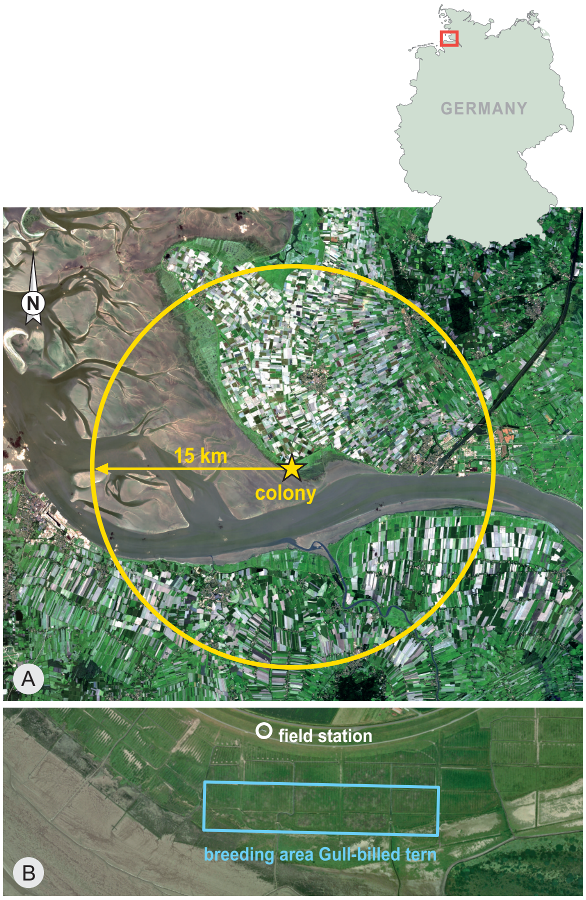

Figure 1. Location of the Gull-billed Tern colony area in Germany, in the Neufelderkoog area (yellow star) with (A) a 15-km foraging radius (yellow circle), and (B) in close-up (blue square). The current environment consists of agriculture (c. 40%), the Elbe estuary (c. 40%), saltmarshes and dikes (c. 15%) and human infrastructure (c. 5%). While we know of the deepening of the river Elbe during the study period, we do not have information on variation in the characteristics of some of the other habitat types (e.g. specific crop types grown). The map was created in QGIS (QGIS Development Team 2022) using a satellite image taken on 4 September 2023.

At Neufelderkoog, the colony area is surrounded by salt marshes with dikes, agricultural land with drainage ditches and the Elbe estuary (Figure 1A), all of which are used for foraging. Agricultural land (c. 40%) as well as the Elbe estuary (c. 40%) thereby represent the main habitats within a 15-km radius around the breeding area, which is the distance within which Gull-billed Terns predominantly forage (Scridel *et al.* 2023). Saltmarshes and dikes account for c. 15% of the environment around the colony area, whereas human infrastructure comprises c. 5%.

Diet monitoring

Starting in 2011, whenever weather conditions were favourable (no darkness, heavy rain, wind or mist), two to three volunteers and researchers performed daily observations from May to August (120–122 days per year) to identify prey items eaten or delivered by Gull-billed Terns. At the beginning of each breeding season, after arrival of the first bird and during courtship, egg laying and incubation, Gull-billed Terns were observed as they were foraging at the dike and in the salt marsh surrounding the colony area, or transporting prey back to the colony area until prey type and usage were identified (self-feeding: $n = 314$; courtship: $n = 667$) or missed ($n = 22$). Prey eaten directly after catching were classified as self-feeding, whereas prey being transported to the colony area were assigned to courtship-feeding. If the adult attempted to feed a partner that subsequently rejected the presented prey item, it was still recorded as courtship-feeding. These observations were all 'single-event registrations', as individual birds were not followed or observed at set times of day, and were mostly done from a field station that was set up at the dike about 300 m from the colony area (Figure 1B). After the hatching of the first chick, 'single-event registrations' continued and included 4193 observations of a prey being delivered to a chick, 807 observations of prey being eaten by the adult itself, 261 observations of prey being used as part of a (late) courtship ritual and 289 observations where the fate of the prey could not be assigned.

Starting in 2016, after hatching of the first chick, we added 'hide observations' to the 'single-event registrations'. These were performed between 10:00 and 12:00, and 18:00 and 20:00 from a hide close to the nests. During these standardised observations, the breeding area was scanned and every prey item that was brought into the area was identified, still without accounting for nest or individual identity. To prevent double counts of the same prey item, each adult with a prey was followed until the prey was delivered to the chick ($n = 3244$), eaten by the bird itself while foraging close to the breeding area ($n = 273$), courtship-fed to a partner after the loss of a clutch ($n = 102$), or lost from sight ($n = 48$). After the usage of the prey item was identified, we scanned the breeding area for the next prey item being brought in. Summing all observations being part of 'single-event registrations' and 'hide observations', we recorded 10,220 dietary items of which 359 (3.5%) were excluded from further analysis as they could not be categorized as self-feeding, part of a courtship ritual or provisioned to a chick.

Following previous studies on Gull-billed Terns, we classified prey as crab, worm (mostly Lumbricidae), insect, benthos, vole, fish, bird or frog (Quinn & Wiggins 1990, Goutner 1991, Costa 1984, Dies *et al.* 2005). Furthermore, each prey was assigned to being of aquatic or terrestrial origin. As we could not link observations to individuals, we cannot account for individual specialism, which may lead to bias if individuals with different prey choice were observed unequal numbers of times.

Reproductive parameters

Starting in 2012, the colony area was visited once during the main incubation period to record the number of nests, as well as clutch size. In 2014–2016, as well as 2020–2022, the length and width of each egg (to the nearest mm) were measured using a calliper, to calculate egg volume (cm^3) using the equation volume = (width×width×length/1000) by Harris (1964). These values were averaged to obtain estimates for the annual mean clutch size and egg volume, although we acknowledge that we did not check for renesting events, such that these annual means are based on first clutches produced during the main laying phase only.

We visited the colony area towards the end of the chick rearing period to search for, and ring, the chicks of each season ($n = 415$ across all years), of which 326 were not found dead afterwards and therefore assumed to have fledged. Given that unringed fledglings were observed on the first migration stop in The Netherlands (Kuipers & van Els 2022), and that the nearest other Gull-billed Tern colonies are located in Spain and France (about 1200 km from Neufelderkoog), such that it is highly unlikely that unringed fledglings observed in The Netherlands originate from other colonies rather than ours, some chicks must have escaped our ringing session. To obtain an estimate of the annual fledging rate as accurately as possible, we added up the number of ringed ($n = 326$) and observed unringed chicks ($n = 37$) in The Netherlands each year and divided them by the total number of nests found across the entire breeding season (which sometimes exceeded the number of nests found during the main incubation period). We, however, also repeated our analyses of fledging rate (see below) excluding the unringed chicks, which led to very similar results and the exact same conclusions (see Figure S1).

Data analysis

Diet data were summarised as proportions of each dietary item per year and category (self-eaten, courtship, chick provisioning) since the total number of prey observed differed among years. A Chi-square test and Shannon-Index were used to test for inter-annual variation and the diversity of the diet in each category, respectively.

To test for temporal trends in, and correlations between, diet composition and reproductive parameters, we grouped prey into being of terrestrial or aquatic origin (following Dies *et al.* 2005, Erwin *et al.* 1998). Annual proportions of these two categories were calculated by dividing the annual sum of each group by the sum of all prey in the same year. As the proportion of prey of aquatic and terrestrial origin always added up to 1, only the latter was used in a Pearson correlation test to assess temporal trends in prey that were self-eaten, part of a courtship ritual, or provided to chicks. Similar correlation tests were run for clutch size, egg size and fledging rate. We also used a Pearson correlation test to assess the correlations among annual average clutch size and egg volume and the proportion of terrestrial courtship prey, and among annual fledging rate and the proportion of terrestrial prey observed in the chick diet, because courtship feeding was previously shown to affect egg weight (Nisbet 1973) and enhanced food availability found to increase egg volume (Oro *et al.* 1996) and fledging rates (Vedder *et al.* 2017, 2019).

All statistical analyses were performed using the R programming software (v. 4.2.1; R Core Team 2022) and figures were created with the 'ggplot2' package (Wickham 2016). All variables were tested for being normally distributed. As fledgling rate and the proportion in the self-eaten diet being of terrestrial origin were not normally distributed, we log- and box-cox transformed these variables prior to analysis. For all analyses, the level of significance was set at $P \leq 0.05$.

RESULTS

Diet variation across breeding stages and years

Of the 9861 identified prey items, 1394 (13.6%) were eaten by the birds themselves, whereas 1030 (10.1%) were part of a courtship ritual and 7437 (72.8%) were delivered to chicks.

Adults were observed to feed on only a small range of prey items (Shannon-Index = 1.15). Their predominant prey type was insect (61.4%), followed by worm (19.9%) and crab (12.5%; Figure 2). Inter-annual variation was substantial ($\chi^2_{88} = 597.7$, $P < 0.001$; Figure 3A) with the proportion of insects, for example, ranging between 21.9% in 2013 and 79.8% in 2016. Similarly, the proportion of worms was at a maximum of 48.5% in 2022, while in 2015 it was at a minimum of 6.6%. Crabs represented 53.1% of the adult diet in 2013, but only 3.2% in 2016.

Prey observed to be used in courtship rituals varied more (Shannon-Index = 1.63). Here, the main prey type was crab (48.3%), followed by worm (15.6%) and fish (12.0%; Figure 2). Again, inter-annual variation was substantial ($\chi^2_{88} = 520.29$, $P < 0.001$; Figure 3B). Males fed their partners 29.4% crab in 2015, versus 59.6% in 2018. Worms accounted for 3% of the courtship feeding diet in 2012, but 51.4% in 2022. In 2014, 44.9% of the courtship feeding diet consisted of fish, whereas no fish were observed to be used for courtship feeding in 2015.

The highest diversity of prey was found in the diet provisioned to the chicks (Shannon-Index = 1.70). Crab was predominant (39.6%), followed by worm (18.8%) and insect (18.8%), but as in the other two categories, the relative frequency of these prey types varied across the years ($\chi^2_{88} = 2174.1$, $P < 0.001$;

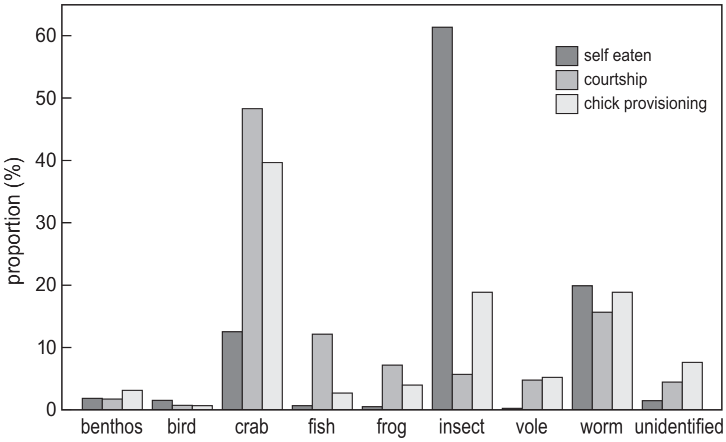

Figure 2. Diet composition of Gull-billed Terns and their chicks between 2011 and 2022.

Figure 3C). Crab ranged in proportion between 54.3% in 2018 and 20.2% in 2022. The proportion of worms varied even more, reaching a minimum of 7.4% in 2012 and a maximum of 28.8% in 2022. The use of insects during chick provisioning fluctuated between 24.6% in 2014 and 5.8% in 2021. In 2017 and 2019, voles represented 19.0% and 14.3% of the chick diet whereas they accounted for less than 6% in the other years.

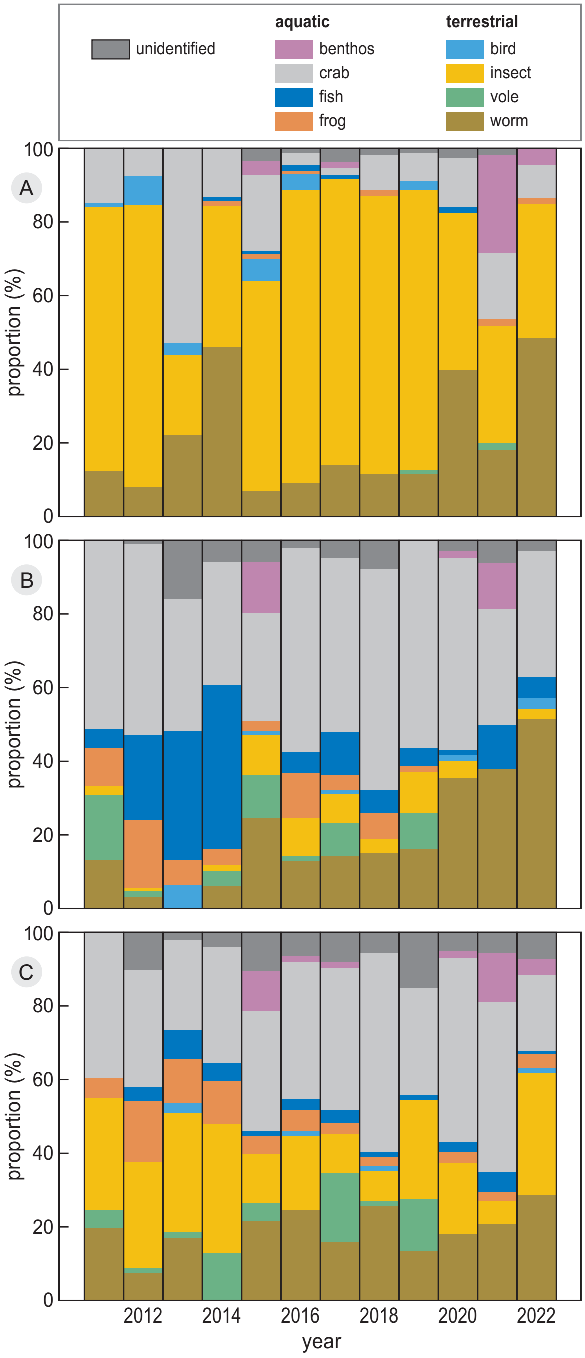

Figure 3. Annual variation in the diet composition of Gull-billed Terns for (A) self-feeding, (B) courtship feeding or (C) chick provisioning.

Categorising prey items into being of aquatic or terrestrial origin showed annual volatility (Figure S2). When regressing the overall proportion against year, the proportion of prey used for courtship feeding being of terrestrial origin was found to increase over the study period ($r_{10} = 0.64$, $P = 0.025$; Figure 4B). This was mainly due to a significant increase in the proportion of worms in the diet ($r_9 = 0.88$, $P < 0.001$). No change was found for self-feeding ($r_{10} = -0.004$, $P = 0.990$; Figure 4A) or for prey delivered to the chicks ($r_{10} = -0.04$, $P = 0.913$; Figure 4C).

Reproductive performance over time and in relation to diet

Mean clutch size ($r_9 = 0.72$, $P = 0.013$, $n = 11$ years; Figure 5A) and egg volume ($r_4 = 0.85$, $P = 0.032$, $n = 6$ years; Figure 5B) increased across the study period, whereas fledging rate did not show any change over time ($r_9 = 0.22$, $P = 0.522$, $n = 11$ years; Figure 5C).

When testing whether variation in reproductive performance measures was correlated with variation in diet composition, the proportion of the courtship feeding diet being of terrestrial origin (which also increased over time; Figure 4B) did not explain a significant amount of variation in either clutch size ($r_9 = 0.50$, $P = 0.117$; Figure 5D) or egg volume ($r_4 = 0.78$, $P = 0.065$; Figure 5E), suggesting that these temporal changes occurred independently of one another. Fledging rate was also not correlated with the proportion of the chick diet being of terrestrial origin ($r_9 = -0.28$, $P = 0.409$; Figure 5F).

DISCUSSION

Based on a 12-year data set, our study provides the first long-term dietary assessment of the last colony of Gull-billed Terns in Central Europe. We quantified dietary variation in prey from self-feeding, courtship rituals and provisioned to offspring and assessed inter-annual variation in reproductive performance measures to test whether variation in fitness components could be explained by dietary variation.

Overall, the Gull-billed Terns of the German Neufelderkoog colony were observed to eat, courtship feed and provision a great variety of prey items. Prey observed to be eaten by adult birds themselves comprised mainly of insects, worms and crabs (c. 94%).

Given that all our observations were done in direct proximity of the colony area, and the surrounding habitats are mainly salt marshes with short vegetation that mostly provides access to insects such as bugs or butterflies, the large amount of insects in the self-feeding category could mainly reflect the habitat and prey availability surrounding our colony area and observation grounds, as also shown in a recent study from Italy (Scridel *et al.* 2023). Prey items such as fish or benthos would (also) have been eaten where they were caught, which would less regularly have been in our field of view or in the vicinity of the colony area, as foraging flights of Gull-billed Terns cover distances up to 15 km (Fasola *et al.* 1989, Scridel *et al.* 2023). Despite prey for self-feeding being the most difficult to accurately quantify, the variation observed across years suggests that our data might still provide a general insight into the relative abundance of available prey used for feeding close to the colony. Although we found considerable variation in prey items across years, we found no trend towards prey being of more terrestrial or aquatic origin across time.

Gull-billed Terns are single prey loaders, such that a short travel distance between the foraging habitats and the colony area, where prey can be presented to partners (or delivered to offspring) should be beneficial (Houston & McNamara 1985). Adults predominantly presented their partners with highly nutritious prey: crabs, worms and fish. Providing nutritious prey to females during courtship could potentially indicate male quality (Nisbet 1973, Tryjanowski & Hromada 2005) and lead to earlier laying, which is often considered beneficial (Smith & Moore 2005, Bejarano & Jahn 2018), or reflect a cost-benefit balance (Charnov 1976, Ledwoń & Neubauer 2018). Whereas insects can easily be eaten by the foraging adults, their nutritional value and therewith the benefit of presenting them to a partner (or chick), likely is smaller than the cost associated with the effort of flying back to the colony area, as shown for Common and Whiskered Tern (Dänhardt *et al.* 2011, Gwiazda & Ledwoń 2016). Still, we found pronounced inter-annual variation in the prey used for courtship, most likely reflecting annual variation in prey abundance, or plasticity in male prey choice.

In addition to general annual variation, we found an increase in the proportion of courtship prey of terrestrial origin across our study period. This change might result from phenotypic plasticity in male prey choice, in this case an increasing specialization towards a terrestrial foraging strategy, for example in response to changes in aquatic food abundance. The colony area is located near the Elbe, a brackish-water river (Figure 1), which was continuously deepened since the beginning of the 20th century (Boehlich & Strotmann 2008). This deepening caused even higher sedimentation rates in the Neufeld harbour, one of the main foraging grounds of the Gull-billed Terns. Additionally, the stream intensified and oxygen concentrations declined (Schöl *et al.* 2014), which can cause fish mortality (Thiel *et al.* 1995). As such, foraging for aquatic prey may have become more time intensive and energetically costly than for terrestrial prey, which can be found in closer vicinity of the breeding area and be caught more efficiently. Finally, the turbidity may have been influenced by enhanced precipitation as part of climate change and have increased the sediment supply to the rivers and lower marshes, thereby decreasing the inundation frequency of the higher elevated saltmarshes (Butzeck *et al.* 2015) and their soil salinity (Bockelmann & Neuhaus 1999). As earthworms, the main prey item

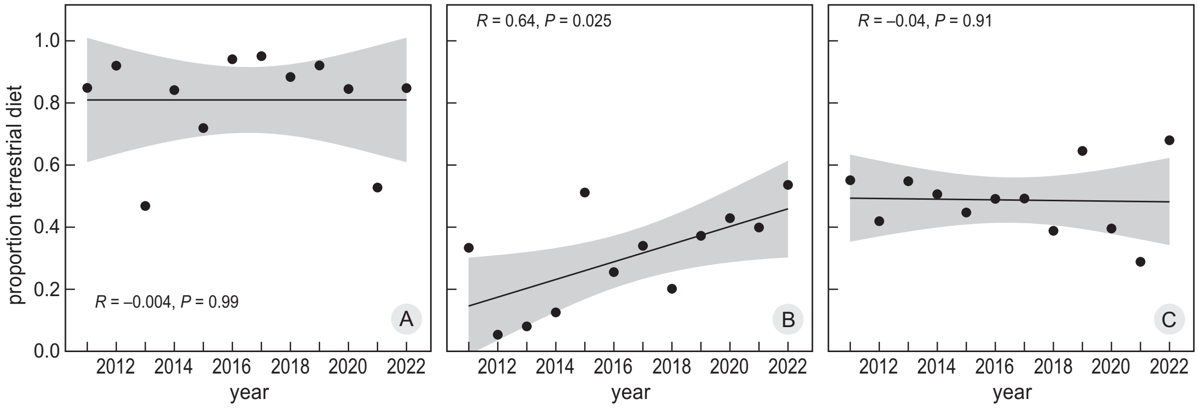

Figure 4. Annual variation in the proportion of Gull-billed Tern prey of terrestrial origin for (A) self-feeding, (B) courtship feeding or (C) chick provisioning.

causing the increase in prey of terrestrial origin in our study, are negatively impacted by salinity (Ivask *et al.* 2012), the potential decrease in soil salinity could have enhanced their numbers near the colony area, facilitating foraging for Gull-billed Terns.

Despite the decline in prey of aquatic origin over time, it is worth pointing out that we found a generally high proportion of crabs taken during courtship, indicating that some adults still manage to catch crabs despite the potentially deteriorated conditions of the aquatic environment caused by anthropogenic impacts. Recently, Goodenough *et al.* (2023) showed that Gull-billed Terns foraged more on terrestrial prey as well as crustaceans when sea surface temperatures were higher than average. Whether the same holds true for the Gull-billed Terns of our study population remains to be

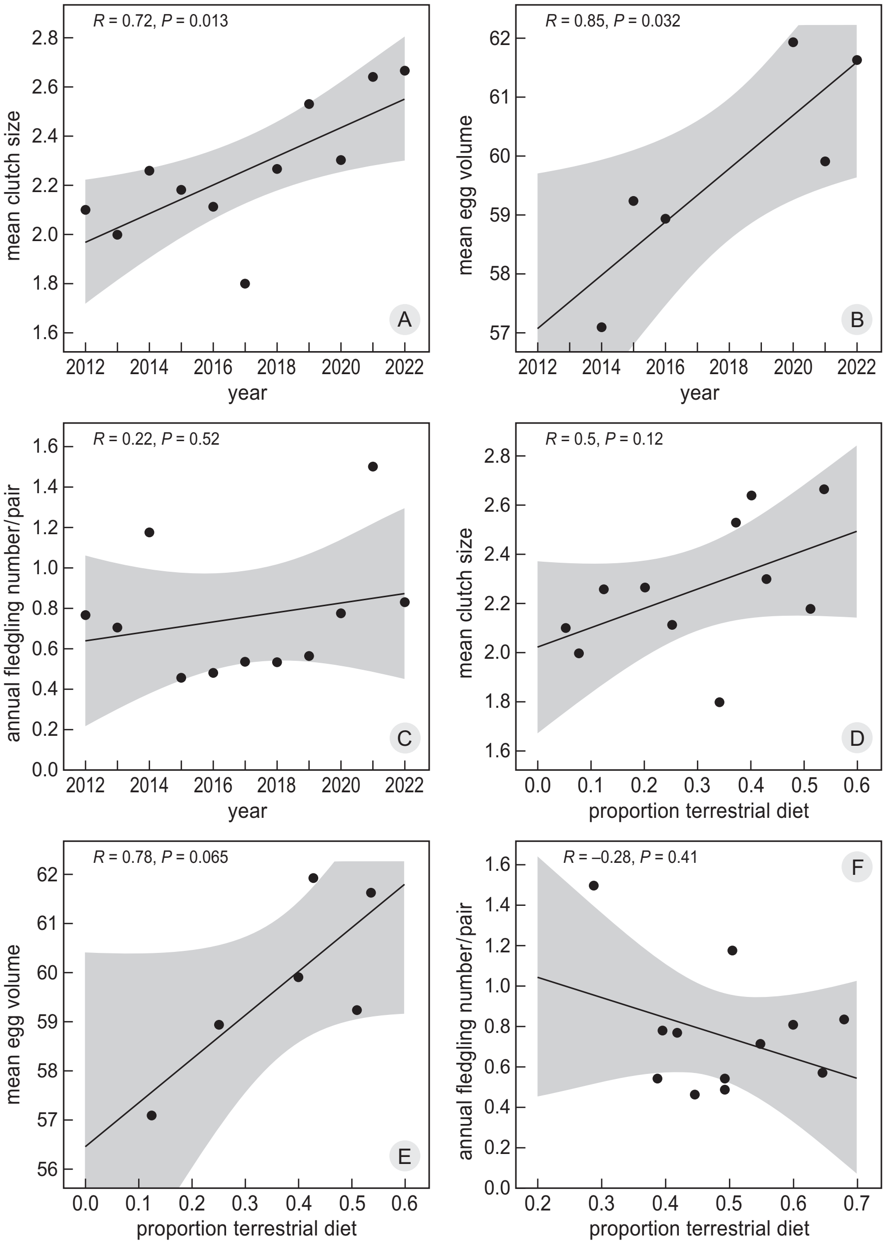

Figure 5. Annual variation in Gull-billed Tern (A) clutch size, (B) egg volume and (C) annual number of fledglings per pair between 2012 and 2022, as well as (D, E) in these same reproductive performance measures in relation to the proportion of the courtship feeding diet and (F) chick diet being of terrestrial origin.

seen, and further studies assessing environmental variables and the abundance of prey items directly, rather than indirectly, will be required to understand the mechanism underlying the patterns we observed.

In our study, the highest diversity in prey items was found in the chick diet. Previous studies of Gull-billed Terns breeding in the Mediterranean (Vargas *et al.* 1978, Costa 1984, Bogliani *et al.* 1990, Znari *et al.* 2013) also showed a high diversity of prey items in the chick diet, thereby suggesting highly opportunistic feeding behaviour of the adults. In further support of this, the exact diet composition differed among study sites. An Italian study by Bogliani *et al.* (1990) showed that reptiles represented more than half of the prey delivered to chicks, whereas crustaceans, shown to be one of the main prey items in another Italian colony (Scridel *et al.* 2023), were not fed. A similar food spectrum comprising of terrestrial invertebrates (such as Orthoptera, Coleoptera), lizards and rarely crustaceans was found by Znari *et al.* (2013) for Moroccan Gull-billed Tern chicks, while Dies *et al.* (2005) and Costa (1984) reported that crustaceans accounted for a major part of the chick diet of Spanish Gull-billed Terns, which is consistent with our findings. The previously mentioned studies, however, only focussed on one or two breeding seasons, potentially missing prey items or underestimating their importance as their abundance may vary between years (Goutner 1991). In our long-term study, we found significant annual variation in prey that were provisioned to chicks, thereby suggesting that adults are highly flexible with respect to their foraging behaviour.

We found significant changes in two of our reproductive performance measures: clutch and egg size. Both increased across the study period, whereas fledging rate, although variable, did not. Using alimental prey with high amounts of protein (Chen *et al.* 2007, Sugimura *et al.* 1984) during courtship feeding was found to affect reproductive parameters such as clutch and egg size in Common Terns *Sterna hirundo* (Nisbet 1973, Wendeln *et al.* 2000). Although we did not find a significant correlation between the proportion of the courtship feeding prey being of terrestrial origin and clutch or egg size, there was a trend. The non-significance of this relationship, however, suggests that the annual increase in clutch size as well as egg volume may be explained by other factors, perhaps parental age (e.g. Zhang *et al.* 2015 for Common Terns), if the age structure of the population changed over time. Moreover, reproductive performance is a complex composite trait, and multiple intrinsic and extrinsic factors as well as their potential interactions have to be taken into account. Therefore, to accurately assess which factor(s) caused the increase in clutch and egg size, further studies are needed. These would ideally adopt an individual-based approach that, however, is hard to realize without being able to track birds during their foraging flights and feeding events.

Despite clutch and egg size increasing across the study period, the number of fledglings did not change accordingly. Neither was it correlated with the proportion of the observed chick diet being of terrestrial origin. The absence of patterns may partly be due to fledging status being difficult to estimate, but could also be indirectly affected by the low amount of vertebrate prey available. Albano *et al.* (2011) showed that chicks fed an invertebrate-based diet grew slower and needed more time to fledge than chicks that were fed a vertebrate-based diet. Such an extended chick phase requires extended foraging by adults, while additionally providing more time and opportunity for predation or the emergence of parasites or diseases. In our study, we did not observe individual nests and chicks, such that finding out whether different aspects of food supply influence the variation in the number of fledglings per breeding pair or whether variation in chick predation, and other environmental factors, such as weather conditions during chick rearing, or behavioural traits, such as kleptoparasitism, are the main factors underlying variation in, and hampering an increase in, reproductive performance will be an important goal for further work on this locally endangered species.

To conclude, our study shows that the last population of Gull-billed Terns in Central Europe uses a wide range of dietary items. The lack of correlations with measures of reproductive success, which themselves were either improving or remaining stable across the 12 years of our study, suggests that the Neufelderkoog birds can cope with variation in food availability and that their breeding success is currently not threatened by a lack of prey availability. However, the increased foraging on prey of terrestrial origin during courtship feeding requires further investigation with respect to its causes and mechanisms. More generally, further studies should do well to address other potential threats for these endangered birds, such as contamination or inbreeding, to help optimise current conservation efforts, as the total breeding numbers of this colony are not increasing although the breeding success is adequate.

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SAMENVATTING

Steeds meer vogelsoorten nemen in aantal af. Om eventuele beschermingsmaatrelen voor die soorten te optimaliseren, is het cruciaal inzicht te hebben in de verschillende aspecten die ten grondslag liggen aan hun populatiedynamiek. Wij bestudeerden tussen 2011 en 2022 de voedselsamenstelling en het voortplantingssucces van de laatste Centraal-Europese broedpopulatie van de Lachstern *Gelochelidon nilotica*. De belangrijkste prooien varieerden zowel tussen de seizoenen als tussen de jaren. Als de sterns voor zichzelf foerageerden, aten ze voornamelijk insecten. Bij baltsrituelen en in het voedsel van de jongen waren krabben en wormen de belangrijkste prooien. Tijdens de onderzoeksperiode nam het aandeel terrestrische prooien in het voedsel bij baltsrituelen toe. Legselgrootte en formaat van de eieren namen in dezelfde periode eveneens toe, maar onafhankelijk van het aandeel terrestrische prooien gevoerd tijdens baltsrituelen. Het uitvliegsucces veranderde niet in de loop van de tijd en was niet gecorreleerd met de variatie in het voedsel van de kuikens. Onze resultaten bevestigen dat de Lachsterns van deze populatie wat hun voedsel betreft generalisten zijn, en maken het waarschijnlijk dat het broedsucces momenteel niet negatief wordt beïnvloed door de beschikbare hoeveelheid voedsel of veranderingen in het voorkomen van bepaalde prooidieren. De verschuiving naar meer terrestrische prooien in het voedsel tijdens baltsrituelen zou echter kunnen duiden op veranderingen in het aquatische ecosysteem, en vraagt om nader onderzoek. Dit geldt ook voor andere potentiële risico's, zoals inteelt en vervuiling, voor deze bedreigde populatie.

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SUPPLEMENTARY MATERIAL

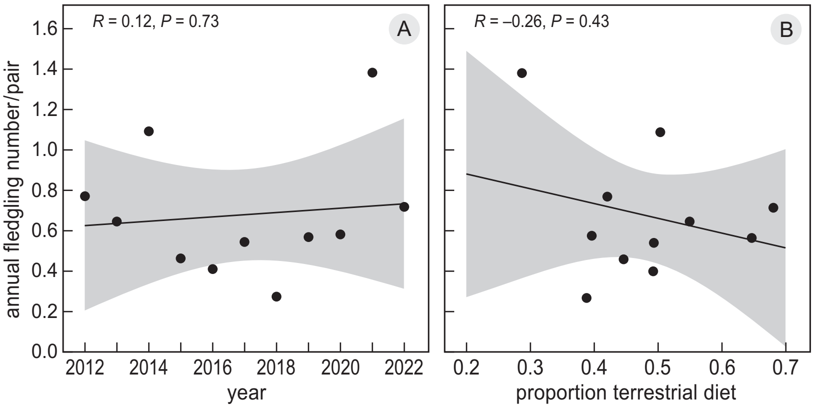

Figure S1. Annual variation in the number of fledglings per pair and (A) correlation between annual variation in annual number of fledglings per pair and (B) the proportion of the diet of chicks being of terrestrial origin, when calculating the number of fledglings per pair excluding unringed chicks observed during their first migration stop in The Netherlands.

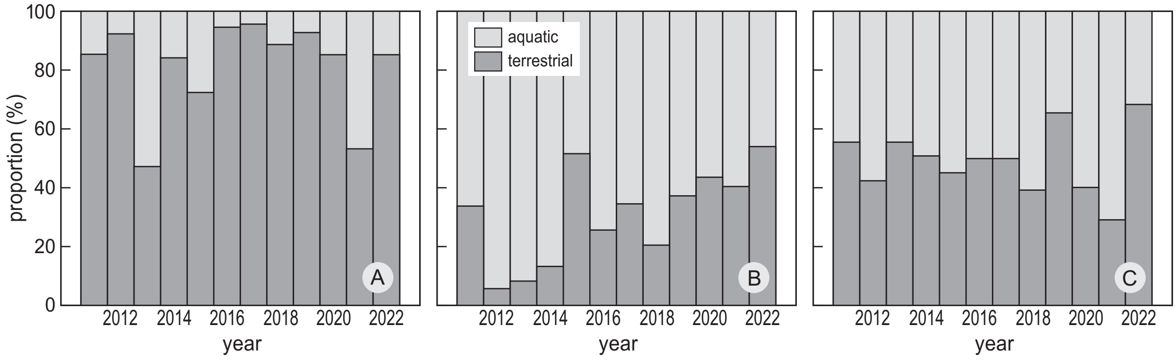

Figure S2. Annual variation in the proportion of Gull-billed Tern prey of terrestrial and aquatic origin for (A) self-feeding, (B) courtship feeding or (C) chick provisioning.