



Original Article

Sex-specific nest attendance rhythm and foraging habitat use in a colony-breeding waterbird

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In most colony-breeding species, biparental care during both egg incubation and chick-rearing is inevitable for successful reproduction, requiring parents to coordinate their nest attendance and foraging time. The extent to which the rhythm of nest attendance is adjusted to temporal and spatial variation in food availability is poorly understood. Here, we investigate whether the rhythm of nest attendance interacts with the spatial and temporal availability of foraging habitats in Eurasian spoonbills *Platalea leucorodia* breeding on Schiermonnikoog, a Dutch Wadden Sea barrier island. Spoonbills are tactile foragers that forage during both day and night in habitats of varying salinity. GPS-tracking combined with acceleration-based behavioral classification of 9 female and 13 male adult spoonbills between 2013 and 2019 revealed that, despite nearby foraging opportunities following a tidal rhythm, nest attendance followed a sex-specific diel rhythm. During incubation and chick-rearing, females attended the nest at night and foraged during the day, while males showed the reverse rhythm. Females made more and shorter foraging trips to, almost exclusively, nearby marine habitats, whereas the larger males often made long trips to forage in more distant freshwater habitats. Before and after breeding, females as well as males foraged primarily at night, suggesting that this is the preferred period of foraging for both sexes. Nevertheless, foraging habitat use remained sex-specific, being most likely explained by size-dependent foraging techniques. To conclude, the sex-specific rhythm of nest attendance is not shaped by the spatial and temporal availability of foraging habitats.

Key words: biparental care, central-place foraging, Eurasian spoonbill, GPS-tracking, *Platalea leucorodia*, sexual size dimorphism.

INTRODUCTION

Biparental care, where both the male and female parent contribute to the incubation of eggs and/or the feeding and protection of chicks, is the prevalent form of care in birds (Lack 1968; Cockburn 2006). It is particularly common in species where the distance between the nest and suitable foraging grounds is

considerable, such as colony-breeding seabirds and waterbirds (Cockburn 2006). In these species, parents need to coordinate their nest attendance and time away from the nest to search for food, for both themselves and their chicks (Schreiber and Burger 2001).

Across colony-breeding species, the distance and quality of foraging grounds around the colony play a key role in shaping nest attendance rhythms. On the extreme side, some pelagic seabird species travel > 1000 km from the colony to reach suitable

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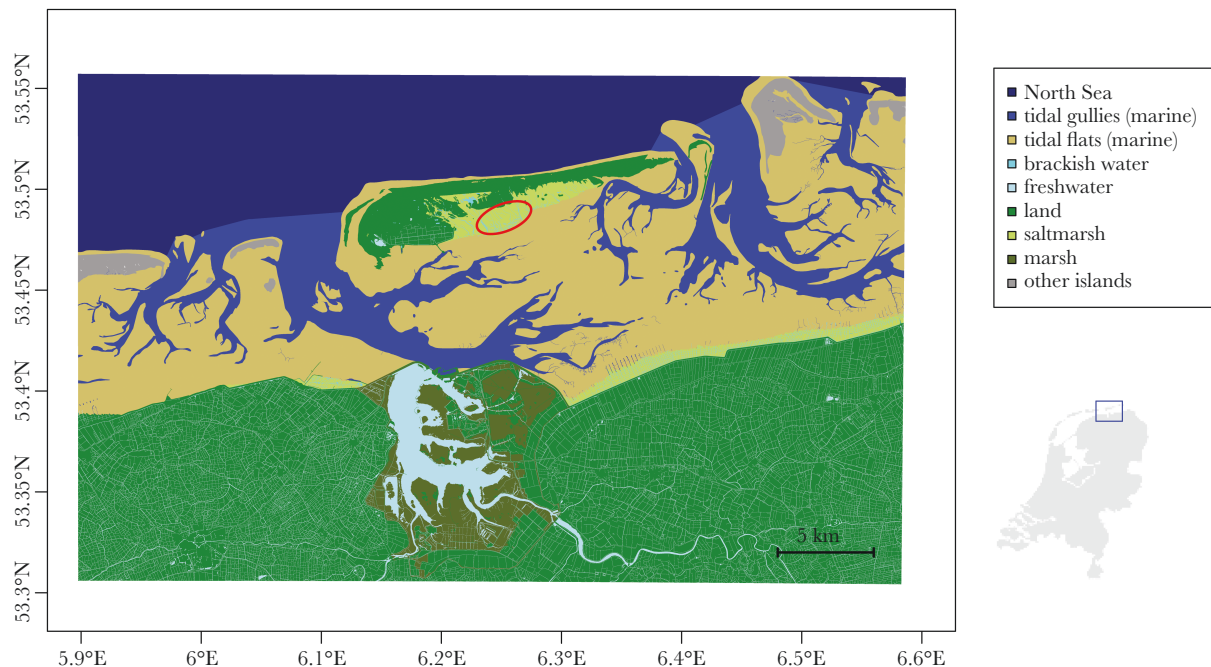


Figure 1

Map of the distinguished habitats on and around the island of Schiermonnikoog, and its location within The Netherlands (the blue rectangle). The large freshwater body on the mainland is called Lake Lauwersmeer. The nests of the tracked spoonbills were all situated within the red ellipse.

foraging grounds, which are often unpredictably and patchily distributed, and stay away for several days while their partner is attending the nest (Weimerskirch 1995; Gonzalez-Solis et al. 2000). However, the majority of seabirds and waterbirds have relatively short foraging ranges and exchange nest attendance duties on a daily basis or more often (Coulson and Wooller 1984; Hafner et al. 1993; Becker et al. 1997; Linnebjerg et al. 2015; Kavelaars et al. 2021). Yet, among the latter species, there is considerable variation in rhythms of nest attendance: some species exchange nest attendance duty multiple times during the diel cycle, even during egg incubation, while in other species, males and females only exchange once or twice (Bernstein and Maxson 1984; Aguilera 1990; Hildén 1994). Also, the proportion of time that the male and female allocate to attending the nest and feeding the young is highly variable across species (Thaxter et al. 2009; Wojczulanis-Jakubas et al. 2009; Riechert and Becker 2017; Kavelaars et al. 2021). The extent to which this variation in diel nest attendance rhythms is caused by temporal and spatial variation in (potentially sex-specific) food and foraging habitat availability has rarely been investigated, as it requires continuous tracking of breeding birds to simultaneously monitor their nest attendance rhythm and foraging habitat use.

Here, we investigate whether and how the rhythm of nest attendance of Eurasian spoonbills *Platalea leucorodia leucorodia* (hereafter spoonbills) interacts with the spatial and temporal availability and use of foraging habitats. Spoonbills are tactile foragers that forage during both day and night in shallow waters of varying salinity, from freshwater lakes to brackish river estuaries and marine tidal areas (Hancock et al. 1992). As a result, environmental contexts around breeding colonies vary considerably. In colonies surrounded by freshwater habitats, foraging habitats are available for 24 h, whereas in colonies on islands surrounded by tidal areas, foraging opportunities are driven by the tidal cycle. Using GPS tracking combined with acceleration-based behavioral classification

(Lok et al. 2023), we simultaneously investigated (1) the rhythm of nest attendance and (2) the foraging range and habitat use of male and female spoonbills breeding in a colony on Schiermonnikoog, a barrier island in the Dutch Wadden Sea. This colony is surrounded by nearby marine foraging habitats, at 2–5 km distance from the colony, that are only available around low tide, whereas the majority of freshwater habitats, available at all times, are at > 10 km distance from the colony (in Lake Lauwersmeer, Figure 1). In an inland colony in Spain surrounded by freshwater foraging habitats, visual observations confirmed a diel (24-h) rhythm in nest attendance during both egg incubation and chick-rearing, with males attending the nest during most of the day and females at night (Aguilera 1990). We investigate whether a similar diel rhythm of sex-specific nest attendance persists under the coastal environmental context in The Netherlands, or whether a tidal rhythm of nest attendance is adopted instead, which would allow both parents to make optimal use of the tidal variation in the availability of nearby marine and brackish foraging habitats.

Second, we monitored the foraging locations and habitats used by males and females before, during, and after the breeding season to investigate whether the rhythm of nest attendance appears to influence the foraging range and habitat use of females and males or vice versa. Spoonbills are sexually size dimorphic, with males being around 20% heavier, having 18% longer tarsi, and 15% longer bills, yet only 5% longer wings (Cramp and Simmons 1977; Lok et al. 2014; Supplementary Table S1). In a variety of colony-breeding species, males and females were shown to have different foraging ranges and locations. In some sexually size dimorphic species, the larger males foraged closer to the colony, a pattern suggested to be caused by their higher flight costs and/or niche specialization (Gonzalez-Solis et al. 2000; Phillips et al. 2004; De Pascalis et al. 2020), while in other species, the opposite pattern was found (Camphuysen

et al. 2015; Militão et al. 2023). Moreover, sex-specific foraging ranges and locations were also found in several monomorphic species and potentially caused by sex-specific nutritional requirements, parental care roles, or risk partitioning (Lewis et al. 2002; Elliot et al. 2010; Pinet et al. 2012; Burke et al. 2015; Ismar et al. 2017). As such, we do not have clear a priori predictions on how male and female spoonbills would differ in foraging range and habitat use. Apart from potential sex-specific differences, we predict that the foraging range will decrease from egg incubation to chick-rearing, as shown for many seabird species (Oppel et al. 2018). By comparing foraging habitat use before, during, and after the period of “nest dependence,” we are able to distinguish whether any sex-specific differences in foraging habitat use are caused by sex-specific habitat preferences or by constraints in foraging range and habitat availability and suitability imposed by the rhythm of nest attendance.

METHODS

Study population

We studied the breeding population of Eurasian Spoonbills on Schiermonnikoog, The Netherlands (53°29'N, 6°15'E), during the breeding seasons of 2012–2019. Schiermonnikoog is one of the five barrier islands in the Dutch Wadden Sea inhabited by people. Most spoonbills on Schiermonnikoog breed on the Oosterkwelder, an extensive saltmarsh on the east side of the island, where nests are built on the ground. During the study period, the number of breeding pairs on the Oosterkwelder varied between 188 and 302 pairs spread over 8–15 colonies varying in size from several up to ca. 50 nests. Distance between colonies on the saltmarsh varied from 100 m to 5 km. A second spoonbill breeding area on Schiermonnikoog with 10–27 breeding pairs was situated in the Westerplas, a freshwater lake on the westside of the island, where they breed in willows or reed.

Adult birds breeding on Schiermonnikoog feed their chicks mainly with small fish and shrimps (El-Hacen et al. 2014; Jouta et al. 2018), which they collect in marine, brackish and freshwater creeks, pools, and lakes with water depths up to 30–40 cm. Marine foraging habitats, tidal creeks, and pools that become available around low tide are situated at 1–6 km distance from the colony, whereas the majority of freshwater habitats, that is, Lake Lauwersmeer, are located on the mainland at ca. 10 km distance from the colony. Brackish water habitats, whose availability is also strongly driven by the tidal rhythm, are present at the saltmarshes on the island (at < 1 km) and along the mainland coast (at ca. 10 km). Habitat types within the study area have been assigned as (1) mainland, (2) island and (3) fresh, (4) brackish, and (5) marine water on the basis of the BRT TOP10NL topographic map from 2011 (resolution 1:20,000; <https://www.kadaster.nl/zakelijk/producten/geo-informatie/topnl>) using expert knowledge and by changing lines into polygons for small waterbodies (e.g., ditches, small gullies) (Figure 1).

GPS tracking

Between 2012 and 2018, 31 adult spoonbills (20 males and 11 females) were caught and equipped with an UvA-BITS GPS/ACC tracker (Bouten et al. 2013; Supplementary Table S1). These trackers collect GPS and accelerometer data following a manually adjustable sampling scheme through communication via a radio antenna network. The most commonly used settings during the

study period were to register a GPS location every 10 or 30 min, along with 0.8 or 1.6 s of 20 Hz accelerometer data.

All birds were caught on the nest using a leg loop. We selected individuals for catching that were strongly attached to the nest (i.e., not flying up when approached until ca. 30 m from the nest). In the majority of cases, these birds were in the second half of incubation. To prevent the eggs from getting damaged during the catching attempt, the eggs were replaced by dummy eggs before capture. In the few cases that a bird was not caught within half an hour, the catching attempt was aborted.

Upon capture, the real eggs were placed back in the nest, and the bird and the catching equipment were taken away from the colony at a distance of ca. 200 m to allow the other breeding spoonbills to return to their nests. The bird was then measured, weighed, and a blood sample was taken for molecular sexing. The bird was ringed with a unique combination of color rings and a flag and a GPS tracker was mounted on the back of the bird using a non-flexible Teflon harness. The tracker including the neoprene pad and Teflon harness (5 g) weighed 31 ± 12 g (mean \pm SD), and the average body masses of the caught adult females and males were 1646 ± 146 g and 1968 ± 162 g, respectively. The tracker contributed 1.1–3.0% to body mass, thus not exceeding the 3% that has been suggested to represent the upper limit for migratory bird species (Phillips et al. 2003). After handling, which took maximally half an hour, the birds were released immediately. We found no difference in breeding success and apparent survival between birds that were equipped with a GPS tracker versus birds that were not (for detailed methods and results of these analyses, see Section S1 of the Supplementary Material).

Determination of breeding phase

In the year of capture, the nest of the tracked adult was marked with a uniquely numbered wooden stick. In subsequent years, and in the cases where the tracked bird deserted the nest after the capture event (in 7 of the 26 catching events, of which 6 nest desertions occurred in a single year, 2016) but renested later in the season (in 6 of the 7 cases, all included in the analyses), we used GPS data of the tracked birds to determine whether a bird initiated a breeding attempt. The timing of the different breeding phases per bird and year are visualized in Supplementary Figure S1. The location of the nest in these cases was determined by selecting the GPS coordinates that the bird visited most frequently (with latitude and longitude in degrees rounded to the nearest 5 and 6 decimals, respectively). Accounting for the inaccuracy of the GPS coordinates, we assumed that the bird was at the nest when within a radius of 10 m and in the colony when within a radius of 50 m from this nest location.

To ensure that the tracked birds were strongly settled to their nest site and presumably had started incubating, we visited the colony for the first time when the bird was estimated to have stayed at the nest site for more than 5 h per 24 h for at least 2 weeks. From ca. 100 m distance, the nests in the colony were observed using a 20–60× telescope. When the tracked bird was observed on the nest, we slowly approached it to determine its nest and marked it with a uniquely labeled wooden stick. When the nest was hidden behind high vegetation, additional observations from a hide or by using a camera trap were needed to locate the nest.

The nest was then visited at intervals of ca. 2 weeks until hatching. Hatch date was estimated from the head-bill length of the largest chick measured during the first visit after hatching, using the

Gompertz growth curve estimated by Lok et al. (2014) ($y_{\infty} = 184$, $k = 0.052$ and $T_i = 7.9$). To know their nest of origin, all chicks in the nest received a uniquely labelled temporary band when the oldest chick was between 7 and 10 days old. When chicks were between 3 and 4 weeks old, they were color-ringed. A breeding attempt was considered successful when at least one chick survived until the age at which it was color-ringed. At this age, spoon-bill chicks are no longer attached to their own nest but gather in crèches (Cramp and Simmons 1977).

We distinguished four breeding phases: pre-breeding (from arrival in the study area until the start of incubation), incubation (25 days prior to hatching; Lok et al. 2014), chick-rearing (from hatching until the oldest chick was 30 days old, or until the last day that the parent was present in the colony for > 5 h during 24 h when this was < 30 days after hatching; this indicated that all chicks had died), and post-breeding (from 30 days old chicks until the last day the bird was in the study area (Figure 1) and transmitted its data before migrating southward). For the post-breeding phase, we distinguished two classes of birds on the basis of their reproductive success: (1) birds that successfully raised at least one chick until the age of color-ringing (“post-breeding, successful”) and (2) birds that failed to raise chicks until the age of color-ringing (“post-breeding, unsuccessful”). We made this distinction because spoonbill chicks are still being fed by their parents for an extended period after they are able to fly (Cramp and Simmons 1977), hence time allocation and foraging behavior of parents that still have chicks are expected to be different compared to parents that no longer have chicks. To achieve balanced sample sizes across breeding phases, we only used data from the last 30 days of the pre-breeding and the first 30 days of the post-breeding phase in the analyses.

Behavioral classification of accelerometer data

The bird’s behavior at each location was predicted from the accelerometer data, using the behavioral classification model developed in Lok et al. (2023). For this, the 20 Hz acceleration data samples were cut into segments of 0.4 s (* 20 Hz = 8 measurements) over which 32 summary statistics were calculated. Together with GPS speed (i.e., current speed of the animal measured by GPS), these summary statistics were used by the classification model to predict the behavior for each segment. Usually, 0.8 or 1.6 s of acceleration data were collected. Therefore, multiple segments of 0.4 s were associated with a single GPS fix. We selected the most often classified behavior as the behavior expressed during a GPS fix. If several behaviors were equally often classified, we randomly selected one of these behaviors.

The model was originally trained to distinguish the following eight behaviors: stand, sit, fly-active (flap), fly-passive (soar or glide), search, handle, ingest, walk, and drink. For this study, we were interested in distinguishing the following behaviors: attending the nest (sitting or standing within 5 m of the nest), resting (sitting or standing away from the nest), foraging (searching, handling, or ingesting prey), flying (using soaring or flapping flight) or other (walking, drinking). Except for the category “other,” these pooled behaviors were previously shown to be predicted with high classification accuracies (i.e., F-measures > 0.90 where F-measure is a balanced measure of precision and sensitivity; Lok et al. 2023). The classification accuracy of the behaviors in the “other” category was estimated at 0.56 for walking and < 0.1 for drinking, the latter being a rarely occurring though biologically relevant behavior (Lok

et al. 2023). Only 5% of the 0.4 s acceleration segments were predicted to be “other” behavior (see Figure 2).

Data selection and definition of foraging trips

For the analyses, we only used GPS fixes that (1) were inside the study area (Figure 1), so that habitat type was known, and (2) were accompanied by a sample of acceleration data, so that the bird’s behavior could be predicted. To make sure that each individual contributed a similar amount of data per day to the analyses, we down-sampled the data to 30-min intervals and only used “bird days” (of 24 h) with (nearly) complete data, that is, where maximally one of the 48 30-min samples was missing. Eventually, data of 22 individuals (9 females and 13 males) were included in the analyses, with 11 individuals contributing data for several (2–4) years, resulting in a total of 3115 bird days and 41 bird years between 2013 and 2019 (Supplementary Table S1 and visualized per bird, year and breeding phase in Supplementary Figure S1).

We assumed that a bird was actually foraging when the bird was classified to be foraging on the basis of the accelerometer data and when the associated GPS coordinates were in foraging habitat (i.e., fresh, brackish, or marine water). When the bird was estimated to be foraging while on land, we assumed that the bird was actually walking (i.e., expressing “other” behavior). These cases mainly concerned locations on the saltmarsh, during which birds (mostly males) were presumably collecting nest material (e.g., branches) rather than food. In the case of small water bodies (e.g., ditches or gullies), the measurement error (mostly 0–5 m) associated with GPS coordinates may sometimes cause a bird to be incorrectly classified as walking along the shore instead of foraging in the water or vice versa. We defined a foraging trip as the period between departure from the colony (< 50 m from the nest location) and return to the colony, which included at least one sample during which the bird was estimated to be foraging. To account for the fact that the bird departed somewhere between 0 and 30 min (i.e., on average 15 min) after the last sample in the colony and returned on average 15 min prior to the sample that it was back in the colony, we subtracted 30 min from the above-calculated duration. In addition to foraging duration, we determined the maximum distance from the nest location.

Data from the day of capture were excluded from analysis, as birds may still behave abnormally as a result of the capture event (e.g., stay away from the nest during “duty hours”). Furthermore, we only used data of a bird for a specific year and breeding phase in the analyses when there were at least 5 days of nearly complete data (see above) available. Moreover, we only included bird years with sufficient data during at least the incubation or chick-rearing phase (i.e., bird years with sufficient data during only pre-breeding and/or post-breeding were excluded).

Statistical analysis

Sex-specific rhythms and overall probabilities of nest attendance and foraging

To investigate whether the probability of nest attendance and foraging showed a diel or tidal rhythm, we used generalized additive mixed models with a binomial error distribution. This allowed us to estimate nonlinear relationships between the explanatory variables, time of the day and tidal phase, and the binary response variables (either or not attending the nest or foraging) and to investigate whether and how these relationships differed between sexes and breeding phases. The time of the day and tidal phase were modeled as cyclic variables using cyclic cubic regression splines and

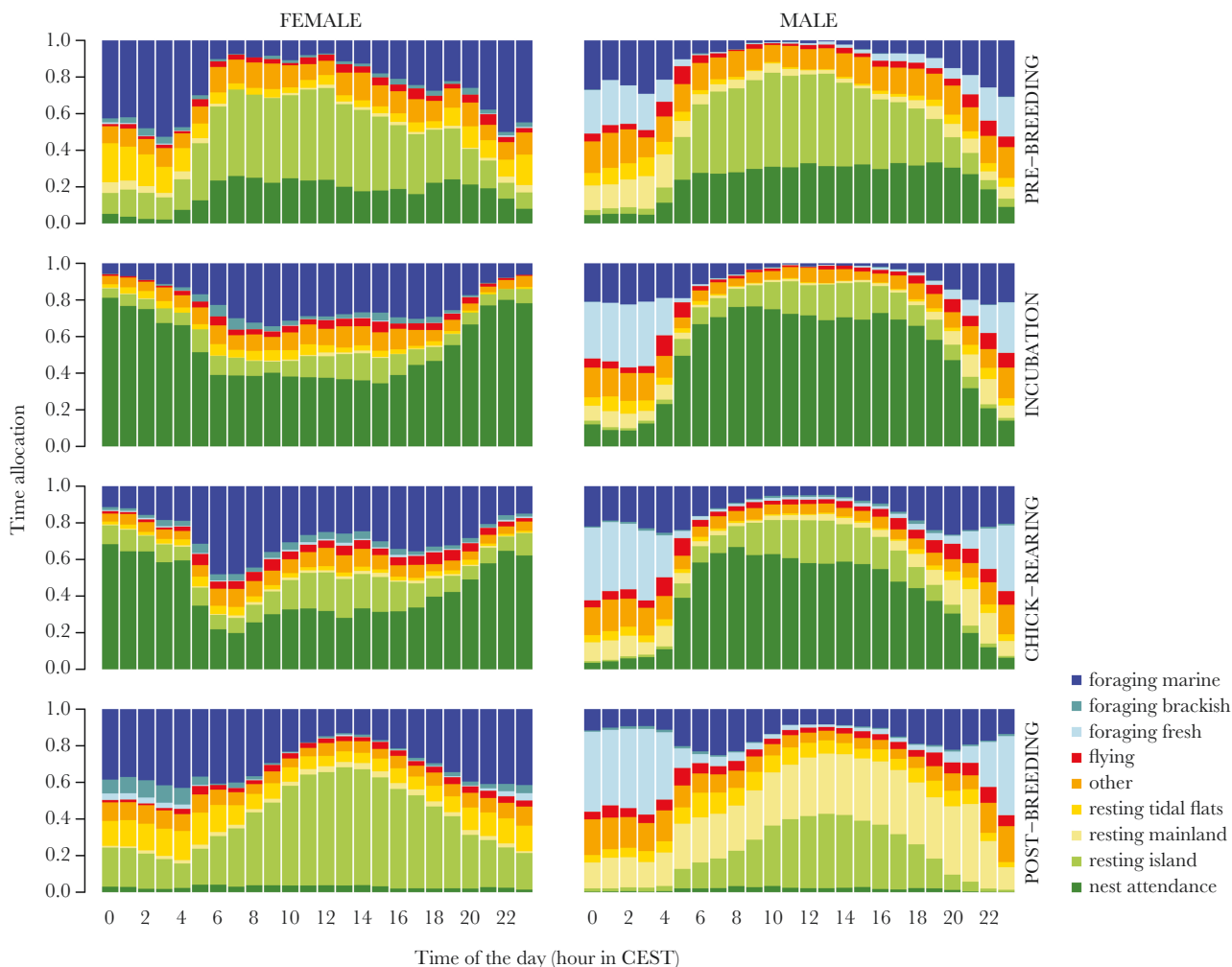


Figure 2

Average time allocated to different activities in different habitats by male and female Eurasian spoonbill parents during pre-breeding, incubation, chick-rearing and post-breeding.

standardized to radians, where 0 and 2π refer to high tide and midnight, and π refers to low tide and noon. We considered the time of the day, tidal phase, sex and breeding phase, and all possible interactions as fixed effects. Year and individual were included as random intercepts in all models.

The overall probability of attending the nest and foraging was modeled using generalized linear mixed models with a binomial error distribution, considering sex and breeding phase and their two-way interaction as fixed effects. Year and individual were included as random intercepts in all models.

Foraging range and habitat use

The daily number of foraging trips, the duration and the maximum distance from the colony of foraging trips, and foraging habitat use (i.e., the probability to be foraging in marine (including brackish) habitat, as opposed to freshwater) were modeled using generalized linear mixed-effects models. The number of foraging trips was modeled using a Poisson distribution, foraging trip duration, and distance using a Gamma distribution, and tidal foraging probability using a binomial distribution. We treated sex, the breeding phase, and their two-way interaction as fixed effects.

To explore whether potential within-sex variation in foraging habitat use could be explained by individual variation in foraging skills, we investigated whether the probability of foraging in tidal habitat of males and females could be explained by their bill and tarsus length, pooling data across all breeding phases. As bill length was more frequently measured than tarsus length (see Supplementary Table S1), we analyzed the relationship with each biometric measurement separately, while reporting the number of individuals included in each analysis. Year and individual were included as random intercepts in all models.

For the analysis of nest attendance probability and number, duration, and distance of foraging trips that had the colony as start and end point, we only compared the incubation and chick-rearing phase. For the analysis of (tidal) foraging probability, all breeding phases were compared, including the pre- and post-breeding phase.

Model selection procedure

All statistical analyses were performed in program R (v. 4.1.3, R Core Team 2022), using package lme4 (Bates et al. 2015) to fit generalized linear mixed models and package mgcv and function bam to fit generalized additive mixed models to large datasets (Wood

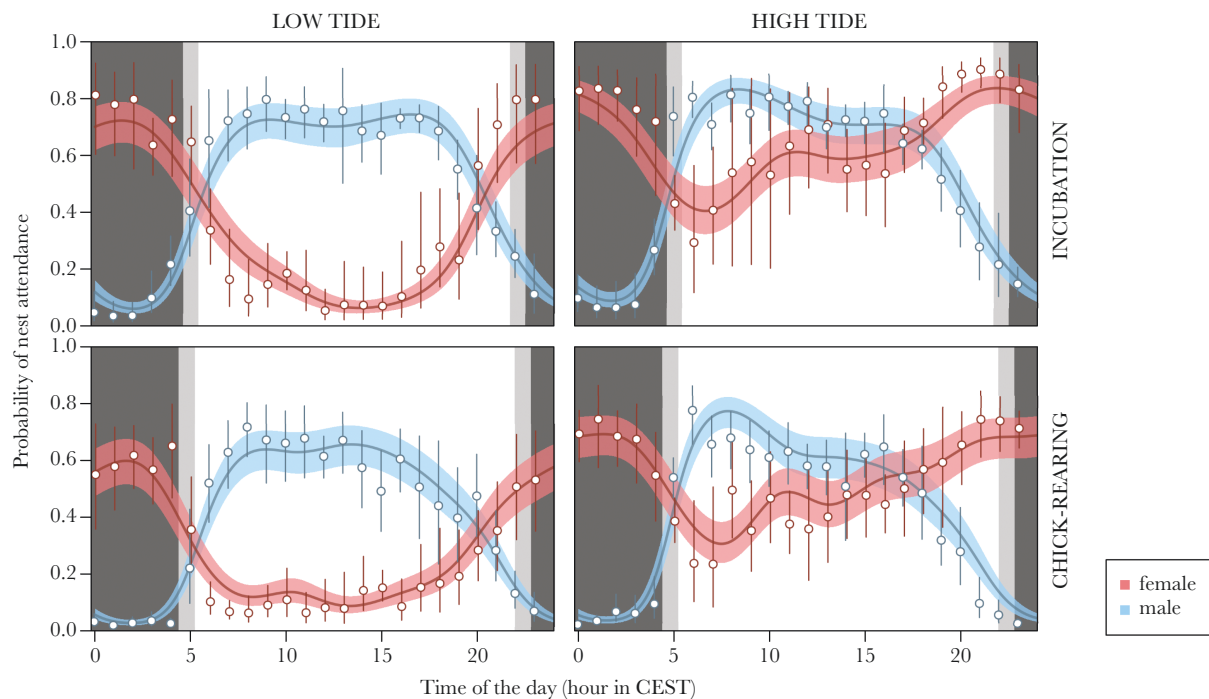


Figure 3

Probability of nest attendance in relation to hour of the day and tidal phase for females and males during incubation and chick-rearing. Dots and error bars show means and 95% confidence intervals calculated over the average logit-transformed probabilities of nest attendance per bird per hour per tidal phase and then back-transformed. The curves and shaded areas show population-level estimates and 95% confidence intervals of the best-supported model from Supplementary Table S2. For plotting the raw data, we pooled radian tidal phases of $> 0.75\pi$ and $\leq 1.25\pi$ to represent low tide and $\leq 0.25\pi$ or $> 1.75\pi$ as high tide, while the curves represent the model estimates at exactly low (π) and high ($0 = 2\pi$) tide. Dark gray is the period between dusk and dawn, and light gray is the twilight period.

2017). We used package DHARMA (Hartig 2022) to confirm that residuals did not deviate from homogeneity. In the additive models, we used $k = 10$ as the upper limit to the degrees of freedom to fit the smooth terms. For the analyses where we considered the potential effects of sex, breeding phase, and their two-way interaction, the candidate model set consisted of all four models with or without these effects. For the nest attendance and foraging rhythm models, we kept sex, breeding phase, and their two-way interaction in all models and built candidate models in which the diel and/or tidal rhythm were allowed to vary between sexes and/or breeding phases. This resulted in 32 candidate models to explain nest attendance and foraging rhythms. Model support was assessed on the basis of the Akaike information criterion adjusted for a small sample size (AIC_c ; Burnham and Anderson 2002). Models were considered to be supported when they were within $2 \Delta AIC_c$ of the best-supported model, except when adding a single parameter increased the AIC_c , as such parameters should be considered uninformative (Arnold 2010). Where applicable, post-hoc pairwise comparisons were performed using R-package emmeans (Lenth 2022).

RESULTS

Sex-specific rhythms and overall probabilities of nest attendance and foraging

Both nest attendance and foraging rhythms were best explained by the statistical four-way interaction between sex, breeding phase, diel phase, and tidal phase, as removing this four-way interaction increased AIC_c by 155 and 310 points, respectively (see

Supplementary Tables S2 and S3). During incubation and chick-rearing, females attended the nest primarily at night and males during the day (Figures 2 and 3), while the foraging rhythm showed the opposite pattern: females foraged mainly during the day and males at night (Figures 2 and 4). The probability that females attend (or at least stay close to) the nest during the day was considerably higher around high tide, while this tidal effect was nearly absent in males (Figure 3, Supplementary Figure S2). During the pre- and post-breeding phase, both males and females showed a higher probability of foraging at night than during the day (Figures 2 and 4). The probability of foraging was more strongly correlated with the tidal cycle in females than in males and was highest around low tide (Supplementary Figure S3).

The overall probabilities of nest attendance and foraging, irrespective of the diel and tidal cycle, were both best explained by an interactive effect of sex and breeding phase (Table 1). The probability of nest attendance decreased from incubation to chick-rearing, with this decrease being more pronounced in males (marginal means [95% CI]: from 0.52 [0.46–0.57] to 0.40 [0.35–0.45]; $z = 22.93$, $P < 0.001$) than in females (from 0.50 [0.45–0.56] to 0.42 [0.36–0.47]; $z = 14.47$, $P < 0.001$). Females and males did not significantly differ in nest attendance probability during either incubation ($z = -0.55$, $P = 0.59$) or chick-rearing ($z = 0.62$, $P = 0.54$), but females foraged more than males during all breeding phases, with the difference being particularly large during pre- and post-breeding (Figure 5a). The foraging probability of females decreased from pre-breeding to incubation but was higher again during chick-rearing and further increased

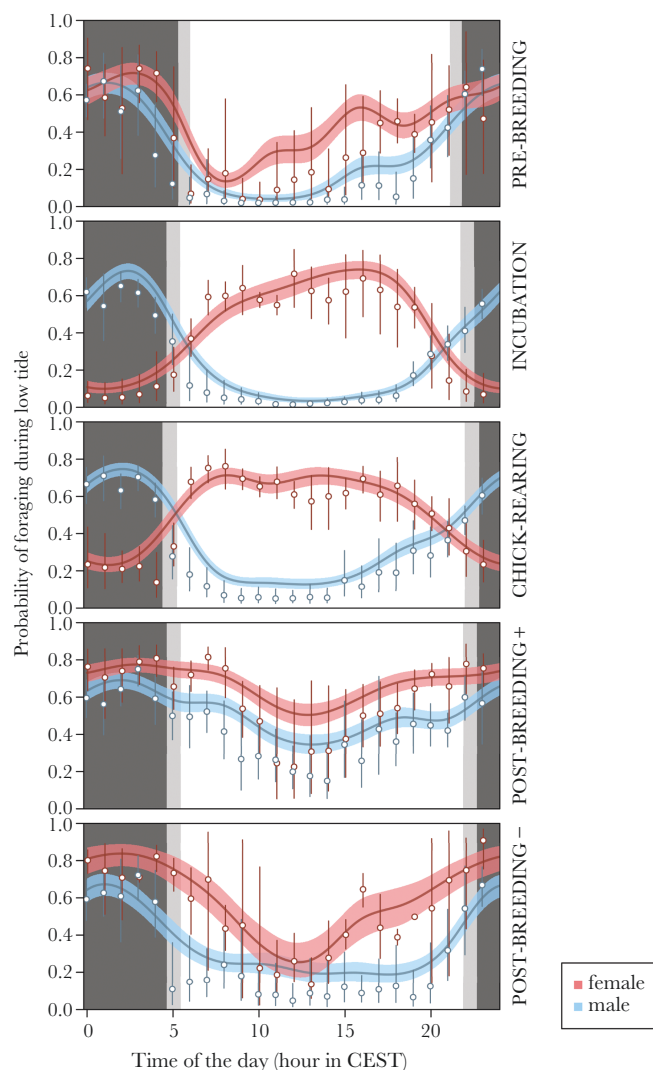


Figure 4 Probability of foraging during low tide in relation to hour of the day for females and males during the different breeding phases, where “post-breeding +” and “post-breeding -” represent post-breeding after a successful and unsuccessful breeding attempt. Dots and error bars show means and 95% confidence intervals calculated over the average logit-transformed probability of foraging per bird per hour, only selecting data around low tide (with radian tidal phase of $> 0.75\pi$ and $\leq 1.25\pi$) and then back-transformed. The curves and shaded areas show population-level estimates and 95% confidence intervals of the best-supported model from Supplementary Table S3 at exactly low tide. Dark gray is the period between dusk and dawn, and light gray is the twilight period.

during post-breeding, irrespective of whether breeding was successful or not (Figure 5a). In males, the foraging probability was lowest during pre-breeding and incubation, increased during chick-rearing and further during post-breeding, and was higher after a successful breeding attempt than when breeding was unsuccessful (Figure 5a).

Foraging range and habitat use

Foraging trip frequency was best explained by an additive effect of sex and breeding phase, whereas in the case of foraging trip duration and foraging trip distance, the selected model included an interactive effect

of sex and breeding phase (Table 2). Females made more foraging trips and stayed closer to the colony than males during both incubation and chick-rearing, while the foraging trip duration of females was only significantly shorter compared to males during chick-rearing (Figure 6). From incubation to chick-rearing, both females and males showed an increase in the number of trips, while only females showed a reduction in foraging trip duration and distance (Figure 6).

Foraging habitat use (i.e., the probability of foraging in marine (including brackish) habitat) was best explained by the interactive effect of sex and breeding phase (Table 1). Females almost exclusively foraged in (nearby) marine habitat, while males only spent about half of their foraging time in marine habitat and showed considerable variation in the probability of marine foraging (Figure 5b). In females, the probability of marine foraging was similar across most breeding phases and was only slightly lower during post-breeding when breeding was successful (Figure 5b). In males, the probability of marine foraging was highest during pre-breeding and chick-rearing and lowest during post-breeding when breeding was unsuccessful (Figure 5b). The spatial distribution of foraging locations of males and females during the different breeding phases is shown in Supplementary Figure S4.

Females showed little variation in foraging habitat use, which was not explained by bill length ($\chi^2 = 0.87$, $P = 0.35$, $N = 9$ individuals) or tarsus length ($\chi^2 = <0.01$, $P = 1.00$, $N = 6$). In contrast, males showed considerable variation in foraging habitat use, which was significantly correlated with bill length ($\chi^2 = 4.32$, $P = 0.04$, $N = 10$), but not with tarsus length ($\chi^2 = 0.53$, $P = 0.47$, $N = 6$). Males with large bills were least likely to forage in marine habitat (Figure 7).

DISCUSSION

In this study, we investigated the rhythm of nest attendance in concert with the foraging rhythm, range, and habitat use of Eurasian spoonbills breeding in a colony on the Wadden Sea barrier island of Schiermonnikoog. Rather than following a tidal rhythm, which would allow both parents to make optimal use of the tidally driven foraging opportunities in the nearby Wadden Sea, the rhythm of nest attendance during both incubation and chick-rearing showed a clear diel pattern, with males mostly attending the nest during the day and females at night. Correspondingly, during these breeding phases, females primarily foraged during the day and males at night. During pre- and post-breeding, however, females as well as males foraged primarily at night, suggesting that this is the preferred time of foraging for both sexes. While nest attendance duties were divided equally, females spent more time foraging during all breeding phases and generally made more and shorter (both in duration and distance) foraging trips per 24 h than males. Moreover, across all breeding phases, females foraged primarily in marine habitat, while about half of the foraging of males (and certainly of males with long bills) took place in more distant freshwater habitats.

Similar to the breeding population in the freshwater Doñana National Park in Spain (Aguilera 1990), spoonbills breeding on Schiermonnikoog showed a strong diel rhythm of nest attendance. Although the probability of females attending the nest during the day was higher during high tide, this was not accompanied by a decrease in the nest attendance probability of males. This indicates that females do not return to the colony because they have “parental duty,” but to rest during the high tide period. While they sometimes take over breeding from their partner during these periods (pers. obs.), males usually stay close to the nest, most likely

Table 1

Model selection results for the overall probability of (i.e., time allocated to) attending the nest, foraging, and foraging in marine habitat in relation to sex and breeding phase

Model	K	$\Delta-2\log L$	ΔAIC_c	Akaike weight
(a) Attending the nest				
phase * sex	6	0.00	0.00	0.99
phase	4	14.06	10.06	0.01
phase + sex	5	13.98	11.98	0.00
c	3	733.42	727.42	0.00
sex	4	733.36	729.36	0.00
(b) Foraging				
phase * sex	12	0.00	0.00	1.00
phase + sex	8	65.43	57.43	0.00
phase	7	71.39	61.39	0.00
sex	4	1322.06	1306.05	0.00
c	3	1325.23	1307.23	0.00
(c) Foraging in marine habitat				
phase * sex	12	0.00	0.00	1.00
phase + sex	8	22.77	14.76	0.00
phase	7	46.78	36.78	0.00
sex	4	189.82	173.82	0.00
c	3	213.66	195.66	0.00

For the probability of attending the nest, we only compared the breeding phases “incubation” and “chick-rearing.” For the probability of foraging and foraging in marine habitat, all breeding phases (“pre-breeding,” “incubation,” “chick-rearing,” “post-breeding successful” and “post-breeding unsuccessful”) were compared. ‘phase’=breeding phase and ‘c’=constant, referring to the ‘intercept-only’ model. Year and individual were included as random intercepts. Supported models are indicated in bold.

to allow females to leave again to forage during the outgoing tide. Indeed, independent of the tidal phase, males are more likely to attend the nest during the day than females (Figure 3). In addition to nearby foraging opportunities following a tidal cycle, foraging conditions appear to be better at night. A possible reason for this is that prey ingestion rates are higher at night, for example, because prey are (1) more active and therefore easier to catch (Verheijen and de Groot 1967; van Donk and De Wilde 1981; Thetmeyer 1997; Ehrenberg and Ejdung 2008), or (2) more accessible at night as they move up from deeper to shallower waters (Mehner 2012) or out of highly vegetated waters that become oxygen-deprived at night (Kersten et al. 1991). Less disturbance by humans at night could also play a role, particularly in the freshwater Lake Lauwersmeer. The diel nest attendance rhythm, therefore, implies that females are forced to forage at suboptimal times of the diel cycle. Altogether, this shows that the rhythm of nest attendance is hardly influenced by the rhythm of foraging opportunities. A similar result was found in the black-faced spoonbill *Platalea minor* breeding in South Korea, which also maintained a diel foraging-incubation rhythm in the midst of a tidal area (Park et al. 2019). Unlike many ground-breeding shorebird species, where nest predation risk was shown to be strongly correlated with rhythms of nest attendance (Bulla et al. 2016), this is unlikely to play a role in most colony-breeding species that are highly conspicuous and, therefore, to avoid nest predation, usually breed on ground-predator-free islands, as was the case in our study population, or in trees.

What could then explain this diel rhythm of nest attendance? Aguilera (1990) hypothesized that males may benefit more than females from being in the colony during the day, as this would allow them to prevent their female partners from engaging in extra-pair copulations and hence reduce uncertainty about paternity. This hypothesis was based on the observation that extra-pair copulations were only observed during daylight hours in the Doñana colony (Aguilera and Alvarez 1989). However, infrared webcams and camera traps in several colonies in The Netherlands have

revealed that extra-pair copulations also occur at night (pers. obs.). Moreover, the fact that the diel rhythm of nest attendance persists during the chick-rearing phase, when extra-pair fertilizations are no longer possible, makes this an unlikely explanation. An alternative explanation could be that males may play a more prominent role in defending the nest from daytime intruders (e.g., conspecifics or avian predators), as found in some seabirds (Paredes and Insley 2010). Another possibility is that there are benefits in this species to foraging with conspecifics of the same sex. Given that males and females seem to prefer different foraging habitats (at least in the ecological context of this study; see below), and assuming that group foraging increases individual foraging success, which could, for example, work via faster detection of shoals of fish or the ability to narrow them down (Clark and Mangel 1986), a sex-specific rhythm of nest attendance would be favored. Although this does not necessarily have to be a diel rhythm, to ensure that all breeding pairs use the same sex-specific rhythm of nest attendance, a day-night rhythm could emerge. More research is needed to unveil which factors are actually playing a role in shaping this seemingly rigid diel rhythm of nest attendance.

The fact that females spent more time foraging than males during all breeding phases may indicate that females require more time to collect the same amount of food than males, for example, because they forage in habitats with lower food availability, at less profitable times of the day (at least during incubation and chick-rearing), or because they feed on smaller prey items. Another possibility is that females have higher energetic demands than males, for example, due to egg production (Walsberg 1983; assuming that spoonbills are income breeders) or because they take a larger share in feeding the chicks. Females indeed make more foraging trips than males, but without information on the amount of food delivered to the chicks after a foraging trip, we do not know whether females indeed deliver more food to the chicks than males. The higher number of foraging trips by females could also be caused by the fact that the availability of their foraging grounds is tidally driven while they are

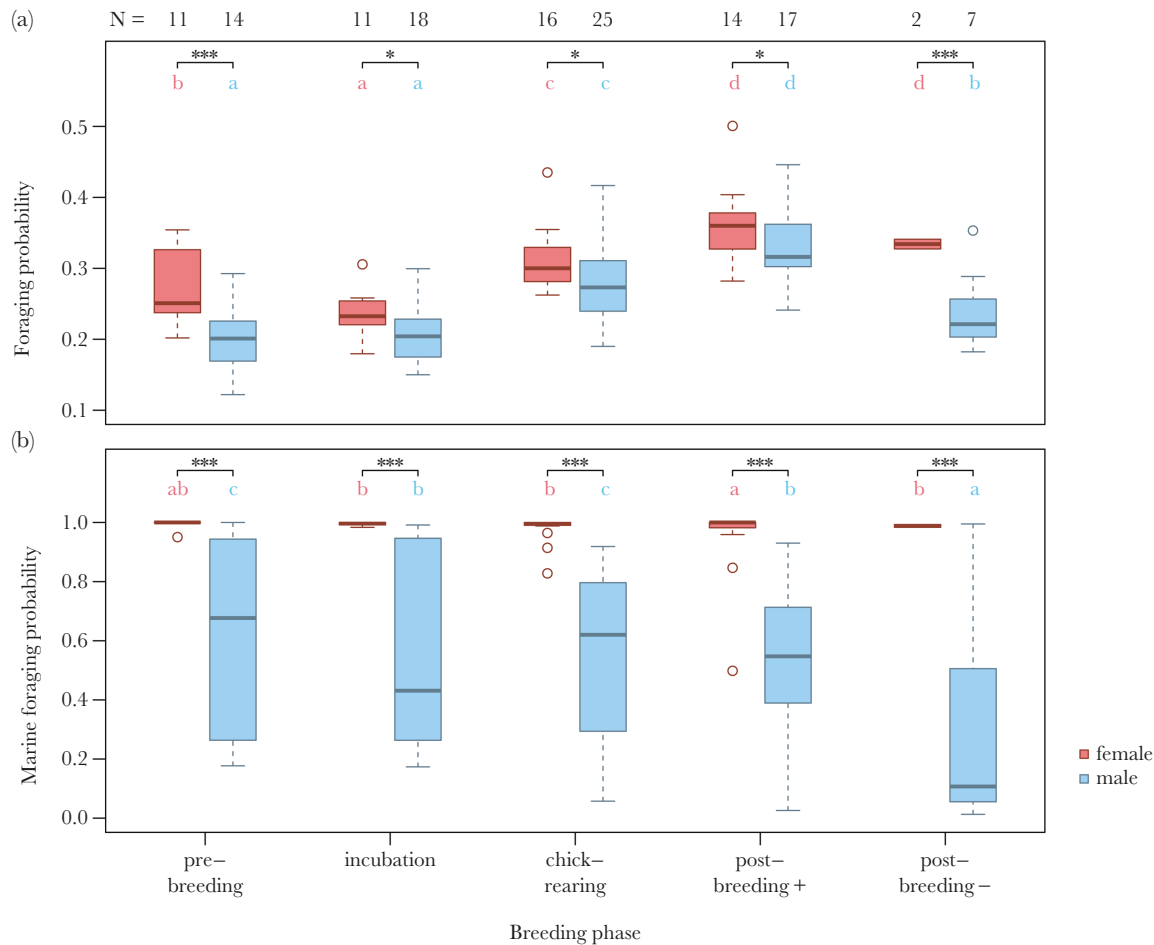


Figure 5
(a) Probability of foraging and (b) probability of foraging in marine (including brackish) water (as opposed to freshwater) as a function of sex and breeding phase, where “post-breeding +” and “post-breeding -” represent post-breeding after a successful and unsuccessful breeding attempt. Mean values per individual, year, and breeding phase are used in the boxplots, with sample sizes reflecting the number of bird years with available data per breeding phase. The significance of pairwise comparisons using the full models in Table 1 among breeding phases within each sex (colored letters) and between sexes within breeding phases (asterisks) are shown on top of the boxplots, where ***= $P < 0.001$, **= $P < 0.01$, *= $P < 0.05$, and n.s. = not significant.

Table 2
Model selection results for foraging trip frequency, duration, and distance in relation to sex and breeding phase

Model	K	$\Delta-2\log L$	ΔAIC_c	Akaike weight
(a) Foraging trip frequency				
phase + sex	5	1.92	0.00	0.51
phase * sex	6	0.00	0.10	0.49
phase	4	23.73	19.81	0.00
sex	4	134.82	130.89	0.00
c	3	150.77	144.83	0.00
(b) Foraging trip duration				
phase * sex	7	0.00	0.00	1.00
phase + sex	6	41.14	39.13	0.00
phase	5	58.01	53.99	0.00
sex	5	74.10	70.09	0.00
c	4	90.99	84.96	0.00
(c) Foraging trip distance				
phase * sex	7	0.00	0.00	1.00
phase + sex	6	29.49	27.48	0.00
sex	5	36.31	32.29	0.00
phase	5	45.85	41.84	0.00
c	4	52.72	46.69	0.00

Only the breeding phases “incubation” and “chick-rearing” were compared. ‘phase’=breeding phase and ‘c’=constant, referring to the ‘intercept-only’ model. Individual and year were included as random intercepts. Supported models are indicated in bold.

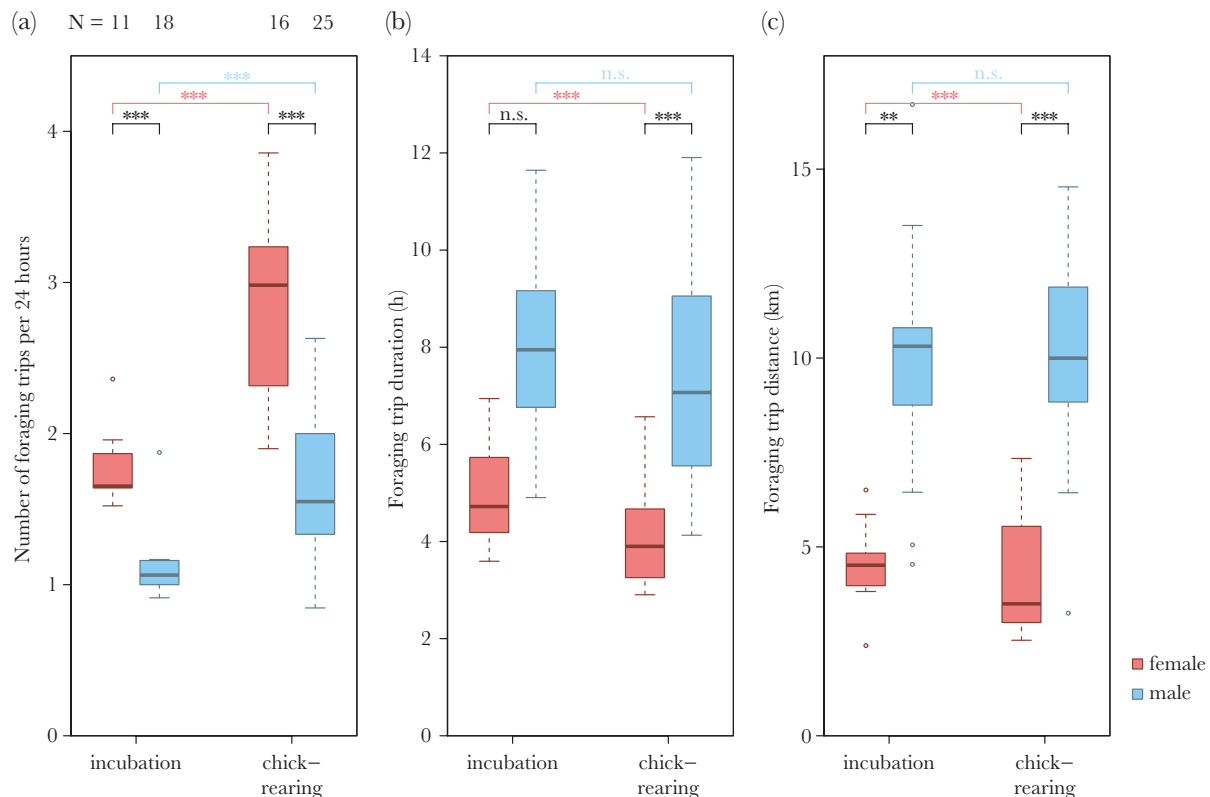


Figure 6

Number of foraging trips per 24 h (a), duration of foraging trips (b), and distance between the nest and the most distant location during a foraging trip (c) by females and males during incubation and chick-rearing. Only trips were included that contained at least one location in foraging habitat (water) during which the bird was predicted to be foraging. Sample sizes reflect the number of bird years with available data. The significance of pairwise comparisons using the full models in Table 2 are shown on top of the boxplots, where ***= $P < 0.001$, **= $P < 0.01$, *= $P < 0.05$, and n.s. = not significant.

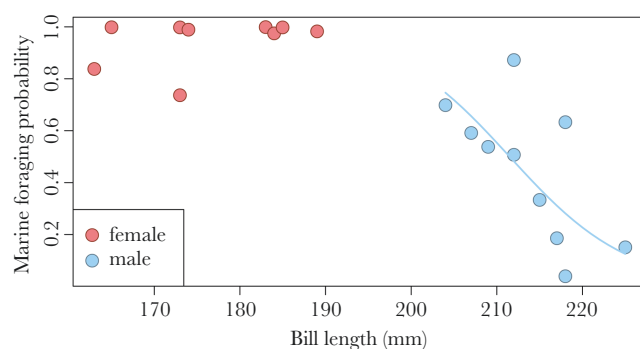


Figure 7

Relationship between bill length and probability of foraging in marine (including brackish) water of spoonbills breeding on Schiermonnikoog. Data are pooled across all breeding phases.

constrained to forage during the day. Consequently, females often have two distinct periods of the day when they can forage, separated by a period of high tide when females tend to return to the colony. Nevertheless, irrespective of whether it is caused by females foraging at less profitable sites, at less profitable times, or on less profitable prey, or because they have higher energetic demands or take a larger share in parental care, females overall work harder during the breeding season, as they spent more time foraging (and thus less time resting) than males.

We found that female spoonbills foraged almost exclusively in the nearby Wadden Sea, while males spent about half of their foraging time in more distant freshwater habitats in the shallow parts of Lake Lauwersmeer. This sex-specific habitat use was not only apparent during incubation and chick-rearing, but also during pre- and post-breeding, which makes it unlikely to be caused by spatial or temporal constraints or other factors related to parental care duties. Moreover, even though females may have different nutritional requirements during pre-breeding and incubation, as a result of preparing and recovering from egg production, this is unlikely to last throughout the entire breeding season. Our findings are, therefore, most likely explained by sex- and size-specific niche specialization, potentially (partly) caused by size-dependent foraging techniques, as supported by the finding that males with longer bills were significantly more likely to forage in freshwater habitats (Figure 7). Being larger and having a longer bill may be beneficial when foraging on fast-swimming pelagic fish that spoonbills predominantly catch in freshwater habitats, compared to foraging on “slower” ground-dwelling species (e.g., shrimp, flatfish, and gobies) that are the main prey species consumed in the Wadden Sea (Jouta et al. 2018). That smaller-billed females forage almost exclusively in marine habitats, irrespective of their bill length, suggests a certain threshold bill length below which foraging in marine habitats (on marine prey) is preferred. As such, size-dependent foraging techniques may result in sex-specific, and even individual-specific, niche specialization and thereby reduce intersexual and intraspecific competition.

To conclude, this study revealed a diel rhythm of nest attendance that was hardly affected by the tidal rhythm of nearby foraging opportunities. In addition, we found strongly sex-specific foraging ranges and habitat use that, rather than from constraints imposed by the rhythm of nest attendance or distance from the nest, most probably resulted from size-dependent foraging techniques and associated habitat (or prey species) preferences.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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AUTHOR CONTRIBUTIONS

Tamar Lok (Conceptualization [Equal], Data curation [Equal], Formal analysis [Lead], Funding acquisition [Supporting], Investigation [Equal], Methodology [Equal], Project administration [Supporting], Visualization [Lead], Writing—original draft [Equal], Writing—review & editing [Lead]), Matthijs van der Geest (Conceptualization [Equal], Data curation [Equal], Formal analysis [Supporting], Investigation [Equal], Methodology [Equal], Project administration [Equal], Visualization [Supporting], Writing—original draft [Equal], Writing—review & editing [Equal]), Petra de Goeij (Investigation [Equal], Methodology [Equal], Project administration [Equal], Writing—review & editing [Supporting]), Eldar Rakhimberdiev (Data curation [Equal], Formal analysis [Supporting], Methodology [Supporting], Resources [Lead], Writing—review & editing [Equal]), and Theunis Piersma (Conceptualization [Supporting], Funding acquisition [Lead], Methodology [Supporting], Project administration [Supporting], Writing—review & editing [Equal])

ETHICAL STATEMENT

This study was conducted under license numbers D6548 and AVD105002016446 following the Dutch Animal Welfare Act and followed the ethical standards of the Dutch Centre for Avian Migration & Demography.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY

Tracking data generated and analyzed in this study are stored at Movebank (www.movebank.org) in the study “SPOONBILL_METAWAD - Eurasian Spoonbills (*Platalea leucorodia*, Threskiornithidae) breeding on Schiermonnikoog, The Netherlands” (Movebank study ID 2596955604) and will be made available upon reasonable request.

Analyses reported in this article can be reproduced using the data provided by Lok et al. (2024).

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