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Abstract  Sex-related differences in foraging habitat are common among seabirds. Streaked Shearwaters Calonectris leucomelas breeding on Awashima Island in the Sea of Japan are considered to exhibit gender differences in foraging habitat: only males cross the windy Tsugaru Strait into the Pacific Ocean. Since males are larger, with greater wing loading than females, winds are expected to increase the effect of sexual size dimorphism on their flight performance, which may determine accessibility to foraging habitats. To assess the sex-related differences in foraging movements among years in which environmental and wind conditions differed, we analyzed foraging trips of male (N=243) and female (N=241) Streaked Shearwaters during the chick-rearing period by using GPS loggers in 2011, 2012, and 2013. Both males and females were found to travel through the Tsugaru Strait into the Pacific Ocean, but the frequency was higher for males than for females. Nevertheless, we found that wind velocities had no effect on the probability of transiting the Tsugaru Strait. Greater wing loading requires higher energy demands for flight; therefore, males possibly needed to travel into the Pacific Ocean to feed on the energy-rich Pacific Saury Cololabis saira. In 2012, when the sea surface temperature (SST) in the Sea of Japan was the highest among the three study years, the frequency of foraging in the Pacific Ocean was similar for males and females. Shearwaters are considered to forage in association with predatory fish, the distribution of which is largely influenced by the Tsushima Warm Current migrating partially into the Tsugaru Strait. Hence, both males and females were more likely to travel into the Pacific Ocean when the Sea of Japan SST was high, generating conditional sex-related differences in foraging habitat.

Key words Calonectris leucomelas, GPS, Sex-related difference, Tsugaru Strait, Wind
et al. 2002, 2005; Weimerskirch et al. 2012), thereby resulting in competitive exclusion between the sexes (González-Solís et al. 2000, 2008). In addition, winds are expected to increase the effect of sexual dimorphism in size on flight performance, which determines the accessibility of foraging habitats for flying seabirds (Shaffer et al. 2001; Phillips et al. 2004; Weimerskirch et al. 2012).

Previous studies of the Streaked Shearwater Calonectris leucomelas population breeding on Awashima Island in the Sea of Japan have assessed their at-sea distribution during the incubation period and found that only males transited the Tsugaru Strait into the Pacific Ocean (Yamamoto et al. 2012). In this study, we investigated the sex-related differences in foraging movements during their chick-rearing period. Male Streaked Shearwaters are larger bodied and have higher wing loading than females (Shirai et al. 2013; Yamamoto et al. 2016); thus it was considered possible that differences in foraging habitat might become obvious when the shearwaters traveled long distances to the Pacific Ocean, owing to differing flight abilities or energy requirements because of their sexual size dimorphism. The wind characteristics of the Tsugaru Strait were also considered as another factor possibly driving the sexual difference. Strong winds prevail in the strait, resulting from a large thermal contrast between the cooler air over the Pacific Ocean and the warmer air over the Sea of Japan (Shimada et al. 2010). The wing loading of seabirds is considered to be a key characteristic in relation to wind strength (Shaffer et al. 2001; Suryan et al. 2008, Navarro et al. 2009); hence, winds in the strait might act as an environmental barrier (Suryan et al. 2008; Navarro & González-Solís 2009) restricting foraging movements, especially of females.

The aim of this study was first to describe sex-related differences in shearwater foraging trips in relation to differing environmental and wind conditions, and second to determine the effect of wind velocity on the passage of the Tsugaru Strait, as a determination of sex-related differences in foraging habitat.

**MATERIALS AND METHODS**

1) **Fieldwork**

Fieldwork was performed on Awashima Island (38°28′N, 139°14′E; Niigata, Japan) located in the Sea of Japan between mid-August and early October in 2011, 2012, and 2013 (Fig. 1). We attached GPS loggers (GiPSy-2, 37×16×4 mm or GiPSy-4, 37×19×6 mm; TechnoSmArt, Roma, Italy) to the back feathers of chick-rearing Streaked Shearwaters with Tesa® tape (Beiersdorf AG; GmbH, Hamburg, Germany) and cyanoacrylate glue (Loctite® 401; Henkel Ltd., Hatfield, UK). The loggers were housed in waterproof heat-shrink tubing and set to record one...
fix per minute. The total weight of the unit was 25 g, which was less than 5% of the mean mass of the birds in our study (mean±SD: 555±68 g, N=112) in accordance to the suggested load limit for flying seabirds (e.g., Phillips et al. 2003). The sex of the birds was determined based on their vocalizations during handling; males give high-pitched calls, whereas females give low-pitched calls (Arima et al. 2014).

One hundred and fifty-one GPS loggers were deployed: 34 in 2011 (on 17 males, and 17 females), 59 in 2012 (31 males; 28 females), and 58 in 2013 (30 males; 28 females). After approximately 11 days (range 4–20 days) of deployment, we recaptured and retrieved the loggers. The recovery rate was 75–100%, with 29 recovered in 2011 (16 males; 13 females), 52 recovered in 2012 (31 males; 21 females), and 51 recovered in 2013 (25 males; 26 females) (Table 1). Some of the retrieved loggers had failed to record data; hence location points were only available for 25 birds in 2011 (12 males; 13 females), 46 birds in 2012 (28 males; 18 females), and 41 birds in 2013 (18 males; 23 females).

During fieldwork in 2011, we randomly selected 50 Streaked Shearwaters (26 males and 24 females) from which to estimate wing loading. For each individual, body mass was measured using a 1 kg spring balance, and wing area was estimated by spreading the right wing over a board (a ruler was placed alongside for reference) and photographing it. The interwing area (i.e., the root box) was measured using a ruler.

### 2) Data analysis

We defined foraging trips as the time birds spent beyond a 3-km buffer zone around the colony. The buffer zone was set in order to exclude location fixes of birds resting on the sea surface off the island’s coast after departing from and before arriving at the nest. To determine the effects of wind on shearwaters passing into the Pacific Ocean, we first selected tracks that reached a distance of 100 km from the line between Cape Tappi (the tip of the Tsugaru Peninsula) and Cape Shirakami (the southernmost tip of the Oshima Peninsula; Fig. 1) which represents a gateway into the windy Tsugaru Strait (Matsuzaka et al. 2003; Yamaguchi et al. 2006). Next, we divided foraging trips into two types, based on whether the birds crossed (assigned as 1) or did not cross over (assigned as 0) the entrance to the strait. Some birds approached the entrance line, but did not immediately cross it, and returned later and crossed it during the same trip. Hence, some trips included “crossed” or “not crossed” more than once (the time between approaches was 29.7±17.3 h; range 6.5–68.5 h, N=13) excluding an extraordinary case of 173.5 h.

The 30-min mean wind direction and speed data corresponding to the time of each approach to the line were obtained from the Japan Oceanographic Data Center (at the Tappizaki and Matsumae meteorological stations: http://www.jodc.go.jp/jodcweb/index_j.html, accessed on 29 November 2016). There was a strong correlation between the wind velocities recorded at the two meteorological stations (Pearson’s r=0.86, P<0.01); the data were averaged for further analysis. Westerly and easterly winds are dominant in the Tsugaru Strait (Yamaguchi et al. 2006); therefore, we calculated westerly (assigned as negative values) and easterly (assigned as positive values) wind components following the formula reported by Garthe et al. (2007). The difference between the flight direction of the birds and the wind direction was considered to be 60° in the formula, which represents the angle of the strait between the Sea of Japan and the Pacific Ocean. Westerly winds correspond

<table>
<thead>
<tr>
<th>Year</th>
<th>Sex</th>
<th>No. of recover/attachment</th>
<th>No. of foraging trips</th>
<th>Foraging trip duration</th>
<th>Maximum foraging distance from the colony</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>Male</td>
<td>16/17</td>
<td>64</td>
<td>2.0±1.8 days (1–8 days)</td>
<td>149±184 km (19–1,013 km)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>13/17</td>
<td>65</td>
<td>2.2±1.7 days (1–7 days)</td>
<td>121±127 km (9–556 km)</td>
</tr>
<tr>
<td>2012</td>
<td>Male</td>
<td>31/31</td>
<td>92</td>
<td>3.2±3.1 days (1–15 days)</td>
<td>244±292 km (14–1,097 km)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>21/28</td>
<td>58</td>
<td>2.9±2.7 days (1–14 days)</td>
<td>158±157 km (14–554 km)</td>
</tr>
<tr>
<td>2013</td>
<td>Male</td>
<td>25/30</td>
<td>87</td>
<td>2.3±2.0 days (1–11 days)</td>
<td>178±188 km (17–753 km)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>26/28</td>
<td>118</td>
<td>1.9±1.8 days (1–9 days)</td>
<td>115±114 km (17–658 km)</td>
</tr>
</tbody>
</table>
to downwind and easterlies to upwind, for birds heading to the Pacific Ocean. The monthly mean sea surface temperature (SST) within 100 km of the colony in September 2011–2013 (0.025° resolution; Aqua-MODIS) was also downloaded via NOAA’s BloomWatch180 (http://coastwatch.pfeg.noaa.gov/browsers/cwbrowser_global180.html, accessed on 29 November 2016) to compare the marine environment condition among the years.

The total wing area (S) is the area of the wing (photographed)×2+inter-wing area (Pennycuick 2008). Wing area was estimated using Image J (Wayne Rasband, US). Wing loading (a measure of force per unit area) was calculated as [(mass×gravity)/S], and expressed as Newton (N)·m⁻² (assuming gravity=9.81 m·s⁻²).

Spatial data were analyzed using ArcGIS 10.2.2 (ESRI, Redlands, CA, USA), and statistical analyses were performed using R version 3.2.2 (R Development Core Team 2014). The area of 100 km from the line between capes Tappi and Shirakami was generated using the ArcMap Buffer tool. Foraging trip duration, maximum foraging distance, and the probability of crossing the line in relation to wind velocities, were all analyzed using generalized linear mixed models (GLMMs), using Gamma, Gaussian, and binomial distributions, respectively. The maximum foraging distance was log-transformed before the statistical analysis. We treated sex and year as response variables and individuals as random factors in the models. We used R package lme4 (Bates et al. 2015) for the linear models. The sex-related differences in the proportion of trips in which the line was crossed were assessed using the proportion test. Annual differences in wind velocity were analyzed using the Kruskal–Wallis test and pairwise Wilcoxon comparisons with Bonferroni correction, and SST was analyzed using ANOVA followed by Tukey’s post hoc multiple comparison. The difference in wing loading between males and females was compared using t-test. The normality and homoscedasticity in data were first checked using the Shapiro–Wilk and Bartlett tests. Values are presented as mean±SD, and statistical significance was set as <0.05.

RESULTS

Over the three year study period, we recorded 243 foraging trips for males and 241 for females (Fig. 2; Table 1). The mean duration of foraging trips did not differ between males and females (GLMM, t=−0.90, P=0.37), but trips were longer in 2012 than in 2011 (t=−3.23, P<0.01). The maximum foraging distance from the colony did not differ between the sexes or the years (GLMM, both t>1.18, P>0.08).

Most foraging trips (>70%) were within 250 km of the colony (Fig. 3). The proportion of trips during which shearwaters crossed into the Tsugaru Strait relative to all trips obtained in each year was: in 2011, 7.8% (5/64 trips) for males, and 0% (0/65 trip) for females; in 2012, 21.7% (20/92 trips) for males, and 12.1% (7/58 trips) for females; and in 2013, 10.3% (9/87 trips) for males and 3.4% (4/118 trips) for females. Males foraged into the Pacific Ocean more frequently than females in 2011 and 2013 (proportion test, \( \chi^2 = 5.28, P<0.05 \) in 2011 and \( \chi^2 = 4.08, P<0.05 \) in 2013), but the frequency did not differ between the sexes in 2012 (\( \chi^2 = 2.25, P=0.13 \)). The probability of crossing the line was not related to wind velocity (GLMM, Z=0.48, P=0.63) for males or females (Z=−1.15, P=0.25). Wing loading was greater in males (46.3±3.7 N·m⁻²) than in females (41.0±2.4 N·m⁻²; t-test, t=−6.1, P<0.01).

The speed of the easterly winds (headwinds for birds moving toward the Pacific Ocean) differed significantly among the years; it was highest in 2012, moderate in 2011, and lowest in 2013 (Kruskal–Wallis test, \( \chi^2 = 97.23, P<0.01 \) with pairwise Wilcoxon comparisons, \( P<0.01 \) for all combinations). SST around the colony was 24.1±0.5°C in 2011, 27.7±0.3°C in 2012, and 25.3±0.4°C in 2013 (Fig. 4), indicating significantly warm conditions in 2012 (ANOVA, F=20689, P<0.01 with Tukey’s post hoc multiple comparison, P<0.01).

DISCUSSION

In this study, we showed that male Streaked Shearwaters travel to the Pacific Ocean during the chick-rearing period, as they do during the incubation period (Yamamoto et al. 2012). In addition, our results indicate that while females also transit the Tsugaru Strait, males are more likely to do so. This frequency was higher for males than females in both 2011 and 2013, but was similar in males and females in 2012. Sex-related differences in habitat use have been observed in seabird species and are often attributed to differences in reproductive roles or niche segregation resulting from sexual size dimorphism (González-Solís et al. 2000; Shaffer et al. 2001; Lewis et al. 2002, Phillips et al. 2004; Elliott et al. 2010; Cleasby et al. 2015). However, despite foraging trip
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duration often being considered related to the respective reproductive roles of males and females (Phillips et al. 2004; Yamamoto et al. 2011), trip duration did not differ between male and female Streaked Shearwaters in this study. Larger bodied male shearwaters (Yamamoto et al. 2016) with greater wing loading than those of females (Shirai et al. 2013; this study) may perhaps have greater tolerance to wind and so be better able to cope with stronger winds (Navarro et al. 2009; Suryan et al. 2008). Nevertheless, we found that wind strength did not affect the probability of shearwaters transiting the Tsugaru Strait where strong winds prevail (Shimada et al. 2010). Thus, the question remains: what is responsible for the difference between the sexes in the proportion of shearwaters foraging in the Pacific Ocean?

Greater wing loading functionally enables birds to fly faster (Pennycuick 1989; Shaffer et al. 2001). Thus, males are potentially more mobile and may have more opportunities to reach distant areas. Alternatively, greater wing loading requires higher energy for flight (Freed 1981; Navarro & González-Solís

Fig. 2. GPS positions of Streaked Shearwaters in (a) 2011, (b) 2012, and (c) 2013 for males, and in (d) 2011, (e) 2012, and (f) 2013 for females. The study colony is indicated by a star.
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2007); therefore, males may need to travel into the Pacific Ocean to feed on energy-rich Pacific Saury *Cololabis saira* (Kurasawa et al. 2012). Saury are more energy-rich prey species than Japanese Anchovy *Engraulis japonicus* (14.6 KJ·g⁻¹ for saury, versus 7 KJ·g⁻¹ for anchovy: Ochi et al. 2016), their dominant prey in the Sea of Japan (Maki Yamamoto unpublished). Such foraging behavior may be similar to the dual foraging strategy (Weimerskirch et al. 1994; Baduini & Hyrenbach 2003), involving the alternation of short-range foraging trips to maximize the frequency of food deliveries to chicks, and long-range trips to recover their own energy reserves. In fact, males were more likely to show a stronger bimodality in foraging distance than females (Fig. 3).

The proportion of trips to cross the line into the Tsugaru Strait did not differ between males and females in 2012, even though winds that year were the strongest among the three years. This result counters our assumption (discussed above) that males might have more opportunities to reach distant areas owing to their greater mobility.

The Japanese Anchovy, the dominant prey species of the Streaked Shearwater in the Sea of Japan, prefers SST from 12°C to 18°C (Mihara 1998), and migrates northward in association with the northern expan-

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**Fig. 3.** Histogram of the maximum foraging trip distance and cumulative proportion of trips relative to the maximum foraging trip distance in (a) 2011, (b) 2012, and (c) 2013 for males, and in (d) 2011, (e) 2012, and (f) 2013 for females.
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In 2012, SSTs in the Sea of Japan (measured within 100 km of the colony) were warmer than those in the other years (see also Fig. 4). The availability of anchovy around the study colony was probably reduced in 2012, because the sea became warmer than the anchovy’s optimal temperature range. However, it is still unclear why the shearwaters traveled through the windy Tsugaru Strait into the Pacific Ocean rather than northward in the Sea of Japan to the western coast of Hokkaido. One possibility is that foraging efficiency becomes lower in warmer water. Streaked Shearwaters are surface-feeding seabirds and are considered to forage in association with predatory fish such as yellowtails and skipjacks (Oka 1994; Takahashi 2000). Yellowtail Seriola spp. are common in the Sea of Japan (Lee et al. 2009), and are greatly influenced by the Tsushima Warm Current, migrating northward to northern Hokkaido as well as into the Tsugaru Strait (Mitani 1959; Watanabe 1979; Tian et al. 2006, 2012), although the proportion of fish migrating into each region is yet not known. Hence, both male and female Streaked Shearwaters were perhaps more likely to travel into the Pacific Ocean in 2012, which could account for the difference in the foraging trip duration between warmer 2012 (27.7±0.3°C) and cooler 2011 (25.3±0.4°C). Foraging trip duration is generally related to the distance traveled (Weimerskirch 2007), but the maximum foraging trip distance and duration did not differ significantly between the sexes in the Streaked Shearwater, even though males made a higher proportion of their trips into the Tsugaru Strait. This is probably because most trips were within 250 km of the colony (i.e., trips into the Pacific Ocean were considerably fewer relative to the overall number of trips).

Our results suggest that whereas male Streaked Shearwaters may forage more frequently in the Pacific Ocean in order to recover their body condition, females enter the Tsugaru Strait when environmental conditions (e.g., high SST) in the Sea of Japan were unfavorable, generating a conditional

Fig. 4. The mean surface temperatures in September (a) 2011, (b) 2012, and (c) 2013. The study colony is indicated by a star.
sex-related difference in foraging habitat.

Previous studies have suggested that wind strength and direction mediate the movements of seabirds, such as the direction of foraging excursions, migratory routes, and timing (e.g., Felicísimo et al. 2008; González-Solís et al. 2009; Paiva et al. 2010; Nourani & Yamaguchi 2017). Optimal use of wind enables seabirds to save their energy for traveling (González-Solís et al. 2009). Furthermore, we might expect a trade-off between the cost of traveling with unfavorable winds and energy intake, especially during the breeding period, when the energy spent for breeding and survival should be balanced. Future studies need to consider energy expenditure as well in order to better understand the effect of wind on the foraging habitat selection of seabirds.

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