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Sexual segregation in foraging behavior varies with breeding site and year in seabirds

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Abstract

In many animals, behavioral sex differences can produce spatial or temporal segregation, known as sexual segregation, which is thought to reduce competition and satisfy sex-specific physiological demands. In seabirds that engage in central-place foraging during the breeding season, such sexual segregation is likely to be accentuated by spatiotemporal constraints. Among the potential drivers of these behavioral sex differences are interannual variation in resource availability and environmental heterogeneity among breeding sites. However, it remains unclear whether sex differences in seabird foraging represent consistent species-wide traits or instead emerge only under particular local environmental conditions, because most studies focus on sexual size dimorphism or a single breeding site. We collected and analyzed GPS tracking data from streaked shearwaters (*Calonectris leucomelas*) breeding at three colonies located in oceanographically distinct regions (the Sea of Japan and the Pacific Ocean) from 2018 to 2024. We tested for sex differences by year and breeding site for behavioral metrics, including maximum distance from the colony, total travel distance, and behavioral states. In addition, we extracted oceanographic variables such as sea surface temperature and chlorophyll a concentration experienced by birds during each trip to evaluate their association with observed sex differences. Males were consistently larger than females, but behavioral sex differences were not universal. Clear sex differences in movement emerged mainly at the Sea of Japan colony, where birds can access both the Sea of Japan and the Pacific Ocean, whereas few or none were detected at colonies that forage exclusively in the Pacific. Patterns of sex differences varied among years within the same colony. Our findings indicate that the expression of behavioral sex differences varies with the spatial context in which birds forage, with clearer differences observed at colonies spanning multiple marine regions. By integrating multi-colony and multi-year data, this study highlights the importance of considering environmental context when evaluating sexual segregation in seabirds.

Introduction

Behavioral sex differences in animals can sometimes manifest as sexual segregation, where males and females differentially use space, time, or resources. Sexual segregation has been widely documented in birds, mammals, and reptiles [1, 2] and has been shown to enhance fitness [3]. Such behavioral differences likely evolved as adaptations to reduce intraspecific competition and meet sex-specific energetic demands and reproductive roles [4].

Central-place foraging animals including breeding seabirds must repeatedly carry resources back to a particular site, requiring them to forage within strict temporal and energetic constraints [5]. Under such spatial and temporal limitations, differences between the sexes in movement capacity, efficiency, and energetic demands are more likely to manifest as sex-specific foraging behaviors and resource use [6]. Consequently, resource utilization during the breeding season tends to reflect these sex differences. Moreover, when parental roles or offspring-rearing burdens differ between the sexes, foraging strategies may become further differentiated, potentially amplifying sexual differences [7].

In breeding seabirds, sexual differences have been reported in trip duration during the breeding season [8], home range size [9], and provisioning rates [10], which may result from sexual size dimorphism (SSD). This is particularly evident in species with pronounced SSD, where differences in behavior and resource use have been documented [7, 11]. Such size differences may contribute to sex-specific patterns through differences in foraging capacity, energetic requirements, or competitive exclusion. SSD can lead to variation in flight performance due to differences in body mass, wing length, and wing area. For example, larger males typically have higher wing loading (body mass divided by wing area), which is suited for fast, straight-line flight, whereas smaller females, with lower wing loading, are better able to generate lift at lower speeds and can fly efficiently in weaker wind conditions [12]. These morphological and aerodynamic differences may form the basis for sex-specific spatial use and foraging strategies.

Sexual segregation arising from SSD-related competitive exclusion or differences in locomotor ability may be influenced by environmental variability, particularly changes in oceanographic conditions and prey distribution [13]. For instance, in years with abundant food resources, males and females often share similar foraging areas, whereas in resource-poor years, spatial segregation may emerge as a strategy to avoid intraspecific competition, reflecting behavioral flexibility [14]. Moreover, the availability and spatial heterogeneity of marine resources accessible from the breeding colony also play a critical role. When the surrounding environment is relatively homogeneous, behavioral sex differences may not emerge. In contrast, when multiple distinct habitats are available, differences in movement capacity between sexes may lead to spatial segregation [7, 13]. Taken together, these observations suggest that sex differences in behavior are context-dependent and may vary according to environmental conditions. Therefore, to understand the influence of environmental variability, it is essential to examine sex differences in behavior across years with differing oceanographic conditions and among breeding colonies with different resource environments. However, most previous studies have focused on a single breeding site [15, 16], making it difficult to determine whether observed sex differences are universal traits across the species or are driven by local environmental conditions.

Streaked shearwaters (*Calonectris leucomelas*) are pelagic seabirds breeding in East and South-east Asia and have been reported to exhibit SSD, with males being generally larger than females [17]. However, the magnitude of SSD may vary among colonies, and such variation can translate into colony-specific behavioral consequences [12, 18]. During the incubation period, a previous study comparing Awashima Island (AW), Mikurajima Island (MI) and another colony (Sangan Islands) found colony-specific differences in incubation shift length, but no significant sex differences [19]. Furthermore, at AW, sex-specific differences have been reported in movement patterns during the chick-rearing period, with males and females differing in their probability of moving into the Pacific Ocean [20].

In this study, from 2018 to 2024, we deployed GPS loggers on streaked shearwaters breeding at three colonies located in oceanographically distinct regions of the Sea of Japan and the Pacific Ocean. The study populations included three breeding colonies: AW, which is located at a northern latitude, where birds forage in both the Sea of Japan and the Pacific Ocean; MI, which lies at a similar latitude, where birds forage exclusively in the Pacific Ocean; and Oshima Island (OS), which is also located at a similar

latitude to MI (Fig. S1). We first quantified SSD at each colony to confirm geographic variation in morphological differences and to examine whether such variation corresponds with sex-specific foraging behavior. Using data from 142 individuals across the three colonies, we evaluated (1) sex-specific differences in multi-scale foraging behavior, such as trip duration, home range and behavioral state, as previous studies in seabirds have reported that sex-specific differences can occur at finer spatial scales, such as foraging locations, even when no differences are observed at macro-scale (e.g., home range) [21–23]. We also evaluated (2) whether the presence or extent of sex differences varies by colony or year. Additionally, by calculating the oceanographic conditions experienced by the birds, sea surface temperature (SST) and chlorophyll-a concentration (Chl-a), we examined (3) whether sex differences are associated with oceanographic conditions. This integrative approach allows us to determine whether sex-specific behaviors represent consistent species-level patterns or emerge only under particular environmental settings.

Methods

Fieldwork

Fieldwork was conducted from August to October in 2018, 2019, 2023, and 2024 at three breeding sites in Japan: AW, Niigata Prefecture (38°28'N, 139°14'E); MI, Izu Islands (33°52'N, 139°14'E); and OS, Mie Prefecture (34°15'N, 136°36'E) (Fig. S1). Data collection years for each site were 2018, 2019, 2023, and 2024 for AW, 2018 and 2019 for MI, and 2023 and 2024 for OS. The sex of each individual was determined based on the pitch of vocalizations emitted during handling, with high-pitched calls indicating males and low-pitched calls indicating females [24].

GPS loggers were attached using one of two established methods, depending on the colony and research objectives for each year. At sites and in years where birds could be recaptured within several days—typically when multiple visits to the colony were permitted within a short period—loggers were attached using small strips of Tesa waterproof tape (Beiersdorf AG, Hamburg, Germany), a standard method for short-term deployments[25]. Tape-mounted loggers are commonly used for short-term deployments and enable high-frequency sampling over short intervals.

To obtain well-resolved behavioral information across multiple temporal scales, we deployed GPS loggers using a lightweight backpack-style harness made of 6-mm Teflon ribbon (TH-25; Bally Ribbon Mills, PA, USA). Because streaked shearwaters show substantial within-individual variability in foraging trip duration, destination, and route choice, short-term deployments may provide a biased representation of typical behavior. Long-duration deployments were therefore required to capture interannual variation during chick rearing, within-season changes, and large-scale post-breeding movements between Japan and equatorial regions. To minimize handling and disturbance to breeding colonies, the same individuals were used across multiple components of the project. The harness consisted of two soft ribbons loosely looped around the wings and joined by a small stainless-steel ring, allowing the logger to rest dorsally without contacting the skin or restricting movement. This design follows a configuration validated by

[24], who reported no adverse effects on reproduction or recapture rates. Consistent with these findings, individuals in our study showed no signs of injury or impaired movement. Because between-year recapture data were incomplete, the absence of interannual resighting cannot be interpreted as reduced survival.

Three types of GPS loggers were deployed: Axy-Trek (55 × 25 × 11 mm, 25 g; Technosmart, Italy), PinPoint VHF-GPS (38 × 32 × 14 mm, 20 g; Lotek Wireless, Canada), and GiPSy-remote (49 × 18 × 12 mm, 12.5 g; Technosmart, Italy). GiPSy units were enclosed in waterproof heat-shrink tubing prior to deployment. All devices weighed < 5% of the species' mean body mass. Sampling intervals differed among colonies for logistical and battery-life considerations (1–5 min at AW, 15 min at MI, and 5 min at OS).

Body mass (BM) was measured using a spring scale (PESOLA 1000 g, 5-g precision), and morphological traits were recorded using digital calipers (Mitutoyo CD-15PSX; 0.01-mm precision) for bill length (BL), bill depth (BD), head length (HL), and tarsus length (TL), and a ruler (1-mm precision) for natural wing length (WL).

Data processing

GPS data were processed following a standardized workflow to ensure positional accuracy and comparability across colonies and years. To remove physically implausible locations, we excluded positions for which the implied travel speed between consecutive fixes exceeded 70 km h^{-1} using the ddfilter function in the SDLfilter package [26, 27]. We removed low-accuracy locations by excluding points with a Horizontal Dilution of Precision (HDOP) > 7, following previous studies that showed that values above this threshold substantially reduce positional accuracy [28]. After filtering, all tracks were resampled at 15-minute intervals using the redisltraj function in the adehabitatLT package [29], which applies linear interpolation between consecutive GPS fixes to obtain regular 15-min trajectories and ensures the temporal spacing required for subsequent behavioral modelling.

Foraging trips were delineated using established criteria for streaked shearwaters. A trip was defined as the continuous movement beginning when an individual departed a 3-km radius around the colony, remaining outside this radius for more than 6 hours, and ending upon return within the same 3-km boundary. This definition follows [27], who demonstrated that streaked shearwaters typically initiate foraging before sunrise and return several hours before or after sunset, resulting in at-sea periods exceeding 6 hours. Tracks that did not meet these criteria, or that contained fewer than five resampled GPS positions due to data gaps or filtering during resampling, were excluded to ensure reliable estimation of movement descriptors.

For each trip, we initially calculated three movement metrics that are commonly used to describe seabird foraging behavior: trip duration, total travel distance, and maximum distance from the colony. Because these metrics are inherently correlated—trips that last longer also tend to involve greater travel distances

and greater offshore reach—we selected maximum distance from the colony as a representative measure of large-scale movement behavior for subsequent analyses. This metric captures the extent of offshore movement while avoiding redundancy among collinear variables. Maximum distance from the colony was estimated using a least-cost path approach implemented with the trans.mat and lc.dist functions in the marmap package [30], which determine the shortest feasible route avoiding land. The farthest point along this least-cost route was taken as the offshore extent of the trip.

Behavioral & spatial metrics

Behavioral states during each foraging trip were inferred using a Hidden Markov Model (HMM) implemented with the fitHMM function in the momentuHMM package [31]. The HMM used a 3-state model with gamma-distributed step lengths and wrapped-Cauchy turning angles, which is standard for seabird movement [31]. Fixes characterized by long step lengths and small turning angles were interpreted as directed travel, those with short step lengths and large turning angles as area-restricted search (ARS), and those with both short steps and small turning angles as resting behavior (Fig. S4).

For each foraging trip, we quantified four fine-scale behavioral metrics. First, we calculated (i) the proportion of fixes classified as ARS and (ii) the proportion classified as directed travel, reflecting the relative composition of behavioral states within each trip. Because trip duration varied substantially among trips, we additionally quantified (iii) the rate of ARS occurrence and (iv) the rate of directed travel occurrence, calculated as the number of GPS fixes classified as each behavioral state per hour of trip duration. Trip duration was defined independently of the number of GPS fixes and could not be inferred directly from fix counts because of variable sampling intervals, missing fixes, and trip delineation procedures. These four trip-level metrics were used to characterize fine-scale foraging and traveling behavior in subsequent analyses of sex differences.

Space-use patterns were quantified using kernel density estimation (KDE). All GPS coordinates were projected into the UTM coordinate system prior to analysis, and only foraging trips containing at least five resampled points were retained. KDEs were computed for each trip using the kernelUD function in adehabitatHR [22] on a 2.5 × 2.5-km grid. A grid of 2.5 × 2.5 km was chosen to balance spatial resolution with computational feasibility. Because smoothing parameters strongly influence UD estimation [32], we calculated the reference bandwidth (href) for each trip and used the overall mean value (h = 6.0 km) to standardize smoothing across individuals and colonies. From each utilization distribution (UD), we extracted the 95% and 50% contours, representing the bird's foraging range and core foraging area, respectively [33]. The areas of these contours (km^2) were used as spatial metrics in subsequent analyses.

To quantify spatial overlap between males and females, we calculated Bhattacharyya's Affinity (BA) [33, 34] between all pairs of trip-specific UD using the kerneloverlaphr function in adehabitatHR. Following standard practice, BA was computed using 95% UD to represent overlap in overall foraging ranges. From the resulting BA matrix, we extracted values corresponding to male–female trip pairs by matching

individual identities and sex labels. For ARS-only overlap, KDEs were recomputed using only GPS fixes classified as ARS by the HMM, using the same bandwidth (h = 6.0 km), and BA was recalculated using the same procedure.

We then evaluated whether opposite-sex overlap was lower than expected by chance using a permutation test following the procedure of [21], as applied in previous studies (e.g. [34]). Sex labels were randomly reassigned to trips 10,000 times, for each iteration, male–female pairs were redefined and their mean BA recalculated. The p-value was computed as the proportion of randomized means less than or equal to the observed opposite-sex mean BA. The same permutation procedure was applied to ARS-only BA values. All analyses were conducted separately for each colony and year to account for spatial and temporal heterogeneity in foraging distribution.

To quantify the oceanographic conditions experienced by birds during foraging, we focused on two environmental variables known to influence prey availability and seabird foraging behavior [35–38]: SST and Chl-a. SST affects the distribution of fish and planktonic prey [35], whereas Chl-a serves as a proxy for primary productivity [36].

Daily SST data were obtained from the NOAA Coral Reef Watch Operational Daily Near-Real-Time Global 5-km Satellite Coral Bleaching Monitoring Products (Dataset ID: dhw_5km), and daily chlorophyll-a data were obtained from the Chlorophyll (Gap-filled DINEOF), NOAA S-NPP / NOAA-20 VIIRS and Copernicus Sentinel-3A OLCI, Science Quality, Global 9-km, 2018–present, Daily dataset (Dataset ID: noaacwNPPN20S3ASCIDINEOFDaily). For each colony and year, all environmental layers corresponding to the GPS tracking period were downloaded, projected to the UTM coordinate system, and cropped to the spatial extent of the utilization distributions.

For each foraging trip, environmental conditions were summarized in two steps: (1) temporal aggregation, in which all daily environmental layers whose timestamps fell within the trip start and end times were extracted and averaged across days; and (2) spatial aggregation, in which the mean value of the temporally averaged raster was calculated within each bird's 95% and 50% utilization distribution (UD). Both 95% and 50% UD were used because broad-scale (95% UD) and core-use (50% UD) environments may reflect different ecological processes. Temporal averaging ensured that longer trips did not disproportionately reflect single-day anomalies, while spatial averaging across the UD captured the environmental conditions of the areas that birds were estimated to use during that trip. Raster extraction was performed using st_join in the sf package [37].

These trip-level summaries of SST and Chl-a concentration, quantified within the 95% and 50% utilization distributions, were then used as response variables to examine sex differences and their behavioral drivers.

Statistical analyses

We analyzed 1,072 foraging trips from 142 individuals (73 males and 69 females) across the three breeding sites (Table S1). All statistical analyses were performed in R v.4.4.2 [38]. Unless otherwise stated, Bayesian models were fitted using the brms package [39].

Guided by our a priori ecological hypotheses, we focused on two primary indicators of sex-specific behavior—spatial overlap and experienced oceanographic conditions—while other behavioral variables were treated as exploratory and are presented in the Supplementary Materials.

Sex differences in morphology

To quantify SSD, we modeled each morphological trait (BM, BL, BD, HL, TL, WL) using Gaussian Bayesian linear models. Fixed effects included sex, colony, and their interaction, while individual ID was included as a random intercept to account for repeated measurements. This structure allowed us to estimate whether SSD varied among colonies. Year was not included because measurements were taken only once per individual per season, providing insufficient within-year replication for reliable estimation of year effects.

Sex differences in large-scale movement behavior (trip metrics)

Trip duration, total travel distance, and maximum distance from the colony were initially calculated for each foraging trip. Because these metrics were strongly collinear, we used maximum distance from the colony as a representative descriptor of large-scale movement behavior in subsequent statistical analyses.

For large-scale movement metrics (maximum distance from the colony), we fitted hierarchical gamma regression models with a log link. Fixed effects were sex, colony (Site), and their interaction. To account for interannual variation within colonies, we included random intercepts and random slopes for sex at the colony–year level, as well as a random intercept for individual identity.

These analyses were treated as exploratory, complementing the primary analyses of spatial overlap by identifying contexts in which sex differences in large-scale movement emerged.

Sex differences in fine scale behavioral states

To test for sex differences in fine-scale behavior, we analyzed four trip-level response variables derived from the HMM state classification: (1) the proportion of fixes in ARS, (2) the proportion of fixes in directed travel, (3) the duration of ARS expressed as a ratio of total trip time, and (4) the duration of directed travel expressed as a ratio of total trip time.

Fixed effects included sex, colony (Site), and their interaction, allowing us to test whether sex differences were consistent across colonies. To account for variability among colony–year combinations, we included a random intercept and random slope for sex at the colony–year level. In addition, a random intercept for logger identity was included to account for repeated measurements arising from devices. All models were fitted assuming Gaussian error distributions. Model diagnostics—including inspection of Markov chain convergence—confirmed adequate performance.

Sex differences in spatial overlap

Sex-specific differences in space use were assessed using BA calculated between all pairs of trip-level 95% UD. Analyses were performed separately for each colony and year to reflect the ecological independence of breeding seasons and distinct oceanographic regimes.

For each colony–year, we calculated the mean BA for male–female trip pairs. To test whether opposite-sex overlap was lower than expected by chance, we performed a permutation test in which sex labels were randomly reassigned to trips (10,000 iterations), holding the number of male and female trips constant. For each permutation, male–female BA values were recomputed and averaged. The one-tailed p-value was defined as the proportion of permutations in which the randomized mean BA was less than or equal to the observed value.

Because spatial segregation may differ between broad-scale travel routes and fine-scale foraging locations, we repeated the same permutation procedure using ARS-only 95% UD, enabling comparison between overlap in overall foraging ranges versus overlap in core foraging behavior.

Permutation results are presented for each colony–year (Table 2). No additional multiple-testing correction was applied, as BA patterns were interpreted as context-dependent and used to identify ecological scenarios under which sexual segregation emerged, rather than to infer species-wide effects.

Table 1
Sample sizes of individuals and foraging trips by site and year.

Site	Year	Sex	No. of individuals	No. of foraging trips
AW	2018	Female	19	140
		Male	20	149
	2019	Female	18	76
		Male	17	87
	2023	Female	5	54
		Male	5	37
	2024	Female	8	16
		Male	8	29
MI	2018	Female	5	32
		Male	10	58
	2019	Female	5	14
		Male	14	62
OS	2023	Female	6	91
		Male	4	47
	2024	Female	11	106
		Male	5	74

Note that 14 individuals were tracked across multiple years; thus, the number of individuals shown for each year represents the cumulative total. AW, MI, and OS indicate Awashima Island, Mikurajima Island, and Oshima Island, respectively.

Table 2
Sex differences in movement, space use, and oceanographic conditions by site and year.

Site	Year	Maximum distance from the colony	Overlap in 95% UD p-value	Overlap in 95% ARS UD p-value	SST in 95% UD	Chl-a in 95% UD	SST in 50% UD	Chl-a in 50% UD
AW	2018	**m > f**	0.07	0.21	**m < f**	N.S.	**m < f**	N.S.
	2019	N.S.	**0.01**	**0.01**	**m < f**	N.S.	**m < f**	N.S.
	2023	**m > f**	**< 0.01**	**< 0.01**	**m < f**	N.S.	**m < f**	N.S.
	2024	N.S.	**< 0.01**	**< 0.01**	**m < f**	N.S.	**m < f**	N.S.
MI	2018	N.S.	**0.04**	0.07	N.S.	N.S.	N.S.	N.S.
	2019	N.S.	0.25	0.39	N.S.	N.S.	N.S.	N.S.
OS	2023	N.S.	0.32	0.44	N.S.	**m < f**	N.S.	**m < f**
	2024	N.S.	**0.01**	0.15	N.S.	N.S.	N.S.	**m < f**

"m > f" indicates that males had higher values than females; "m < f" indicates that males had lower values than females; "N.S." indicates no significant difference. SST refers to sea surface temperature and Chl-a to chlorophyll *a* concentration. Bold text indicates statistically significant sex differences or spatial overlap/segregation. AW, MI, and OS indicate Awashima Island, Mikurajima Island, and Oshima Island, respectively.

Sex differences in experienced oceanographic conditions

To evaluate whether males and females experienced different oceanographic conditions during foraging, we modeled the environmental values extracted from each trip's UD. For each trip, both the 95% UD (representing the full movement extent) and the 50% UD (representing core-use areas) were used to summarize SST and Chl-a, two variables closely linked to prey availability and previously shown to influence the foraging behavior of Procellariiformes seabirds. Using both UD scales allowed us to capture broad- and fine-scale environmental conditions that may differentially reflect sex-specific space use.

For each environmental variable and UD scale, we fitted hierarchical Bayesian linear models. Because UD-based environmental summaries can contain multiple pixels per trip, we generated one environmental value per trip by averaging all raster-extracted values within each UD polygon (i.e., each trip contributed a single mean SST or mean Chl-a value). This ensured that every trip was represented by an equal number of observations and prevented pseudoreplication arising from multiple spatial samples within a single trip.

Fixed effects included sex, colony (Site), and their interaction, allowing us to test whether sex differences were consistent across colonies. To account for variability among colony–year combinations, we included a random intercept and random slope for sex at the colony–year level. In addition, a random

intercept for logger was included to account for repeated measurements arising from devices. All models were fitted assuming Gaussian error distributions. Model diagnostics—including inspection of Markov chain convergence—confirmed adequate performance.

Results

AW birds used coastal waters along both the Sea of Japan and the Pacific side of northern Japan. The MI birds ranged widely, from offshore areas east of Honshu to waters off eastern Hokkaido in the Pacific. The OS birds primarily foraged in coastal areas of central Japan along the Pacific Ocean, but some individuals also reached northern Pacific waters near Hokkaido (Fig. 1).

Males were significantly larger than females in all morphological traits, including BM (Table S3; Figs. 2, S3). The degree of SSD was similar across all breeding sites, as indicated by 95% credible intervals for the sex × colony interaction terms that included zero. In contrast, absolute body size varied among breeding sites, with females from MI having lower BM and shorter HL than those from AW. Additionally, females from OS had smaller bill depths compared to those from AW (Table S3).

In AW, males reached greater maximum distances from the colony than females in 2018 and 2023. No sex differences were observed in maximum distance from the colony in the MI and OS in any year (Table 2).

In AW, males and females were significantly spatially segregated in 2019, 2023, and 2024 (2019: mean BA = 0.19, $p < 0.01$; 2023: mean BA = 0.33, $p < 0.01$; 2024: mean BA = 0.15, $p < 0.01$), whereas their home ranges overlapped in 2018 (mean BA = 0.33, $p = 0.07$ (Table 2; Fig. S6). In the MI, male and female home ranges overlapped in 2019 (mean BA = 0.38, $p = 0.25$) but were spatially segregated in 2018 (mean BA = 0.41, $p = 0.04$) (Table 2; Fig. S6). In the OS, overlap was observed in 2023 (mean BA = 0.41, $p = 0.32$), whereas significant spatial segregation occurred in 2024 (mean BA = 0.38, $p = 0.01$) (Table 2; Fig. S6).

At AW in 2018, males exhibited a significantly higher rate of directed travel (per hour) and a lower proportion of GPS fixes classified as ARS than females, while ARS zones overlapped spatially between sexes (mean BA = 0.32, $p = 0.21$; Table S4; Fig. 3). No significant sex differences were detected in the rate of ARS occurrence or in the proportion of directed travel (Table S4). In 2019, ARS zones were spatially segregated between sexes (mean BA = 0.11, $p = 0.01$), but no sex differences were observed in the proportion of ARS-classified fixes, the rate of ARS occurrence, the proportion of directed travel, or the rate of directed travel (Table S4). In 2023, males showed a significantly lower proportion of ARS-classified fixes than females (Table S4), and ARS zones were spatially segregated (mean BA = 0.29, $p < 0.01$). However, no sex differences were detected in the rate of ARS occurrence, the proportion of directed travel, or the rate of directed travel (Table S4; Fig. S7). In 2024, ARS zones were again spatially segregated (mean BA = 0.07, $p < 0.01$), but none of the ARS or directed travel metrics differed significantly between sexes (Table S4; Fig. S7). At MI, ARS zones overlapped between sexes in both 2018 (mean BA = 0.15, $p = 0.07$) and 2019 (mean BA = 0.12, $p = 0.39$; Table S4; Fig. 3). No significant sex differences were detected in the proportion of ARS-classified fixes, the rate of ARS occurrence, the

proportion of directed travel, or the rate of directed travel in either year (Table S4; Fig. S7). At OS, ARS zones overlapped between sexes in both 2023 (mean BA = 0.36, p = 0.44) and 2024 (mean BA = 0.33, p = 0.15; Table S4; Fig. 3). No significant sex differences were detected in any of the behavioral metrics in either year (Table S4; Fig. S7).

In AW, males consistently used cooler SSTs than females across both the 95% and 50% UD in 2018, 2019, 2023 and 2024 (Table 2, Fig. S8). In MI, no significant sex differences were found for any environmental variable in either year (Table 2, Fig. S8). In OS, females consistently used higher Chl-a waters than males in 2023 in both UD scales, whereas in 2024 sex differences were detected only for the 50% UD, with females using higher Chl-a concentrations than males (Table 2; Fig. S8).

Discussion

We investigated whether behavioral sex differences in seabirds represent species-wide traits or vary in response to environmental context, by analyzing 142 streaked shearwaters breeding at three colonies with different oceanographic conditions. Despite consistent male-biased body size, clear behavioral sex differences were concentrated at AW, the only colony where birds can exploit both the Sea of Japan and the Pacific Ocean. These results suggest that sex differences in the behavior of seabirds may not represent inherent species-level traits nor be solely driven by SSD but might instead emerge in response to local environmental conditions [34, 40]. Therefore, any discussion of the presence or magnitude of sex differences should consider the influence of local oceanographic conditions around breeding sites and interannual variability.

While no sex differences in movement metrics such as maximum distance from the colony were observed in the Pacific colonies of OS and MI, sex differences were detected in AW, located in the Sea of Japan, in some years. This may reflect differences in foraging environments: whereas birds from OS and MI forage exclusively in the Pacific Ocean—dominated by the Kuroshio and Oyashio Currents—AW individuals exploit both the Pacific and the Sea of Japan, the latter influenced by the Tsushima Current and characterized by more variable oceanographic conditions (Fig. S1). These results suggest that when multiple distinct foraging environments are available, differences in movement capacity associated with body size may be more likely to translate into detectable sex differences [41]. Environmental heterogeneity may also help explain why spatial segregation of home ranges occurred only in certain years, even within the relatively homogeneous Pacific colonies. In both OS and MI, males and females exhibited segregation at the home-range scale (95% UD) in some years but not others (Fig. 2). Such year-to-year variation is consistent with a scenario in which predictable and abundant prey promote spatial overlap between sexes, whereas more dispersed or less predictable resources promote divergence in space use depending on movement capacity [42]. Importantly, our results do not indicate a consistent sequence in which sex differences emerge from fine-scale behaviors (e.g., ARS patterns) to broader movement metrics. Instead, the scale at which sex differences become detectable appears to vary across colonies and years, likely reflecting context-dependent interactions between resource distribution, environmental variability, and sex-specific movement capacities. Although trip duration and maximum

distance have traditionally been used as indicators of sexual differences in seabird movement [43, 44], our findings highlight that sex-specific space use can manifest at different spatial scales depending on ecological conditions.

Two main hypotheses have been proposed to explain the emergence of sex differences in behavior: competitive exclusion due to SSD, and differences in movement capacity. Regarding competitive exclusion, for example, in Scopoli's shearwater (*Calonectris diomedea*), males tend to exploit nearby resources under deteriorating environmental conditions, while females are displaced and forage over longer distances and broader areas [13]. Similar patterns have been suggested in African penguin (*Spheniscus demersus*) and Adélie penguin (*Pygoscelis adeliae*), where females forage over larger areas and at different depths during the breeding season under limited foraging space and resource conditions, likely due to competitive exclusion [45, 46]. While no behavioral sex differences were observed in most colonies and years in our study, males with larger body size tended to travel farther than smaller females in some years at AW. This result contrasts with previous studies that support the competitive exclusion hypothesis and instead may be better explained by differences in movement capacity.

Regarding movement capacity, the sex with larger body size and higher wing loading generally has greater movement capacity and energy requirements and tends to undertake longer trips to access productive foraging sites [47]. Males of wandering albatrosses (*Diomedea exulans*), which are larger in body size, tend to travel farther and reach more productive areas than females [48]. In our study, during particular years at AW, males exhibited greater maximum distances from the colony than females. Additionally, males in this population experienced lower SST than females, as these conditions are typically associated with higher primary productivity and greater availability of prey such as small fish and plankton [36]. Our results suggest that movement capacity related to body size may contribute to behavioral sex differences, facilitating males' access to more productive marine environments than females. Additionally, a geographic barrier—the Tsugaru Strait—between the Sea of Japan and the Pacific Ocean may contribute to the observed behavioral sex differences, as these were mainly detected at AW, where individuals utilize both oceanic regions. At AW, sex-specific differences in movement patterns have been demonstrated, such as differing probabilities of traveling to the Pacific Ocean [20]. While males consistently crossed the strait, females appeared more affected by wind conditions due to their smaller body size, potentially leading to more restricted home ranges in certain years [20]. However, it is noteworthy that females did access the Pacific Ocean in nearly all years, indicating that such movement is possible under favorable conditions. This interannual variation in the frequency with which females accessed the Pacific suggests that female movement behavior, rather than a fixed capacity difference, plays a pivotal role in determining whether behavioral sex differences emerge. Specifically, our results suggest that when females more frequently reach productive foraging grounds in the Pacific, behavioral sex differences may be reduced, whereas in years when fewer females do so, such differences may become more evident.

At the Pacific colonies, even when sex differences in home-range size were observed, no significant differences emerged in core foraging locations or behavioral metrics, suggesting that males and females exhibited broadly similar foraging behavior. In MI, males and females differed in their broad-scale movement ranges in 2018 (95% UD), whereas their core-use areas overlapped (50% UD). This pattern suggests that the two sexes may have traveled through partially different routes or ranges but ultimately converged on similar core foraging areas. A comparable mismatch between large-scale travel patterns and fine-scale foraging locations has been reported in red-footed boobies (*Sula sula*), where males and females use different movement strategies en route yet exploit similar foraging zones [49]. Our results may reflect a similar mechanism although we did not track flight paths at a resolution sufficient to evaluate route-level differences directly. Such convergence in foraging location despite differences in home-range extent implies that both sexes may be concentrating on a limited number of high-quality foraging sites. Indeed, individuals from MI frequently reached productive waters near Hokkaido [50, 51], suggesting that both sexes may have targeted the same profitable foraging grounds.

Environmental variables showed colony- and year-specific patterns in sex differences. Across all years at AW, males consistently tended to use cooler waters (lower SST) than females, whereas no sex differences were detected in Chl-a. This pattern is consistent with males traveling farther offshore or reaching Pacific waters more frequently, where SST is lower, but productivity is not necessarily higher. In MI, no sex differences in any oceanographic variable were observed, supporting the interpretation that both sexes accessed similar foraging environments in this relatively homogeneous region. In OS, sex differences emerged only in Chl-a, and only in certain years (e.g., higher Chl-a used by females in the 50% UD in 2024). These intermittent differences suggest that fine-scale productivity patches, rather than broad-scale temperature structure, may underlie sex-specific habitat use in this colony. Collectively, these results reinforce that sex differences in environmental use are highly context-dependent, varying not only among colonies but also across years and environmental variables.

Conclusion

This study revealed that sex differences in seabird behavior are not universal traits of the species but rather vary depending on breeding site and oceanographic conditions [40]. Such context dependence suggests that size-related differences in movement capacity may contribute to behavioral variation under certain environmental conditions, particularly when birds can access multiple distinct marine habitats. We captured the variability in sexual differences that may be overlooked when focusing on a single site or year, highlighting the importance of evaluating sexual segregation under diverse environmental contexts [13]. Additionally, in regions with relatively homogeneous environments, sex differences tended to be less evident. Previous studies have shown that behavioral differences between sexes tend to diminish in years with abundant food resources and become more pronounced in years with limited resources [13, 52], and that extreme weather events driven by climate change can temporarily create sex-specific foraging conditions [53]. Future studies incorporating finer-scale indicators—such as oceanic frontal structure or wind fields—may help clarify the mechanisms underlying sex-specific foraging behavior. Overall, our findings underscore that sexual segregation in seabirds is

highly context-dependent, and understanding its drivers requires broad spatial and temporal perspectives.

Additional_file 1: Supplementary Figures. (PDF)

Additional_file 2: Supplementary Tables. (PDF)

Description: Additional figures and table supporting the main analyses.

Declarations

Ethics approval and consent to participate

All experiments were approved by the Animal Experimental Committee of Nagoya University (GSES 2018–2024), as well as by the Awashimaura Village Office, Niigata Prefecture; the Kihoku Town Office, Mie Prefecture; and the Mikurajima Village Office, Tokyo.

Consent for publication

Not applicable.

Competing interests

The authors declare no conflict of interest.

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Author Contribution

C.Y. and K.Y. conceived the ideas and designed the methodology. C.Y., K.S., W.T., and S.K. collected the data. C.Y. and Y.G. analyzed the data. All authors contributed to drafting the manuscript. All authors provided critical feedback and approved the final version for publication.

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Data Availability

The dataset collected at Awashima Island (2018–2024) is available from Biologging intelligent Platform (BiP; https://www.bip-earth.com/ja). The datasets obtained at Oshima Island (2023–2024) and Mikurajima Island (2018–2019) are available from the corresponding author(s) upon reasonable request.

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Figures

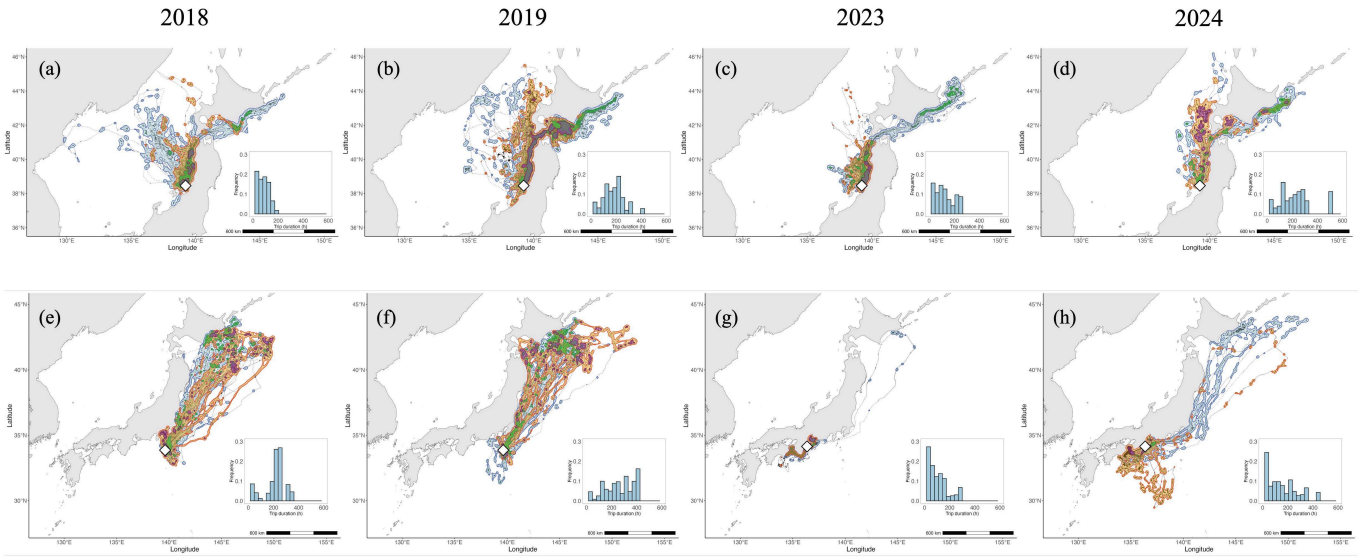


Figure 1

Sex-specific utilization distributions and GPS tracks across breeding sites.

UD colors indicate sex: orange represents female 95% UD, purple represents female 50% UD, light blue represents male 95% UD, and green represents male 50% UD. White circles indicate colony locations, gray areas indicate land, and the black line represents a 500 km scale bar. Histograms within each map show the distribution of trip durations (hours), with the x-axis representing trip duration and the y-axis representing proportion. Panels (a)–(d) show data from Awashima Island, (e) and (f) from Mikurajima Island, and (g) and (h) from Oshima Island.

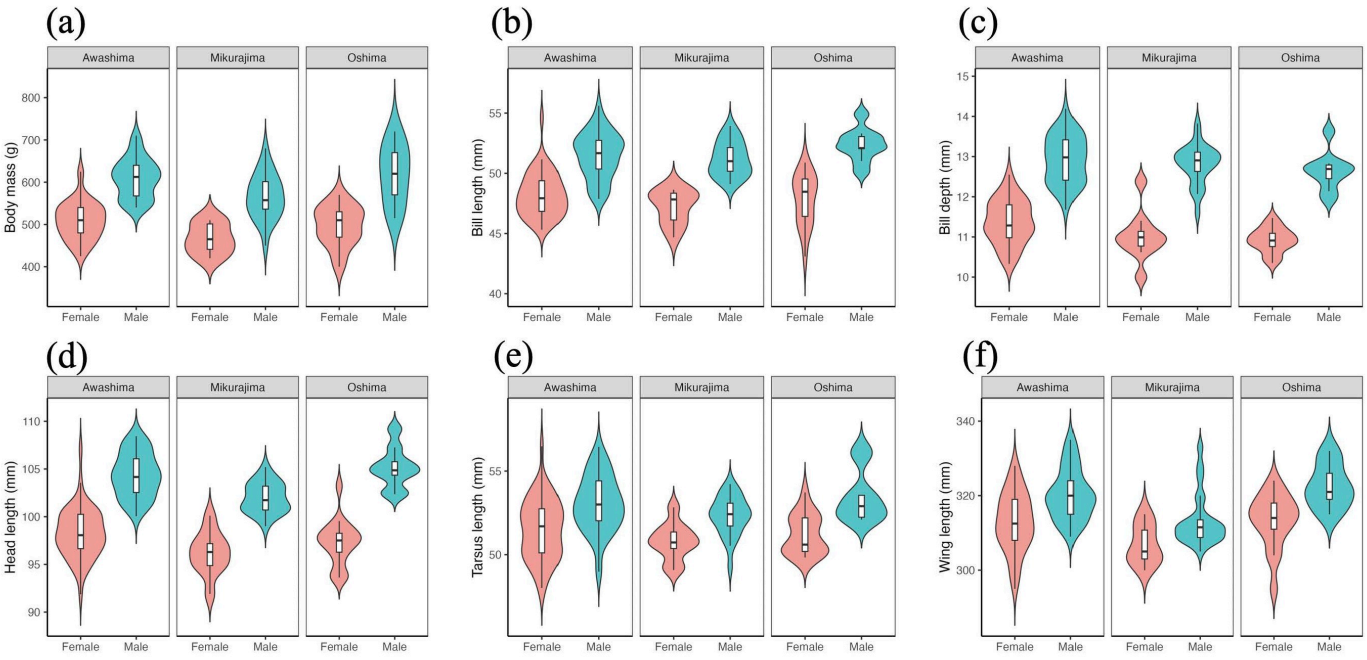


Figure 2

Sex differences in body mass and morphological traits across breeding sites.

Panel (a) shows body mass (BM); (b) bill length (BL); (c) bill depth (BD); (d) head length (HL); (e) tarsus length (TL); and (f) wing length (WL).

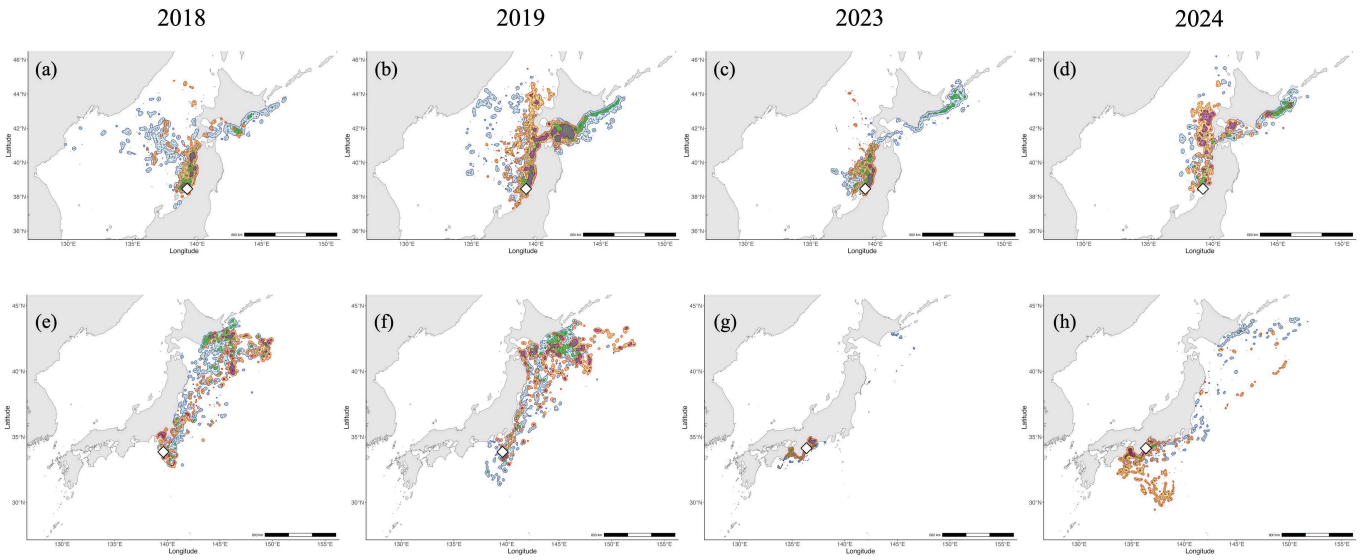


Figure 3

Sex-specific ARS (area-restricted search) distributions and core foraging areas across breeding sites.

UD colors indicate sex: orange for female 95% UD, purple for female 50% UD, light blue for male 95% UD, and green for male 50% UD. White circles represent colony locations, gray areas represent land, and the black line indicates a 500 km scale bar. Panels (a)–(d) show data from Awashima Island, (e) and (f) from Mikurajima Island, and (g) and (h) from Oshima Island.

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