








Sex-mediated changes in foraging behaviour according to breeding stage in a monomorphic seabird adapted to rural habitats

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In contrast to sexually size-dimorphic species, monomorphic ones rarely show sexual differences in foraging behaviour as such variations have been primarily attributed to dissimilar body size. To investigate this aspect, we analysed foraging behaviour in breeding gull-billed terns, *Gelochelidon nilotica*, a monomorphic seabird adapted to rural habitats. We equipped 19 breeding birds with GPS devices and assessed differences in foraging behaviour and habitat use according to sex and breeding stage. Foraging trip distance and duration and daily frequencies were influenced by both breeding stage and sex, with females, but not males, performing closer, more frequent and shorter duration trips during chick rearing than incubation. Females, but not males, increased the repeatability of foraging metrics from incubation to chick rearing, while both sexes increased individual foraging site fidelity between the two breeding stages. Agricultural fields were the most exploited habitat for both sexes, but females made more use of aquatic habitats than males, especially during chick rearing. By foraging in different ways and in different habitats, the breeding pair can provide a wider range of prey types to their offspring, maximizing the chances of delivering high quantity and quality of food items under different environmental conditions. Our work provides new additional evidence of sex differences in foraging behaviour of monomorphic species, while highlighting the need to better understand underlying mechanisms driving foraging niche divergence and the consequences for fitness.

Food availability plays a central role in determining the survival, reproductive success and movement behaviour of animals (Fenn et al., 2021; Whelan et al., 2020). With respect to foraging behaviour, optimal foraging theory predicts that animals make decisions that maximize fitness, while taking the dependence of energy intake rate on the forager's ability to detect, capture and handle each prey item into account (Schoener, 1971; Stephens & Krebs, 1986). In addition, individuals within a population can show extensive variation in their foraging niche and behaviour due to intrinsic (i.e. sex, age and personality; Zandberg et al., 2017) and/or

extrinsic factors (e.g. weather, competition, distribution of food resources; Araújo et al., 2011; Sheppard et al., 2018).

In birds, the breeding period is suggested to be one of the most energetically demanding and time-constraining phases of the annual life cycle (Nord & Williams, 2015; Reid et al., 2000). Within the breeding period, differences in foraging behaviour and diet have emerged with respect to the breeding stage considered. For example, many studies have demonstrated that chick-rearing adults tend to travel shorter distances and perform higher frequency foraging trips compared to the incubation stage (e.g. Cecere et al., 2013; De Pascalis et al., 2021; Harris et al., 2020). Indeed, chick rearing is regarded as one of the most energetically expensive processes of reproduction (Drent & Daan, 1980; Weathers & Sullivan, 1993) as birds need to allocate energy between the

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competing demands of self-maintenance and constant offspring care.

Sexual variation in foraging behaviour during the breeding period has been described for many bird populations, suggesting that the relative costs and/or benefits of adopting a specific tactic may vary according to sex and/or a different reaction of males and females to extrinsic dynamic factors (e.g. wind, temperature, precipitation; De Pascalis et al., 2020). Examples of sexual differences in foraging behaviour have been described mostly for sexually dimorphic species and are thought to be responsible for observed differences in dominance, flight efficiency and competitive ability (Clay et al., 2020; González-Solís et al., 2000; Miranda et al., 2018). In contrast, examples of sexual differences in foraging behaviour for monomorphic birds during the breeding period are rarer in the literature and restricted to a few species (see Elliott et al., 2010; Hedd et al., 2014; Lewis et al., 2002; Reyes-González et al., 2021).

In this study, we aimed at assessing potential sexual differences in parental foraging behaviour across breeding stages (incubation and chick rearing) in gull-billed tern, *Gelochelidon nilotica*, a sexually monomorphic seabird able to forage in freshwaters, coastal-marine and terrestrial habitats. It is a poorly studied yet cosmopolitan species breeding in scattered localities across Europe, Asia, northwest Africa, Australia and the Americas. It is a highly opportunistic bird with a variable diet, feeding across a broad range of habitats and taxa such as aquatic and terrestrial invertebrates and vertebrates (Bogliani et al., 1990; Molina et al., 2020). In our study area in northern Italy, the species seems to forage mainly in terrestrial habitats and shows a wide trophic niche including invertebrates, lizards, frogs, crayfish and fish (D. Scridel, J. G. Cecere, J & M. Basso, personal observations of bill loadings and remains at the nesting site). In detail, we aimed at assessing differences in foraging behaviour (i.e. daily number of foraging trips, duration, maximum and total travelled distance and repeatability of these behavioural metrics), individual foraging site fidelity and habitat use between the sexes and breeding stages. In line with the above-mentioned studies, we expected foraging trips to be less frequent and longer in both duration and distance during incubation compared to the chick-rearing stage, when birds are more constrained by offspring food demand. Moreover, in accordance with the available literature on gull and tern behaviour (Isaksson et al., 2016; Molina et al., 2020; Navarro et al., 2010; Pais de Faria et al., 2021; van Donk et al., 2017), we expected both males and females to exploit aquatic (i.e. marine and freshwater) and terrestrial habitats but we predicted a more frequent use of the former during the chick-rearing stage, when chicks could require high-energy and easily digestible food items such as fish. Finally, given the monomorphic nature of this species with males being only 3.5% larger than females (male body mass: mean \pm SD = 197 \pm 21 g, N = 15; female body mass: 190 \pm 25 g, N = 25; this study; see also Molina et al., 2020), we did not expect any differences in foraging behaviour or in habitat use between the sexes.

METHODS

Study Area

The study was conducted in the northern wetlands of the Po Delta (44°59'15.9"N 12°19'36.2"E; in 2019 and 2020) and in the southern part of the Lagoon of Venice (45°22'39.5"N 12°09'21.4"E; in 2021) in the Veneto region, Italy (Fig. 1). These areas comprise some of the largest complexes of wetlands in Europe hosting thousands of breeding, migrating and wintering birds of conservation concern (Keller et al., 2020; Zenatello et al., 2014). These natural and seminatural environments are intertwined with densely populated and agricultural reclaimed areas, as well as with

wetlands dedicated to fish farming and industrial activities. Both gull-billed tern colonies considered in this work bred on artificial islets (i.e. mud mounds) surrounded by shallow brackish water basins used for extensive fish farming and/or as waterfowl hunting reservoir. Gull-billed tern colonies were mostly monospecific although mixed colonies with a few breeding black-headed gulls, *Chroicocephalus ridibundus*, common terns, *Sterna hirundo*, pied avocets, *Recurvirostra avosetta*, and redshanks, *Tringa totanus*, were observed in the area.

GPS Deployment

To minimize chances of nest abandonment, all birds were captured during the late incubation stage (ca.7 days before hatching; range 31 May–24 June) in the 2019–2020–2021 breeding seasons, using a modified drop trap designed to cause little disturbance to incubating birds. To minimize chances of nesting failure, only one bird per nest was tagged. Each bird was equipped with a Milsar (Milsar Technologies S.R.L., Gheorghieni, Romania) or TechnoSmArt GPS-UHF (TechnoSmArt Europe Srl, Roma, Italy) nanotag attached on the back using a leg-loop harness adjusted to body size. On average, tags (including the Teflon harness) weighed 3.5 g, accounting on average for 1.84% of the bird's body mass (SE = 0.05; range 1.54–2.66%). After inspecting preliminary GPS data and checking that gull-billed terns do not move at night, we set all tags to record locations at 15 min intervals between 0500 and 2100 (local time), which is the daily interval when birds actively foraged. Upon capture, we recorded body mass using a spring balance (\pm 10 g) and sampled three to four body feathers for molecular sex determination.

Birds were molecularly sexed according to the following procedure. DNA was extracted from the feather calamus using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Manchester, U.K.) following the manufacturer's instructions except for the lysis step, which was carried out overnight and, for the final elution, performed in 75 μ l of water (Milli-Q at 56 °C, Merck, Darmstadt, Germany) to increase final DNA concentration. To standardize the extraction procedure and minimize the risk of cross-contamination, the extraction process was performed using the automated QIAcube device (Qiagen). Molecular sexing was carried out by means of polymerase chain reactions (PCR) using the primer pair P2/P8 (Griffiths et al., 1998) with a modification of the P8 primer which was labelled with a 6-FAM fluorophore. The thermal profile was set as in Çakmak et al. (2017). PCR conditions and amplicons visualization were performed following the protocols illustrated in Costanzo et al. (2020). All reactions were performed with negative (i.e. no DNA template) and positive controls (i.e. DNA extracts from one male and one female gull-billed tern). Overall, we relied on GPS data of 19 sexed breeding birds (12 females and seven males) collected across 3 consecutive years (2019–2021).

Ethical Note

The research described in this study adheres to the ASAB/ABS Guidelines for the Use of Animals in Research. Capture, handling, ringing and tagging procedures were carried out by the Italian Institute for Environmental Protection and Research (ISPRA), under prescriptions of Law 157/1992 [Art.4(1) and Art 7(5)], which regulates research on wild bird species. Birds were handled and ringed by experienced staff only. Overall, we captured 32 birds, but six abandoned their nests immediately after tagging while three, despite evidence that they bred successfully (i.e. repeatable foraging trips clearly observable from tracks after the tagging period), had to be excluded from the analyses due to issues with GPS and setting of camera traps. Our abandonment rate was

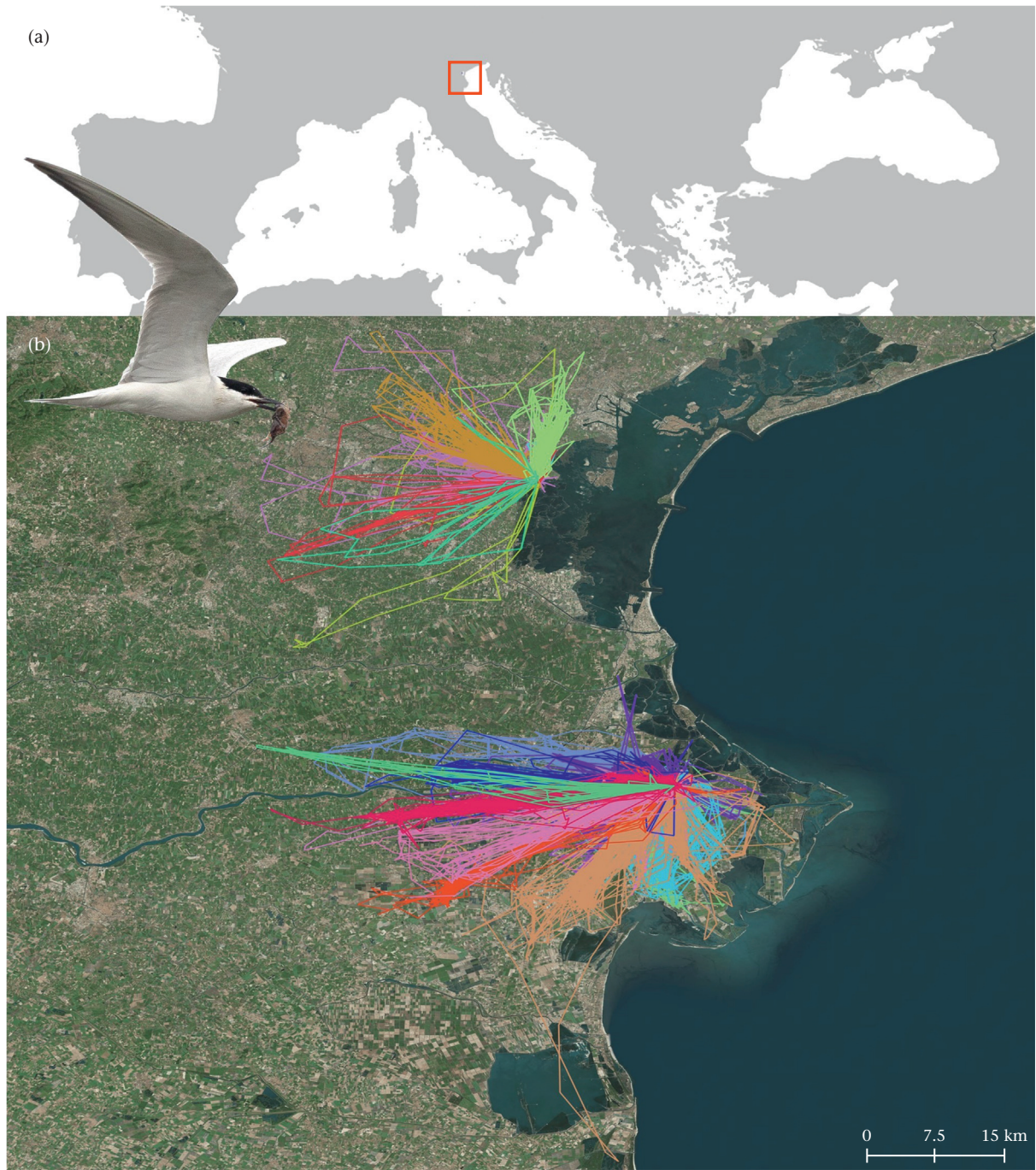


Figure 1. (a) Location of the area comprising the wetlands of the Lagoon of Venice and the Po Delta (Italy) where breeding birds were tagged. (b) Foraging tracks of incubating and chick-rearing gull-billed terns equipped with GPS.

therefore 18.8% (6/32). Unfortunately, this result cannot be compared with a control group as we do not have information on natural nest abandonment. From the remaining 23 birds, we had to exclude four that were not sexed.

Foraging Trips and Breeding Stage Identification

To identify single foraging trips, starting and ending at the breeding site, we used the function 'tripSplit' implemented in the package 'track2kba' (Beal et al., 2021) running in R software (R version 4.0.4; R Core Team, 2021). Parameters set in the function to constitute a trip were (1) individual identity, (2) date and time of

each GPS location, (3) the geographical coordinates of the breeding site and (4) a buffer with radius 0.6 km used by the function to define the starting and ending area of each trip from its place of origin (i.e. the colony). This distance was estimated via QGIS (version QGIS 2.18; QGIS Development Team, 2016) by judging the average size of the breeding islets and the surrounding basin where birds may rest after a foraging trip. Thus, a foraging trip was considered to occur when a bird left and returned to this buffer zone. Using site embankments as physical boundaries of each breeding area, we then excluded, via visual inspection in QGIS, all excursions that only covered the water body surrounding the colony, because birds generally do not forage in these areas and these

movements may be more ascribable to nonforaging behaviours such as disturbance by predators, local human activities or movements to nearby isles for interaction with conspecifics (J.G. Cecere, S. Imperio, D. Scridel & L. Serra, personal observations). Upon bird capture, a camera trap (Digital Scouting Camera SG2060-X, Scubla Srl, Remanzacco, UD, Italy) was set on a 1.5 m wooden pole planted 0.5 m in the ground and 2 m from the nest of each tagged bird. To collect information on daily nest fate (i.e. brood abandonment or predation) and hatching date, all cameras were programmed to take a photo every 2 h. Each foraging trip was then assigned as being part of the incubation stage (if no eggs hatched on the day of the trip) or the chick-rearing stage (if at least one chick was present). Camera traps could not be used to define the end of the chick-rearing stage (i.e. fledging date) as gull-billed tern chicks are more precocious than other terns, walking around the colony a few days after hatching (J.G. Cecere, personal observations). Thus, for all chick-rearing trips we assumed that fledging did not occur before 25 days after hatching (Cramp et al. 1977–1994; Molina et al., 2020) and therefore we considered for analyses only trips that occurred within this period. We assessed that the brood was alive (e.g. no dead chicks/adult abandonment) throughout this period by visualizing bird locations in QGIS and by checking that tagged birds moved regularly to and from their nesting site (i.e. chick feeding). Visual inspection of tracking data suggested no evidence of birds re-nesting in other locations.

Trip Metrics and Adjusted Repeatability

To assess differences in foraging behaviour between the sexes and breeding stages, we calculated the following foraging trip metrics (i.e. response variables) commonly used in similar studies for other bird species (Cecere et al., 2020; Votier et al., 2017): (1) 'total duration', calculated as the time elapsed from departure to the return to the colony across all trips; (2) 'maximum trip distance', calculated as the most Euclidean distant point from the breeding site across all trips; (3) 'total travelled distance', calculated as the sum of the distances between consecutive locations from departure to the return to the colony across all trips using the 'distGeo' function in the 'geosphere' R package (Hijmans, 2019). In addition to these metrics at the foraging trip scale, we calculated (4) the 'daily number of trips' as the total number of trips performed by an individual over a day.

For all these metrics, we assessed differences between the sexes and breeding stages by means of linear and generalized mixed-effects models (LMMs and GLMMs) using the R package 'lme4' (Bates et al., 2015). All models were tested for within-group collinearity by calculating the variance inflation factor (VIF) using the package 'car' (Fox & Weisberg, 2019) and no issue of violation (VIF value ≥ 3 ; Zuur et al., 2009) for any of the fixed effects was detected. Model assumptions (i.e. linearity, independence and normality of errors, equal variance) were verified by inspection of model outputs via the R package 'performance' (Lüdtke et al., 2021). Preliminary assessments of models for trip maximum distance, total distance and duration indicated evidence of residuals heteroscedasticity. We therefore verified which distributions fitted our response variables better by means of Cullen and Frey plots and Akaike information criterion (AIC) performance using the package 'fitdistrplus' (Delignette-Muller & Dutang, 2015). Log-transformed LMMs and GLMMs with gamma distribution outperformed standard Gaussian LMMs for models evaluating trip duration and distance (maximum and total), respectively. To model the daily number of trips (i.e. count data) we used a GLMM with Poisson error structure and no signs of overdispersion were observed (dispersion ratio = 0.75). For each metric we fitted separate models including as fixed effects the year of the trip, sex and breeding stage

(including an interaction term between the latter two), entering bird identity (i.e. ring number) as a random intercept. When the interaction between sex and breeding stage was not significant, this was removed from the analysis to estimate the effects of sex and breeding stage alone. Multiple comparison tests for interacting significant factorial variables (i.e. breeding stage and sex) were also calculated using the R package 'emmeans' (Lenth, 2020) with P values for each variable combination corrected according to Bonferroni methods. In the first 2 years (2019–2020) we sampled birds from the same colony located in the Po Delta, while in the third year (2021) we worked on a different colony located in the Lagoon of Venice. This implied that the variables year and colony encoded similar information and could not both be included in the same models. We opted to use year rather than colony as a fixed factor as the former always performed better than the latter (i.e. models had lower AIC values when compared via maximum likelihood; Zuur et al., 2013).

For each trip metric we calculated the adjusted repeatability with the 'rptR' R package (Stoffel et al., 2017). The adjusted repeatability is an estimate of repeatability controlling for fixed effects and was calculated as $R = V_A / (V_A + V_W)$, following Nakagawa and Schielzeth (2010), where V_A is the variance across random intercepts (i.e. the among-individual variance) and V_W is the residual variance (i.e. the within-individual variance). The index of repeatability ('R') ranges from 0 (low repeatability, high within-individual variance) to 1 (high repeatability, low within-individual variance). In this work we used a qualitative classification of repeatability following Potier et al.'s (2015) definition (i.e. highly repeatable: $R > 0.50$; moderately repeatable: $0.25 < R < 0.50$; poorly repeatable: $R < 0.25$). To obtain repeatability values of trip metrics for the two sexes during the two breeding stages, we fitted a series of GLMMs (with Poisson error for daily number of trips) and log-transformed LMMs (for trip distance and duration) for each trip metric (i.e. response variables), using the wrapper function 'rpt' while setting year as a factorial fixed effect and bird identity as a random effect. Models were run for each data group (i.e. incubating females, incubating males, chick-rearing females and chick-rearing males), an approach also used in other studies (Harris et al., 2020; Ramellini et al., 2022). We used a default parametric bootstrap replicate setting ($N = 1000$) and 1000 permutations for calculating asymptotic P values. In addition, following Votier et al. (2017) and Sztukowski et al. (2018), we assessed the individual foraging site fidelity by estimating the individual repeatability of the distal point of each foraging trip (proxy of the foraging site, Hamer et al., 2009; Votier et al., 2013; Ramellini et al., 2022) by means of LMMs with the longitude and the latitude of the distal point as dependent variables, year as a fixed factor and bird identity as a random factor.

Changes in Habitat Use

To evaluate changes in habitat use according to breeding stage and sex, we associated GPS locations of tagged birds with land cover data retrieved from the Carta Natura project (Brentan et al., 2008; Cardillo et al., 2021). This layer identifies 230 habitats in Italy based on the Corine-Biotopes classification system (Devilleers & Devilleers-Terschuren, 1993) and it has been preferred to other continent-wide databases (Copernicus Corine) for being more up to date. To aid interpretation, we merged similar habitats into broader categories considered ecologically relevant for gull-billed terns (see Appendix Table A1). Specifically, these were: (1) agricultural: areas defined by the presence of nonperennial crops; (2) rice fields; (3) coastal lagoon habitats: coastal and lagoon areas characterized by brackish and saltwater (including islets and associated halophilic vegetation); (4) freshwater habitats: rivers, streams, lakes and associated vegetation (i.e. reedbeds, riparian forests,

embankments, islets, etc.); (5) woodlands and perennial crops: mostly commercial plantations and vineyards; (6) grassland; (7) urban; (8) other habitats: all other habitats in our study site. Given the potential role of small freshwater features for foraging gull-billed terns, a further layer, the 'reticolo idrografico' (accessible at <http://www.pcn.minambiente.it/mattm/>), representing a fine-scale hydrographic network that includes agricultural drainage ditches, canals and small streams, was merged with the freshwater habitats class of the Carta Natura project layer. We then used the function 'intersect' in QGIS to assign to each GPS location of tagged birds the associated habitat type. We considered all GPS locations occurring within the buffer with radius 0.6 km around the colony as the location associated with nest attendance (incubating, chick feeding, nest guarding) or with the departure and return of foraging trips. These locations were reclassified as 'water body surrounding the colony' and excluded from further analyses ($N = 3894/12\,494$ or 31.17% of all locations). Changes in habitat use were modelled separately only for the most representative habitats (namely, agricultural, freshwater, coastal lagoon). To investigate changes in the proportional use of a foraging habitat type during foraging trips between breeding stages, we ran binomial GLMMs using the 'cbind' function with the two vectors 'number of GPS locations in the target habitat' and 'number of locations in all other habitats' of a single trip bound together and fitted as the dependent variable (i.e. habitat X/all locations). Year and the interaction between sex and breeding stage were initially included as fixed effects while bird identity was entered as a random effect (i.e. random intercept

model). As for the abovementioned modelling metrics approach, interactions were removed if not significant in order to estimate the effects of sex and breeding stage alone. Fitted models did not show evidence of violation of model assumptions, including collinearity (tested following the procedure described previously).

RESULTS

Foraging Trip Identification

Overall, 1779 complete foraging trips were identified from 19 individuals (Fig. 1), 287 of which were recorded during the incubation stage (females: $N = 173$; males: $N = 114$) and 1492 during the chick-rearing stage (females: $N = 1053$; males: $N = 439$). Thirteen birds were tracked during both breeding stages and six birds only during incubation due to rat, *Rattus* spp., predation on eggs, detected by means of camera traps. Summary statistics showing annual average values of daily number of trips, trip duration, maximum trip distance and total travelled distance across years, colony, breeding stage and sex are reported in Appendix Table A2.

Sex and Breeding Stage Differences in Trip Metrics

During incubation, males and females showed similar trip metrics (Fig. 2, Table 1), but during chick rearing, female gull-billed terns performed significantly more foraging trips per day and shorter duration foraging trips than males (Fig. 2, Table 1). Females

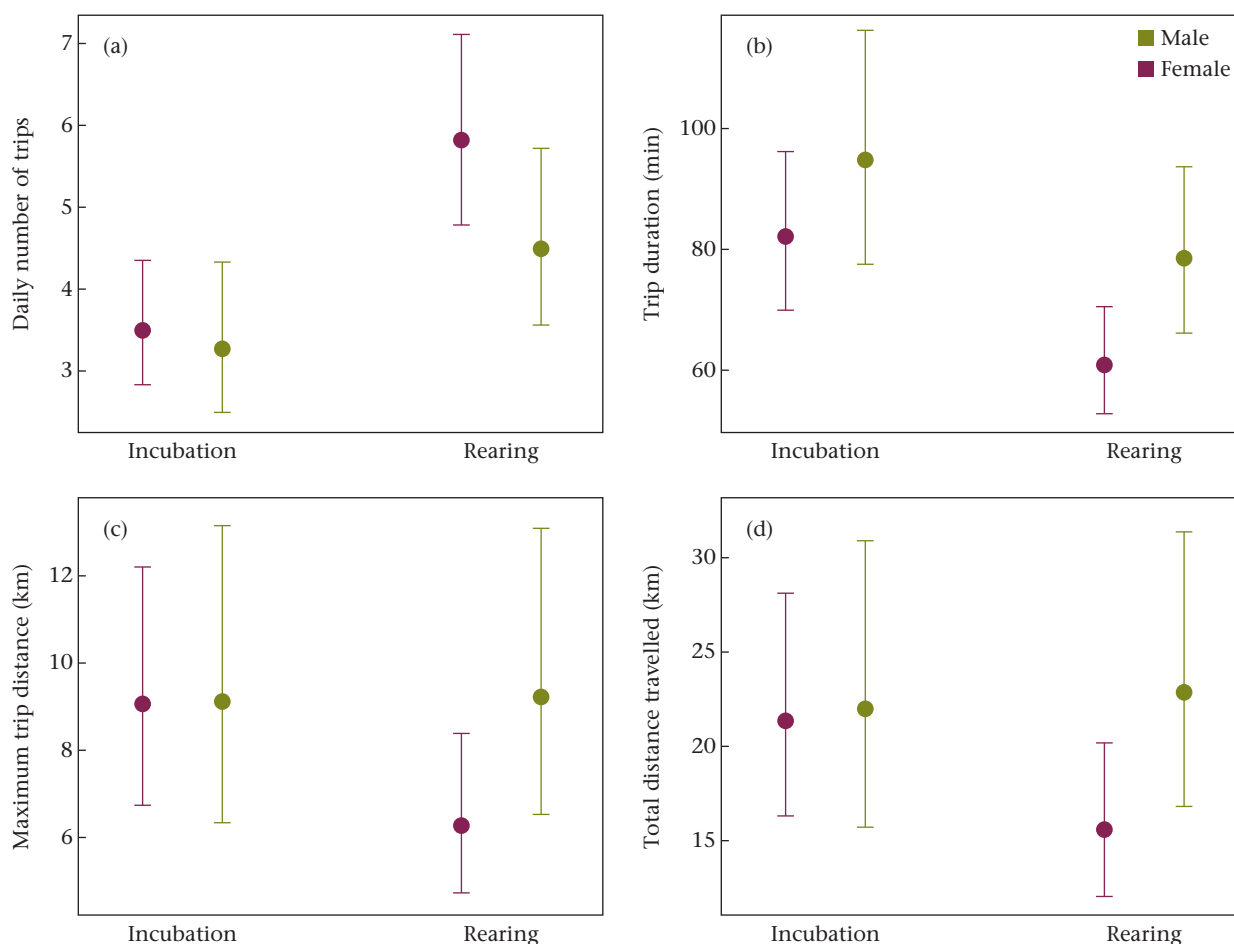


Figure 2. Intersexual differences in trip metrics (mean \pm 95% confidence interval) according to GLMMs and LMMs for (a) daily number of trips, (b) trip duration, (c) maximum trip distance and (d) total distance travelled of gull-billed terns in respect to breeding stage and sex.

Table 1
Model summaries of GLMMs (daily number of trips, trip maximum distance, total travelled distance) and LMMs (trip duration) of gull-billed terns foraging trip metrics

Predictors	Estimate [95% CI]	F/χ^2	df	P
Daily number of trips				
Breeding stage	I: 2.65 [2.25–3.12]; R:4.98 [4.43–5.61]	80.21	1	<0.0001
Sex	F: 3.73 [3.26–4.28]; M: 3.54 [2.93–4.28]	0.27	1	0.601
Sampling year	2019:3.63 [2.90–4.54]; 2020: 3.32 [2.78–3.97]; 2021: 3.99 [3.27–4.86]	2.73	2	0.255
Breeding stage*Sex	IF: 2.49[1.99–3.11]; IM: 2.83[2.12–3.77]; RF: 5.61 [4.83–6.51]; RM: 4.42[3.58–5.47]	6.35	1	0.012
Conditional R^2 : 0.36; marginal R^2 : 0.30				
Trip duration (min)				
Breeding stage	I: 119.1[106.1–136]; R:92.4[85.3–101]	33.49	1	<0.0001
Sex	F: 99.2 [90.4–110]; M: 109.4[95–129]	1.5	1	0.221
Sampling year	2019: 100.6 [85.9–122]; 2020: 126.2 [108.4–151]; 2021: 91.2 [80.2–106]	10.25	2	0.006
Breeding stage*Sex	IF: 119 [102.3–143.0]; IM: 119 [97.9–151.6]; RF: 85[77.3–94.3]; RM: 101 [87.1–120.6]	5.69	1	0.017
Conditional R^2 : 0.10; marginal R^2 : 0.07				
Trip maximum distance (km)				
Breeding stage	I: 9.86 [7.68–12.67]; R: 6.91 [5.41–8.82]	35.14	1	<0.0001
Sex	F: 7.39[5.59–9.78]; M: 9.22 [6.26–13.56]	1.36	1	0.261
Sampling year	2019: 8.18 [4.86–13.78]; 2020: 10.46 [7.01–15.59]; 2021: 6.58 [4.47–9.68]	2.58	2	0.112
Breeding stage*Sex	IF: 10.03 [7.17–14.04]; IM: 9.70 [6.17–15.23]; RF: 5.45 [3.94–7.53]; RM: 8.76 [5.59–13.72]	18.43	1	<0.0001
Conditional R^2 : 0.30; marginal R^2 : 0.12				
Trip total distance (km)				
Breeding stage	I: 21.6 [16.6–28.26]; R: 14.6 [11.3–18.9]	30.78	1	<0.0001
Sex	F: 15.7 [11.7–21.0]; M: 20.2 [13.5–30.3]	1.66	1	0.218
Sampling year	2019: 18.6 [10.78–32.0]; 2020: 22.2 [14.61–33.6]; 2021: 13.7 [9.07–20.6]	2.54	2	0.112
Breeding stage*Sex	IF: 21.5 [15.09–30.7]; IM: 21.7 [13.50–35.0]; RF: 11.4 [8.11–16.0]; RM 18.8 [11.73–30.1]	12.34	1	<0.0001
Conditional R^2 : 0.23; marginal R^2 : 0.10				

CI: 95% confidence intervals; I: incubation; R: chick rearing; F: female; M: male. Significance tests are F tests for LMMs and χ^2 for GLMMs. Predictors with significant P values ($\alpha = 0.05$) are shown in bold. Marginal and conditional R^2 were calculated according to Nakagawa et al. (2017). Multiple comparison tests for significant interactions with P values corrected according to Bonferroni methods are shown in Appendix Table A3.

also foraged at shorter distances and travelled less during each trip than males during chick rearing (Fig. 2, Table 1).

Individual Repeatability of Trip Metrics and Foraging Site Fidelity

Males showed generally poor and nonsignificant adjusted repeatability (' R ') of trip metrics during both breeding stages (range <0.01 to 0.25), while females increased repeatability of trip metrics from incubation to the chick-rearing stage, particularly for distance metrics (Table 2). Interestingly, adjusted repeatability for individual foraging site fidelity assessed by R scores for latitude and longitude of distal points was high for males during incubation but not for females (Table 2). For both males and females individual foraging site fidelity increased throughout the breeding period and was high for both sexes, with R values ranging between 0.55 ± 0.15 and 0.84 ± 0.32 during chick rearing (Table 2).

Change in Habitat Use

Agricultural land was the most used habitat, accounting for 69.25% ($N = 5956$) of all locations (excluding colony locations) belonging to foraging trips, followed by freshwater habitats (16.67%, $N = 1434$). The remaining 14.08% occurred on rice fields (4.31%, $N = 371$), coastal lagoon habitats (3.31%, $N = 285$), urban (3.49%, $N = 300$), woodlands and perennial crops (2.85%, $N = 245$) and grassland (0.12%, $N = 9$). According to our models, the proportional use of agricultural land was constant throughout the breeding season and did not vary according to sex or breeding stage (ca. 72% of all GPS locations in both stages and sexes; Table 3). For freshwater habitats and coastal lagoon habitats, the interaction between breeding stage and sex was significant (Fig. 3). During the incubation stage, the percentages of GPS locations in freshwater habitats were similar between the sexes while females were recorded more in rice fields than males (males = 3.52%, females = 10.73%; During chick rearing, the proportional use of freshwater habitats increased in both sexes, but the percentage change was significantly greater for females (+39.84%) than males

(+15.25%; Table 3). Although poorly represented, both sexes reduced their proportional use of rice fields during the chick-rearing period, but this reduction was much greater for females (–66.08%) than males (–20.86%). Chick-rearing females increased their proportional use of coastal lagoon habitats (+468.70%) whereas males' usage declined (–32.57%).

DISCUSSION

The foraging activity of breeding birds generally varies between incubation and chick rearing according to different energy demands required during each breeding stage. Moreover, it may differ between the sexes, particularly in sexually dimorphic birds or in species where males and females have different breeding tasks. With this study, we present novel and additional evidence of differences in foraging behaviour and habitat use between the sexes in a sexually monomorphic colonial bird.

As expected, we found that gull-billed terns' foraging trips were longer in distance and duration, and the terns made fewer daily trips, during incubation than the chick-rearing stage, yet our results also varied with sex. Shorter duration and more frequent trips per day during the chick-rearing stage than incubation is a common pattern described for several bird species (Baert et al., 2021; Camphuysen et al., 2015; Cecere et al., 2020; Ito et al., 2010; Lerma et al., 2020; Phillips et al., 2021), which reflects the constraints associated with chick provisioning and growth. Indeed, as chick development progresses, parents must balance their time–energy budget between self-maintenance (i.e. finding food for themselves) and constant parental investment (i.e. frequent provisioning of food). Incubating birds have generally more time available to feed themselves in the surrounding landscape. Unexpectedly for a monomorphic species, gull-billed terns showed sex-mediated differences in foraging behaviour between the two breeding stages, with females, but not males, performing more frequent, closer distance and shorter duration foraging trips during chick rearing than incubation. Sex-related foraging differences in sexually monomorphic seabirds have been hypothesized and demonstrated

Table 2

Model results for the adjusted repeatability analyses performed on trip metrics, latitude and longitude of the distal point (to assess individual foraging site fidelity) tested across separated data sets according to sex and breeding stage

Trip metrics	Male			Female		
	$R_{\pm SE}$	D (df)	P	$R_{\pm SE}$	D (df)	P
Incubation						
No. of trips/day	<0.01±0.11	<0.01(1)	1	<0.01±0.02	<0.01(1)	1
Trip duration	<0.01±0.04	<0.01(1)	1	0.03±0.04	<0.01(1)	1
Maximum trip distance	0.21±0.14	0.88(1)	0.173	0.03±0.04	<0.01(1)	1
Total travelled distance	0.25±0.15	1.96(1)	0.08	0.02±0.04	<0.01(1)	0.5
Latitude	0.54±0.19	33.3(1)	<0.0001	0.49±0.14	66(1)	<0.0001
Longitude	0.45±0.17	23.7(1)	<0.0001	0.03±0.04	<0.01(1)	1
Chick rearing						
No. of trips/day	<0.01(1)	<0.01(1)	0.5	0.14±0.06	16.5(1)	<0.0001
Trip duration	0.11±0.12	2.71(1)	0.05	0.04±0.03	10.6(1)	0.0005
Maximum trip distance	0.02±0.01	<0.01(1)	0.5	0.29±0.12	134(1)	<0.0001
Total travelled distance	<0.01±0.03	<0.01(1)	1	0.23±0.10	106(1)	<0.0001
Latitude	0.84±0.32	3.9(1)	<0.0001	0.55±0.15	431(1)	<0.0001
Longitude	0.66±0.06	121(1)	<0.0001	0.59±0.12	745(1)	<0.0001

Fixed effects included year as factor and bird identity as random intercept. R : adjusted repeatability; D : test statistic. P value is for $\alpha = 0.05$.

Table 3

Model summary of GLMMs evaluating differences in proportional use of the three most representative habitats across sexes and breeding stages for gull-billed tern foraging trips

Predictors	Estimate [95% CI]	χ^2	df	P
Agricultural				
Breeding stage	I: 0.72 [0.65, 0.78]; R: 0.72 [0.65, 0.78]	0.06	1	0.813
Sex	F: 0.72 [0.65–0.79]; M: 0.72 [0.61–0.81]	0.01	1	0.919
Sampling year	2019: 0.64 [0.491–0.776]; 2020: 0.713 [0.602–0.802]; 2021: 0.79 [0.702–0.865]	4.65	2	0.098
Breeding stage*Sex	IF: 0.74[0.65–0.81]; RF: 0.71 [0.62–0.79]; IM: 0.71 [0.58–0.81]; RM: 0.73 [0.60–0.82]	2.09	1	0.148
Freshwater				
Breeding stage	I: 0.09 [0.06–0.14]; R: 0.13 [0.09–0.19]	12.63	1	<0.0001
Sex	F: 0.10 [0.06–0.15]; M: 0.13 [0.07–0.23]	0.85	1	0.919
Sampling year	2019: 0.26 [0.14–0.44]; 2020: 0.11 [0.06–0.20]; 2021: 0.04 [0.02–0.09]	15.41	2	<0.0001
Breeding stage*Sex	IF: 0.07[0.04–0.11]; RF: 0.14 [0.09–0.22]; IM: 0.14 [0.071–0.26]; RM: 0.12 [0.06–0.23]	23.42	1	<0.0001
Coastal lagoon				
Breeding stage	I: 0.10 [0.06–0.14]; R: 0.13 [0.09–0.19]	15.38	1	<0.0001
Sex	F: 0.01 [0.007–0.03]; M: 0.03 [0.02–0.05]	10.95	1	<0.0001
Sampling year	2019: 0.02 [0.008–0.07]; 2020: 0.01 [0.006–0.03]; 2021: 0.02 [0.01–0.06]	1.38	2	0.5
Breeding stage*Sex	IF: 0.005 [0.002–0.01]; RF: 0.02[0.01–0.05]; IM: 0.04 [0.01–0.09]; RM: 0.04 [0.01–0.09]	10.51	1	<0.0001

CI: 95% confidence intervals; I: incubation; R: chick rearing; F: female; M: male. The test statistic is Wald's χ^2 , type III. Predictors with significant P values ($\alpha = 0.05$) and with 95% CI not overlapping zero are shown in bold. For cases where the interaction between sex and breeding stage was not significant (i.e. agricultural) this was removed from the analyses to estimate the effects of sex and breeding stage alone and are presented in [Appendix Table A4](#). Multiple comparison tests for significant interactions (freshwater and coastal lagoon) with P values corrected according to Bonferroni methods are shown in [Appendix Table A5](#).

to be related to the energetic and/or nutritional constraints of egg-laying females (Ismar et al., 2017; Rishworth et al., 2014), to intraspecific, intersexual competition for food (Botha et al., 2017; Fraser et al., 2002; Peck & Congdon, 2006), to potential sex-related differences in moulting patterns (Lewis et al., 2002; Thiebot et al., 2014) or to different investment in parental care (Thaxter et al., 2009). In our study, by performing trips of shorter distance and duration females appeared to be able to invest more parental care than males by achieving ca. 30% more foraging trips per day than males. These results contrast with other gull and tern studies where male-biased feeding rates were observed (Fasola & Saino, 1995; Ledwoń and Szczys, 2022).

Similar to another colonial bird species foraging in rural habitat (i.e. the lesser kestrel, *Falco naumanni*; Ramellini et al., 2022), gull-billed terns also increased individual foraging site fidelity from incubation to chick rearing. An individual foraging consistently in the same area is likely to increase its foraging efficiency by gaining familiarity with the sites that it repeatedly visits and by improving local knowledge on patch profitability and persistence over time (Piper, 2011). This could be more advantageous for breeders during chick rearing, when energy requirements for self-maintenance and

raising chicks is very high and parents must make the right decision on where to forage successfully and in an appropriate time span. Moreover, individual foraging site fidelity implies that individuals consistently exploit spatially distinct foraging areas, likely lowering the chances of intraspecific competition, which is a particularly advantageous strategy for colonial species that breed in large aggregations (Ramellini et al., 2022). However, differently from lesser kestrels, this behavioural pattern in gull-billed terns was sex biased, with females being more repeatable in foraging behaviour than males during chick rearing. This result is in line with what we found in our analyses on foraging metrics (Table 1) and provides further evidence of sex-mediated differences in foraging behaviour between the two breeding phases.

In terms of habitat use, breeding gull-billed terns made consistent use of both agricultural and freshwater habitats. These preferences are in line with findings of previous studies on this species in Italy (Fasola & Bogliani, 1990; Grussu et al., 2020). In central Spain, gull-billed terns breeding on lakes were observed foraging on cereal crops and ploughed fields and avoiding vertical habitat structures such as vineyards, arboreal and urban areas (Britto et al., 2018). In contrast to other studies (Goutner, 1991;

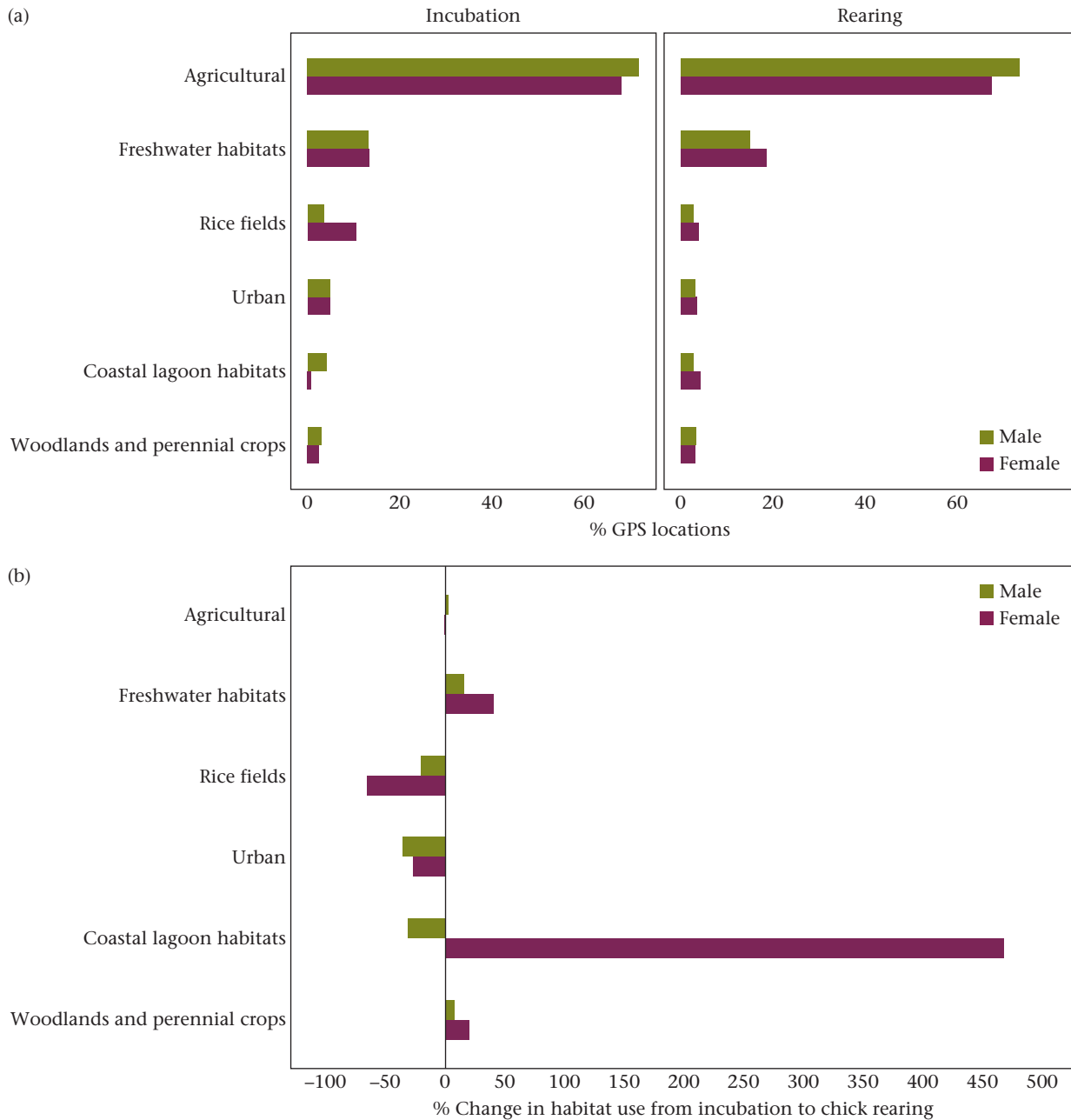


Figure 3. (a) Bar charts showing the percentage of GPS locations ($N = 8600$) within sex and breeding stage from all foraging trips ($N = 1975$) associated with each habitat type. (b) Diverging bar chart expressing the percentage change in the number of GPS locations between incubation and chick-rearing stages grouped by sex. Grassland habitats were rare and are not included in the plot ($N = 9$).

Goodenough, 2014), coastal lagoon habitats were little explored for foraging purposes, and we had no evidence of foraging in marine habitats, highlighting that in our study system gull-billed terns did not seem to be a marine species.

Changes in habitat use through the breeding season have been commonly observed in many seabird species, including gulls and terns (Baert et al., 2021; Camphuysen et al., 2015; Gaglio et al., 2018; Ludynia et al., 2005; Navarro et al., 2010). For example, the lesser black-backed gull, *Larus fuscus*, a dietary generalist species foraging in both terrestrial and marine habitats, increased its marine foraging after hatching, probably to feed its chicks with high-energy marine fish, which are more easily digested than terrestrial invertebrates (Isaksson et al., 2016). In our case, females seemed to explore aquatic habitats more than males during both

breeding stages, with a stronger difference between the sexes during chick rearing. During incubation, females explored rice fields more than males, but their use of this habitat declined during chick rearing, probably because of increased vegetation growth or drying of formerly flooded rice fields which occurs every year towards mid-summer. Such events may have a strong influence on prey availability and detectability. To compensate for this habitat loss during the chick-rearing stage, females increased their proportional use of freshwater and coastal lagoon habitats more than males, potentially due to the exploitation of different food resources or intraspecific and intersexual competition. Indeed, it is possible that male gull-billed terns, which foraged more on agricultural areas also exploited by gulls (Mediterranean gull, *Ichthyophaga melanocephalus*, black-headed gull and yellow-legged gull,

Larus michahellis), adopted a 'risk-prone' strategy characterized by higher competition, while females adopted a 'risk-averse' strategy, foraging more on canals and small rivers, where competition should be comparatively lower, and feeding on fish or the hyper-abundant alien red swamp crayfish, *Procambarus clarkii* (D. Scridel, J.G. Cecere, & M. Basso, personal observations). This strategy has been observed for both sexually dimorphic (e.g. lesser black-backed gulls; Camphuysen et al., 2015) and monomorphic species, such as thick-billed murre, *Uria lomvia*, where sex specialization with males feeding on 'risk-averse' prey (consistent across time and space) and females being 'risk-prone' has been associated with different parental roles (Elliott et al., 2010). Different foraging specialization of males and females is likely to result in an increase in the foraging abilities of the pair compared to a strategy where both sexes are equally generalist.

Surprisingly for a monomorphic species where no foraging niche divergence between the sexes was expected, we found sex-mediated differences in both foraging trip metrics (trip distance, duration and frequency), repeatability and habitat use between incubation and chick-rearing stages. This female-biased difference in the allocation of foraging effort between parents could be due to various factors (e.g. prolonged period of male-only postfledging care, parental differences in time spent in nest defence, differences in competitive ability during foraging) and future studies should evaluate this particular aspect of our study species. Based on the results, we cannot rule out any of these hypotheses, even that gull-billed terns show a combination of a risk-partitioning strategy and sex specialization in prey choice that may ultimately maximize breeding success (Elliott et al., 2010). Overall, our study supports the idea that sexual differences in foraging behaviour might be more common in monomorphic bird species during the breeding period than previously believed. This foraging strategy is likely to be particularly useful for animals exploiting heterogeneous habitats, with the goal of increasing reproductive success by expanding the trophic niche of the offspring and ensuring adequate prey delivery to them under different environmental conditions.

Author Contributions

Conceptualization: D.S., L.S., S.I. and J.G.C. Investigation: D.S., M.B., A.F., L.S., S.P., A.C., C.M., F.R., E.V. and J.G.C. Analysis: D.S., S.I. and J.G.C. Writing original draft: D.S., with inputs by S.I., L.S. and J.G.C. Writing-review & editing: all authors.

Data Availability

GPS data are available in the MoveBank repository (project ID: 1347882924) upon request to the corresponding author. The R scripts used for the analyses are also available upon request to the corresponding author.

Declaration of Interest

The authors have no relevant financial or nonfinancial interests to disclose and no competing interests to declare that are relevant to the content of this article. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or nonfinancial interest in the subject matter or materials discussed in this manuscript. The authors have no financial or proprietary interests in any material discussed in this article. There are no additional activities to disclose.

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Appendix

Table A1

Macrohabitats considered in our study area obtained by merging various habitats classified by the Carta Natura project (Brentan et al., 2008; Cardillo et al., 2021)

Macrohabitat	Carta habitat codes
Urban	87, 86.6, 86.31, 86.32, 86.41, 86.1_m, 85.1, 86.41, 86.3, 86.1
Woodlands & perennial_crops	83.325_m, 83.31_m, 83.21, 83.15_m, 45.31, 44.4, 45.31, 42.83, 42.82, 41.L_n, 41.F1, 41.88_m, 32.3_m, 31.8A, 84, 31.81, 32.4_m, 32.A, 31.8A, 31.88_m, 41.4, 41.731, 41.732, 41.741, 41.81, 41.9, 42.G_n, 44.3, 45.32, 4D_n, 45.32, 83.11, 83.12, 83.321, 83.325, 83.324, 83.15, 83.11, 45.324, 44.44, 42.83, 42.611, 42.54, 42.52, 42.322, 42.321, 42.31, 42.222, 42.221, 42.21, 42.1B, 42.13, 42.12, 42.11, 42.611, 42.54, 42.52, 42.322, 42.321, 42.31, 42.222, 42.221, 42.1B, 42.13, 42.12, 41.B, 41.9, 41.81, 41.74, 42.731, 41.59, 41.41, 41.39, 41.282, 41.281, 41.16, 41.15, 41.13, 41.11, 31.8A, 31.88, 31.81, 31.611, 31.52, 31.42.
Rice fields	82.41
Agricultural	82.1, 82.3
Grassland	81, 38.2, 37.4_m, 37.1, 34.8_m, 34.32, 37.1, 31.863, 34.8_m, 34.332
Freshwater habitats and related vegetation	89.2, 24.1_m, 24.3_m, 24.52, 53.1, 53.6, 44.D2_n, 44.D1_n, 44.61, 44.13, 83.321, 22.4, 22.2_m, 22.1_m, 53.3, 53.2, 44.9, 44.21, 44.13, 44.12, 44.11, 24.221, 24.1, 22.1, 51.1, 22.4, 44.91 + Aste Fluviali Geoportale Nazionale.
Coastal lagoon habitats and related vegetation	13.2, 14.1, 15.1, 15.21, 15.2, 15.5, 15.6, 89.1, 21.2_m, 21.1_m, 16.3, 16.28, 16.29, 16.21, 16.1, 15.81, 16.11, 16.12, 16.27, 16.25, 16.22,
Other	16.21, 15.1, 14, 23, 21, 15.5, 15.21
	63, 62.15, 62.21, 62.211_m, 61.31, 61.23, 61.22, 61.11, 62.7_n, 67_n, 64.4

Macrohabitats were created specifically for this study according to the ecological requirements of the gull-billed tern.

Table A2

Summary trip statistics showing average values \pm SD of daily number of trips, trip duration, maximum trip distance, total travelled distance and daily trips according to colony, year, breeding stage and sex

	Incubation		Chick rearing	
	Males	Females	Males	Females
Daily number of trips				
Po Delta (Rovigo) 2019	2.50 \pm 0.71 (1;5)	2.23 \pm 1.03 (3;58)	5.04 \pm 1.31 (1;126)	5.77 \pm 2.67 (2;283)
Po Delta (Rovigo) 2020	3.00 \pm 1.36 (2;48)	2.52 \pm 1.4 (5;53)	3.38 \pm 1.89 (2;169)	5.67 \pm 2.31 (5;482)
Lagoon of Venice 2021	2.90 \pm 0.83 (4;61)	2.69 \pm 1.06 (4;62)	5.76 \pm 2.43 (1;144)	5.76 \pm 1.73 (2; 288)
Total	2.92 \pm 1.06 (7;114)	2.47 \pm 1.16 (12;173)	4.39 \pm 2.14 (4;439)	5.72 \pm 2.26 (9;1053)
Trip duration (min)				
Po Delta (Rovigo) 2019	118.80 \pm 43.3 (1;5)	105.22 \pm 50.62 (3;58)	94.25 \pm 50.07 (1;126)	88.91 \pm 73.22 (2;283)
Po Delta (Rovigo) 2020	136.52 \pm 89.43 (2;48)	156.02 \pm 118.92 (5;53)	123.07 \pm 112.33 (2;169)	100.86 \pm 86.68 (5;482)
Lagoon of Venice 2021	130.28 \pm 92.59 (4;61)	108.49 \pm 48.66 (4;62)	91.75 \pm 78.17 (1;144)	69.25 \pm 41.57 (2;288)
Total	132.41 \pm 89.23 (7;114)	121.96 \pm 80.51 (12;173)	104.53 \pm 88.13 (4;439)	89.0 \pm 74.21 (9;1053)
Trip maximum distance (km)				
Po Delta (Rovigo) 2019	10.06 \pm 6.93 (1;5)	10.77 \pm 4.86 (3;58)	10.50 \pm 3.87 (1;126)	6.27 \pm 3.98 (2;283)
Po Delta (Rovigo) 2020	15.66 \pm 7.65 (2;48)	16.85 \pm 12.15 (5;53)	14.06 \pm 7.71 (2;169)	8.64 \pm 9.09 (5;482)
Lagoon of Venice 2021	8.77 \pm 6.32 (4;61)	12.14 \pm 8.57 (4;62)	5.69 \pm 2.49 (1;144)	5.92 \pm 4.25 (2;288)
Total	11.73 \pm 7.66 (7;114)	13.13 \pm 9.22 (12;173)	10.30 \pm 6.44 (4;439)	7.26 \pm 6.97 (9;1053)
Total travelled distance (km)				
Po Delta (Rovigo) 2019	55.42 \pm 9.83 (1;5)	52.61 \pm 23.77 (3;58)	127.72 \pm 34.98 (1;126)	96.86 \pm 36.41 (2;283)
Po Delta (Rovigo) 2020	34.93 \pm 19.34 (2;48)	36.88 \pm 27.89 (5;53)	31.24 \pm 20.35 (2;169)	19.77 \pm 21.19 (5;482)
Lagoon of Venice 2021	19.59 \pm 15.88 (4;61)	26.32 \pm 19.61 (4;62)	13.11 \pm 10.93 (1;144)	12.41 \pm 9.92 (2; 288)
Total	26.16 \pm 18.81 (7;114)	28.64 \pm 21.07 (12;173)	23.58 \pm 17.54 (4;439)	16.92 \pm 17.48 (9;1053)

Sample sizes are shown in parentheses (number of individuals; number of foraging trips).

Table A3

Summaries of multiple comparisons tests derived from trip metrics models (GLMMs: number of daily trips, maximum and total distance; LMM: trip duration) for which significant interactions between sex (F = female, M = male) and breeding stage variables were detected

Contrasts	Estimate	SE	z	P
Number of daily trips				
Incubating F–Rearing F	0.443	0.0409	8.818	<0.0001
Incubating F–Incubating M	0.879	0.1282	–0.884	1
Incubation F–Rearing M	0.562	0.0693	4.673	<0.0001
Rearing F–Incubating M	1.984	0.256	5.311	<0.0001
Rearing F–Rearing M	1.268	0.1299	2.317	0.123
Incubating M–Rearing M	0.639	0.0707	4.046	0.0003
Trip duration (min)				
Incubating F–Rearing F	–0.003	0.0005	–6.281	<0.0001
Incubating F–Incubating M	0.00001	0.0009	–0.019	1
Incubating F–Rearing M	–0.001	0.0008	–1.781	0.450
Rearing F–Incubating M	0.003	0.0009	3.953	0.001
Rearing F–Rearing M	0.002	0.0008	2.409	0.096
Incubating M–Rearing M	–0.001	0.0006	–2.521	0.070
Trip maximum distance (km)				
Incubation F–Rearing F	0.611	0.079	7.721	<0.0001
Incubating F–Incubating M	0.034	0.203	0.169	0.998
Incubating F–Rearing M	0.135	0.199	0.681	0.903
Rearing F–Incubating M	–0.576	0.198	2.913	0.043
Rearing F–Rearing M	–0.475	0.193	–2.453	0.1
Incubating M–Rearing M	0.101	0.089	1.126	0.673
Trip total distance (km)				
Incubating F–Rearing F	1.892	0.175	6.874	<0.0001
Incubating F–Incubating M	0.991	0.215	–0.041	1
Incubating F–Rearing M	1.146	0.242	0.645	1
Rearing F–Incubating M	0.524	0.11	3.081	0.038
Rearing F–Rearing M	0.606	0.123	–2.462	0.159
Incubating M–Rearing M	1.156	0.122	1.373	1

P values have been adjusted according to Bonferroni corrections performed via the package 'emmeans' (Lenth, 2020). Comparisons with significant P values (alpha = 0.05) are shown in bold.

Table A4

GLMM on agricultural use analysis testing main effects excluding the interaction between breeding stage (I = incubation, R = chick rearing) and sex (F = female, M = male)

Predictors	Estimate [95% CI]	χ^2	df	P
Breeding stage	I: 0.73 [0.65, 0.78]; R: 0.72 [0.65, 0.78]	0.24	1	0.621
Sex	F: 0.72 [0.65–0.79]; M: 0.72 [0.61–0.81]	0.01	1	0.999
Sampling year	2019: 0.64 [0.49–0.78]; 2020: 0.713 [0.602–0.80]; 2021: 0.79 [0.702–0.86]	4.3	2	0.116
Conditional R ² : 0.10; marginal R ² : 0.02				

Table A5

Summaries of multiple comparisons tests derived from habitat use analysis (GLMMs) for freshwater and agricultural habitats where significant interactions between sex (F = female, M = male) and breeding stage variables were detected

Contrasts	Odds ratio	SE	z	P
Freshwater				
Incubating F/Rearing F	0.440	0.059	6.11	<0.0001
Incubating F/Incubating M	0.444	0.170	–2.118	0.204
Incubating F/Rearing M	0.508	0.19	–1.811	0.421
Rearing F/Incubating M	1.008	0.374	0.021	1
Rearing F/Rearing M	1.154	0.417	0.396	1
Incubation M/Rearing M	1.145	0.164	0.941	1
Coastal lagoon				
Incubating F/Rearing F	0.201	0.081	3.981	<0.0001
Incubating F/Incubating M	0.138	0.081	3.356	0.005
Incubating F/Rearing M	0.139	0.080	3.421	0.004
Rearing F/Incubating M	0.692	0.339	–0.751	1
Rearing F/Rearing M	0.695	0.329	–0.769	1
Incubating M/Rearing M	1.005	0.290	0.019	1

P values have been adjusted according to Bonferroni corrections performed via the package 'emmeans' (Lenth, 2020). Comparisons with significant P values (alpha = 0.05) are shown in bold.