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Inter-colony Differences in the Incubation Pattern of Streaked Shearwaters in Relation to the Local Marine Environment

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Abstract.—Foraging trip duration of breeding seabirds is affected by characteristics of available feeding habitat in the marine environment, which may, in turn, generate inter-colony difference in the patterns of nest attendance. Here, nest attendance patterns and foraging areas of Streaked Shearwaters (*Calonectris leucomelas*) during their incubation period were examined using global location sensors. The study was conducted at Sangan (SI) and Mikura Islands (MI) in the northwestern Pacific, and Awa Island (AI) in the Japan Sea during 2006-2009. The duration of incubation shifts showed significant inter-colony difference, but no sex-related difference. Shearwaters from SI had shorter mean incubation shifts (5.6 days on average; range 3.0-8.0 days) than those from MI (7.2 days; range 4.8-10.7 days) and AI (6.9 days; range 6.0-9.7 days). During the incubation period, SI and MI shearwaters foraged in the northwestern Pacific's Kuroshio-Oyashio transition area, while shearwaters from AI mostly foraged in the Japan Sea. The Northwestern Pacific represents a high-productivity zone, and SI shearwaters appeared to forage in these waters, where foraging efficiency is potentially high, leading to shorter incubation shifts. Also, although MI shearwaters foraged in the northwestern Pacific, the distance between their colony and foraging areas was greater (645 km on average; range 546-756 km), compared to SI (272 km; range 244-297 km) and AI birds (228 km; range 75-518 km). In this study, inter-colony differences in incubation shift length of Streaked Shearwaters appeared to be related to differences in foraging areas associated with the local marine environment. *Received 3 July 2011, accepted 17 January 2012.*

Key words.—*Calonectris leucomelas*, foraging area, global location sensor, incubation, inter-colony difference, Streaked Shearwater.

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Reproduction schedules and associated energetic constraints often reduce opportunities for foraging (Williams 1966; Lack 1968). In seabirds, males and females often take alternate shifts during incubation duties (Lack 1968). During incubation period individuals may lose body condition, and must recover energy reserves during available foraging opportunities, as well as accumulate energy for their next incubation shift (Warham 1990). Thus, incubation represents a conflict between egg care and foraging, and birds have to allocate time and energy between incubating (i.e. fasting) and self-feeding. Typically, foraging trip duration of breeding seabirds is thought to reflect the distance from breeding colony to foraging area, patchiness of prey distribution, and prey abundance levels in the local marine environment (e.g. Lewis *et al.*

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2004; Peck and Congdon 2005) which, in turn, generate the observed inter-colony differences in the patterns of incubation routine (Warham 1990; Mallory *et al.* 2008). Information on the patterns of incubation and foraging, therefore, should yield insights into the relationship of a seabird species with its local marine environment.

Ground nesting seabirds are more easily observed than species breeding in burrows. Because ca. 65% of species nest in deep burrows on remote islands in Procellariiformes, the nest attendance pattern of petrels is usually difficult to observe, as they often come ashore only at night (Lack 1968; Warham 1990). In addition, some burrow-nesting species are known to be sensitive to disturbances such as multiple handling events or nest destruction (Warham 1990). Thus, alternative methods are required to study the nest attendance pattern of burrow-nesting species. Previous studies have examined colony attendance pattern of burrow-nesting species using a variety of methods, including temperature sensors inserted into the nest chamber (e.g. Shoji *et al.* 2011), electronic balances (e.g. Ochi *et al.* 2010), electronic event recorders (e.g. Granadeiro *et al.* 1998) and video camera systems installed either inside or outside burrows (Simons 1985). However, such studies do not provide information about foraging areas used by the birds and, therefore, cannot reveal how nest attendance patterns may be correlated with the local marine environment (but see Shoji *et al.* 2011). Recently, miniaturised global location sensor loggers have been used to track bird movement and behavior at sea during both breeding and non-breeding periods (Croxall *et al.* 2005; Shaffer *et al.* 2006; Yamamoto *et al.* 2008), as well as identify the day of return to the breeding colony (Yamamoto *et al.* 2011). Therefore, both the timing of nest attendance and foraging areas of individuals can be examined at the same time using these global location sensors.

Streaked Shearwater (*Calonectris leucomelas*) is a Procellariiform seabird which usually nests in deep burrows (Yoshida 1981). The reproductive biology and foraging behavior of this species have been studied during the chick-rearing period at several breeding colonies in Japan and Korea (Oka *et al.* 2002; Lee and Yoo 2004; Ochi *et al.* 2010); however, little information is available for the incubation period. Breeding colonies of Streaked Shearwater are distributed widely from 24°N to 42°N in latitude and from 121°E to 142°E in longitude in East and Southeast Asia, and, thereby, the characteristics of local marine environment may differ depending on the location of a breeding colony (Oka 2004). Furthermore, previous studies reported that the foraging trip duration of Streaked Shearwaters differed between the sexes depending on the reproductive stage, as females take longer trips during the prelaying period (Yamamoto *et al.* 2011) and males tend to take longer trips during chick-rearing period (Ochi *et al.* 2010). Therefore, we might expect to observe the inter-colony and sex-related differences in the share of incubation duties in Streaked Shearwaters.

In this study, we recorded the nest attendance pattern of Streaked Shearwaters during their incubation period at three breeding colonies using global location sensors. As regulation of the incubation shift is considered to relate to the time spent at sea (Chaurand and Weimerskirch 1994; Weimerskirch 1995; Tveraa *et al.* 1997), we examined the foraging trip duration and foraging area of Streaked Shearwaters. Our goal was to examine how characteristics of the incubation routine differed between sexes as well as among the colonies in relation to the local marine environment.

METHODS

Fieldwork

We conducted fieldwork on Sangan Island (39°18'N, 141°58'E, Iwate, Japan), Mikura Island (33°52'N, 139°14'E, Izu Islands, Japan), and Awa Island (38°27'N, 139°13'E, Niigata, Japan). Streaked Shearwaters return to the breeding colony in mid-March following a migration to tropical regions: the seas off northern New Guinea, Arafura Sea, and South China Sea (Yamamoto *et al.* 2010). They lay a single egg in mid- to late June, which they incubate for 50-55 days (Yoshida 1981). Chicks hatch in early to mid-August, and parents provision them for 78-82 days (Oka *et al.* 2002). We used global location sensors (GLS-Mk4: 25 × 18 × 7mm, 4.5g or GLS-Mk5: 18 × 18 × 6.5mm, 3.6g, British Antarctic

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Survey, UK) to examine the incubation shift length, foraging trip duration and foraging area of Streaked Shearwaters during incubation period. We fitted GLSs to 48 Streaked Shearwaters breeding on Sangan Island (SI) in mid-September 2006 using a plastic leg ring (Takahashi *et al.* 2008). In the following breeding season, we recaptured 38 birds in early August 2007 (incubation period), and reattached GLSs to 35 of the 38 recaptured birds. Subsequently, we recaptured 27 birds in the following year of early August 2008 (incubation period), thereby obtaining the complete data for the 2007 incubation period for these birds. At Mikura Island (MI), we fitted GLSs to 16 birds each in early October 2006 and late August 2007. In the following year of each attachment, we recaptured seven and 13 birds in late August 2007 and late September 2008, respectively (both chick-rearing period). In addition, three birds instrumented in 2006 were recaptured in 2008, two years after the attachment. At Awa Island (AI), we fitted GLSs to 20 birds each in mid-August 2007 and late August 2008, and recaptured 16 and 15 birds in late August 2008 and late August 2009, respectively (both chick-rearing period).

Of the recovered GLS loggers, five from SI and two from AI had recording errors, and the data were partially or completely unusable. We excluded six birds from SI, seven birds from MI, and seven birds from AI from the analysis, because they failed to hatch eggs. Failed breeders possibly behave differently after losing or abandoning an egg and, thereby, may bias results. We used data from twelve breeding birds (five males and seven females) from SI, 14 breeding birds (eight males and six females) from MI, and 18 breeding birds (nine males and nine females) from AI, including nine breeding pairs in total. We also used data from four non-breeding birds (two males and two females) from SI, two non-breeding birds (two males) from MI, and four non-breeding birds (one male and three females) from AI.

The total mass of the GLS, including the plastic leg ring, was ca. 1.3% of the mean body mass of the study birds. The attachment of GLS on a congener, the Cory's Shearwater (*Calonectris diomedea*), did not appear to cause any adverse effects on foraging behavior or the breeding success of birds (Igual *et al.* 2005). Upon recovery, we removed the logger and plastic leg ring from each individual. We did not observe any obvious injuries to their legs.

We determined the sex of all the birds based on their vocalizations during handling. The calls of males are high pitched whereas those of females are low pitched (Arima and Sugawa 2004). We also measured chicks of the GLS-equipped birds at the time of recapture to estimate their hatching date using external measurements (Oka *et al.* 2002).

Data Analysis

The GLS loggers record time, light intensity, the percentage of time immersed in seawater and water temperature. The loggers were programmed to measure light levels at 60 s intervals, and record the maximum value during each 10 min period. Immersion in seawater was measured every 3 s and compiled over each 10 min recording period, thereby providing the proportion of time the logger was in the water during the 10 min period. Water temperature was only recorded after continuous immersion for 20 min, as the temperature sensors require 10 min to stabilize. Light data were processed following the procedures in Takahashi *et al.* (2008) and Yamamoto *et al.* (2010). We calculated times of sunrise and sunset from light records and converted these to estimates of location using TransEdit and BirdTracker software (British Antarctic Survey, UK). Day length is used to provide an estimate of latitude, while the timing of recorded midday or midnight is used to provide an estimate of longitude (Hill 1994). A previous study using GLS loggers showed a mean location error of 202 km in temperate regions (Shaffer *et al.* 2005). However, the location data in our study should be more accurate because we corrected positions by comparing water temperature records with available satellite remotely-sensed 8-day composite sea surface temperature (SST) images (Yamamoto *et al.* 2010). We obtained monthly composite chlorophyll a concentrations and SST data (resolution of 9 km, measured by Aqua-MODIS) in July, representing their incubation period (see 'Results'). The oceanographic data were obtained from http://oceancolor.gsfc.nasa.gov, and extracted using the SeaWiFS Data Analysis System (SeaDAS, version 5.2). Values outside of mean ± 2SD were excluded from the analysis due to error. Bathymetry data were obtained from www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html. These data were used to identify the oceanographic characteristics in foraging area of Streaked Shearwaters from each colony.

The foraging distributions of Streaked Shearwaters from each colony were established by fixed kernel-density maps using the Spatial Analyst toolkit in ArcGIS 9.3 (ESRI®). We identified the date of return to the breeding colony using light and immersion data (Yamamoto *et al.* 2011). Because most Streaked Shearwaters land at the breeding colony after dusk, and depart the colony before dawn (Yoshida 1981), immersion data were recorded as 0 (out of water) over the substantial period of the night that birds were at the colony.

Petrels usually conduct the pre-laying exodus after copulation, and females lay a single egg almost immediately after returning to the colony (Warham 1990). Therefore, we defined the start of the incubation period as the return from the pre-laying exodus for females, and as occupancy of the burrow over a period of more than three days for males. Note that Streaked Shearwaters usually do not stay in their burrows for more than two days continuously prior to the incubation period (Yamamoto *et al.* 2011). The end of the incubation period was defined as the hatching date of each egg. Hatching date was estimated by the back calculation of the chick age using external measurements (Oka *et al.* 2002).

For our analysis, we determined the breeding status of the birds either by direct observation of eggs or chicks at the time of recapture, or by examining whether the GLS data included repeated periods of darkness,

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assumed to represent time spent within the nest burrow during incubation. On SI and MI, artificial nests (Kuroki *et al.* 1998) are buried. Our study birds were breeding either in artificial nests or relatively shallow burrows (ca. 1.0 m long), and, therefore, we were able to access to birds and chicks (or eggs) in the nest by hand. For non-breeding birds, we analysed data recorded in July to compare with the results from breeders during the incubation period, as it was inappropriate to define the start and end of the incubation period for non-breeders.

Statistical Analysis

Statistical analyses were carried out in R software (version 2.5.1, R Development Core Team) and Minitab (version 14.20, Minitab Inc.). Data were tested for normal distribution using the Shapiro-Wilk test. Sex-related and inter-colony differences in pre-laying exodus period were tested using two-way ANOVA (with Tukey Multiple Comparisons tests). To test the differences in incubation shift length, foraging trip duration, and maximum foraging distance from the colony between sexes as well as among colonies, we fitted a generalized linear mixed model (GLMM) with a Gaussian error distribution. Bird identity was set as a random factor in the models. The maximum foraging distance was log-transformed prior to statistical analysis. The models with and without information on sex or colony were compared using a likelihood ratio test. Then, we examined the difference among colonies using Tukey Multiple Comparisons tests, based on the mean values from individual birds. Confidence intervals of the fitted model terms were calculated using Markov Chain Monte Carlo (MCMC) methods. We used R package lme4 and function lmer for the linear models, and package coda and function mcmcsamp for MCMC methods. Data were available for one year, 2007, for SI, two years, 2007 and 2008, for MI, and two years, 2008 and 2009, for AI. Although annual conditions in the marine environment appear to influence incubation scheduling and shift in some seabird species via differences in food availability (Hatch 1990; Warham 1990; Mallory *et al.* 2008), no significant differences were found for foraging trip duration between years in MI (likelihood ratio test, $\chi^2 = 0.44$, P = 0.51) and AI ($\chi^2 = 1.89$, P = 0.17) (data from SI were available for only one year). Furthermore, substantial proportion of foraging area (95% kernel density) was overlapped between the years in MI (93.2% of foraging area in 2007 overlapped with foraging area in 2008, and correspondingly 80.6% of foraging area in 2008 overlapped with foraging area in 2007) and AI (99.5% of foraging area in 2008 and correspondingly 83.7% of foraging area in 2009). Data from different years were, therefore, pooled for further analyses. Values are presented as the mean ± SD. Statistical significance was set at <0.05.

RESULTS

Pre-laying Exodus

In early June, just prior to egg laying, female Streaked Shearwaters undertook a single long foraging trip, lasting 13-17 days, while males conducted shorter trips, lasting four to seven days, in mid-June (Table 1). Trip durations significantly differed between sexes, but did not differ among the colonies (Two-way ANOVA: sex $F_{1, 38} = 140.34$, P < 0.01; colony $F_{2, 38} = 1.69$, P = 0.20; interaction $F_{2, 38} = 2.82$, P = 0.10). During the pre-laying exodus, females from Sangan Island foraged in northern and southern coastal areas away from the colony, while females from Mikura Island foraged in eastern offshore areas in the Pacific Ocean (Figs. 1a and 1b). In contrast, females from Awa Island foraged in northern coastal areas close to the colony in the Japan Sea (Fig. 1c).

Table 1. The pre-laying exodus in Streaked Shearwaters from Sangan, Mikura and Awa Islands in 2007-2009; 2007 for Sangan Island, 2007 and 2008 for Mikura Island, and 2008 and 2009 for Awa Island. Values are presented as means ± SD with ranges in parentheses.

Colony	N	Sex	Days in pre-laying exodus	Start date	Finish date
Sangan Island	5	Male	4.6 ± 1.8 (3-7)	17 June ± 4.3 (15-25 June)	21 June ± 3.5 (18-27 June)
	7	Female	13.6 ± 2.4 (11-18)	9 June ± 5.2 (1-14 June)	21 June ± 3.7 (17-27 June)
Mikura Island	8	Male	7.5 ± 2.9 (4-12)	16 June ± 5.3 (9-26 June)	23 June ± 3.5 (17-30 June)
	6	Female	17.2 ± 2.4 (14-21)	3 June ± 2.4 (1-8 June)	19 June ± 1.3 (18-21 June)
Awa Island	9	Male	4.3 ± 2.1 (1-7)	13 June ± 3.6 (8-19 June)	16 June ±2.6 (14-21 June)
	9	Female	16.8 ± 3.4 (12-21)	3 June ± 4.3 (27 May - 9 June)	18 June ± 2.7 (16-24 June)

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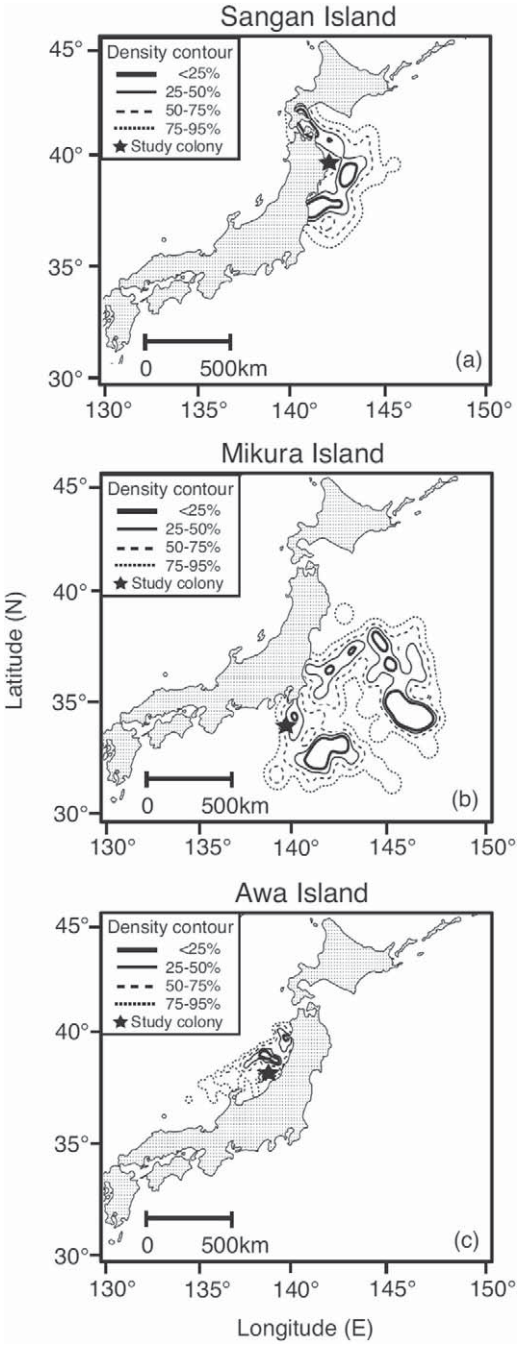


Figure 1. Density distribution (kernel contours) of female Streaked Shearwaters during the pre-laying exodus period: (a) Sangan Island, (b) Mikura Island, and (c) Awa Island.

Incubation Shift

Streaked Shearwaters started their incubation routines in mid- to late June (Table 2). Females stayed in the burrows for 0.9-1.9 days after returning from the pre-laying exodus. Typical incubation shift duration, excluding the first long shift by females, did not differ between sexes (likelihood ratio test: $\chi^2 = 0.02$, $P = 0.88$), but differed among the colonies ($\chi^2 = 15.51$, $P < 0.01$). The mean duration of incubation shift on Sangan Island (SI) (5.6 ± 1.6 days) was significantly shorter than Mikura Island (MI) (7.2 ± 1.4 days; Tukey Multiple Comparisons tests: $P < 0.05$) and Awa Island (AI) (6.9 ± 1.2 days; $P < 0.05$) (Table 2). Between members of a pair, the mean incubation shift length was similar to that of the partner ($r^2 = 0.57$, $P < 0.05$, $N = 9$; Fig. 2). Birds completed their incubation routines by mid-August, meaning the incubation period for Streaked Shearwaters in this study was 50.5 ± 3.2 days (45-58 days).

Foraging Trip Duration and At-sea Distribution

Foraging trip duration for Streaked Shearwaters during the incubation period showed significant inter-colony differences (likelihood ratio test: $\chi^2 = 28.37$, $P < 0.01$), but no sex-related difference ($\chi^2 = 1.88$, $P = 0.17$), with a shorter mean duration for birds from SI (4.8 ± 1.4 days) than birds from MI (7.9 ± 1.6 days; Tukey Multiple Comparisons tests: $P < 0.01$) and AI (6.2 ± 1.3 days; $P < 0.01$). Foraging trip duration was positively correlated with the preceding incubation shift duration (Fig. 3).

During the incubation period Streaked Shearwaters from SI foraged in northern coastal and eastern offshore areas (Fig. 4a), while MI shearwaters foraged in northern areas along the coast and also in offshore areas of the wider Pacific Ocean (Fig. 4b). In comparison, AI shearwaters mainly foraged in southern and northern areas along the coast in the Japan Sea (Fig. 4c). Streaked Shearwaters from SI foraged in relatively productive and cold waters, compared to shearwater from MI and AI, and shearwaters from AI foraged over shallower waters (Table 3). For SI and MI 54.0-66.9% of the core foraging area (<50% kernel density) overlapped between sexes within the same

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Table 2. Incubation shift duration, number of incubation shifts, and incubation period in Streaked Shearwaters from Sangan, Mikura and Awa Islands in 2007-2009; 2007 for Sangan Island, 2007 and 2008 for Mikura Island, and 2008 and 2009 for Awa Island. Values are presented as means ± SD with ranges in parentheses.

Colony	Sangan Island		Mikura Island		Awa Island	
Sex N	Male 5	Female 7	Male 8	Female 6	Male 9	Female 9
Incubation shift (days)[1]						
First incubation	6.0 ± 1.6 (4-8)	0.9 ± 0.7 (0-2)	5.8 ± 1.0 (4-7)	1.7 ± 2.0 (0-5)	6.6 ± 1.7 (4-10)	1.9 ± 1.3 (0-4)
Second incubation	6.0 ± 3.2 (2-9)	3.9 ± 2.4 (1-7)	8.0 ± 1.9 (5-10)	6.8 ± 1.0 (6-8)	6.6 ± 1.3 (5-9)	7.4 ± 3.6 (3-12)
Third incubation	5.6 ± 1.5 (3-7)	6.1 ± 3.4 (2-10)	10.0 ± 0.8 (9-11)	9.3 ± 1.5 (8-12)	7.3 ± 0.7 (7-9)	8.1 ± 1.7 (5-11)
Fourth incubation	5.2 ± 3.0 (1-9)	5.1 ± 3.0 (1-9)	3.5 ± 2.6 (1-7)	5.8 ± 4.1 (1-13)	6.4 ± 0.9 (5-8)	6.8 ± 2.4 (3-11)
Fifth incubation	5.7 ± 1.5 (4-7)	4.2 ± 3.0 (1-7)	— —	2.0 —	3.3 ± 1.5 (2-5)	6.4 ± 1.5 (5-9)
More than sixth	4.0 —	4.9 ± 2.4 (2-9)	— —	— —	— —	— —
No. of total incubation shift	5.0 ± 1.0 (4-6)	5.6 ± 1.5 (4-8)	3.4 ± 0.7 (2-4)	4.2 ± 0.4 (4-5)	4.2 ± 0.7 (3-5)	4.6 ± 0.5 (4-5)
Incubation period (days)	47.2 ± 2.9 (45-52)	48.9 ± 2.5 (46-53)	50.1 ± 3.8 (46-57)	51.3 ± 2.3 (47-53)	52.0 ± 3.2 (48-58)	51.9 ± 1.8 (49-54)
Start date	23 June ± 4.4 (19-29 June)	22 June ± 4.0 (17-28 June)	25 June ± 2.6 (23 June-1 July)	20 June ± 1.3 (19-22 June)	17 June ± 2.6 (15-22 June)	19 June ± 2.7 (17-25 June)
Finish date[2]	10 August ± 4.0 (3-15 August)		13 August ± 3.9 (8-20 August)		9 August ± 3.9 (4-18 August)	

[1]Incubation shift length for 0 means that birds stayed at the colony only for a single night.
[2]The end of incubation period was defined as hatching date of each bird's egg.

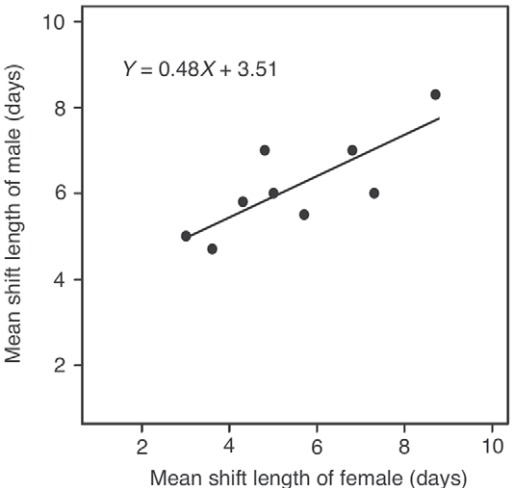


Figure 2. Correlation of the mean incubation shift length between pair members in Streaked Shearwaters.

colony, but this was less pronounced for AI (20.9% in males and correspondingly 32.4% in females) (Table 4, Fig. 4). The core foraging areas for SI and MI birds overlapped to some extent, but these Pacific-breeding populations used completely separate areas from those used by AI breeders (Table 4).

Maximum foraging distance did not significantly differ between sexes (likelihood ratio test: $\chi^2 = 2.63$, P = 0.11), but differed among colonies ($\chi^2 = 53.9$, P < 0.01). Maximum foraging distance from the colony was greatest for shearwaters from MI (645 ± 73 km; N = 14), and less for shearwaters from AI (228 ± 117 km; N = 18) than the birds from SI (272 ± 19 km; N = 12) (Tukey Multiple Comparisons tests: P < 0.01 for all combinations). The maximum foraging distance was positively correlated to the foraging trip duration (Fig. 5). Furthermore, the effect of trip duration on foraging distance was stronger for shearwaters from MI (viz. the slopes of the fitted regression lines from the generalized linear mixed models: $Y = 0.09X + 5.70$) than shearwaters from AI ($Y = 0.08X + 4.75$) and SI ($Y = 0.06X + 5.29$).

Behavior of Non-breeding Birds

For non-breeding birds, both males and females returned to the breeding colony frequently in July, after short foraging trips (1.8

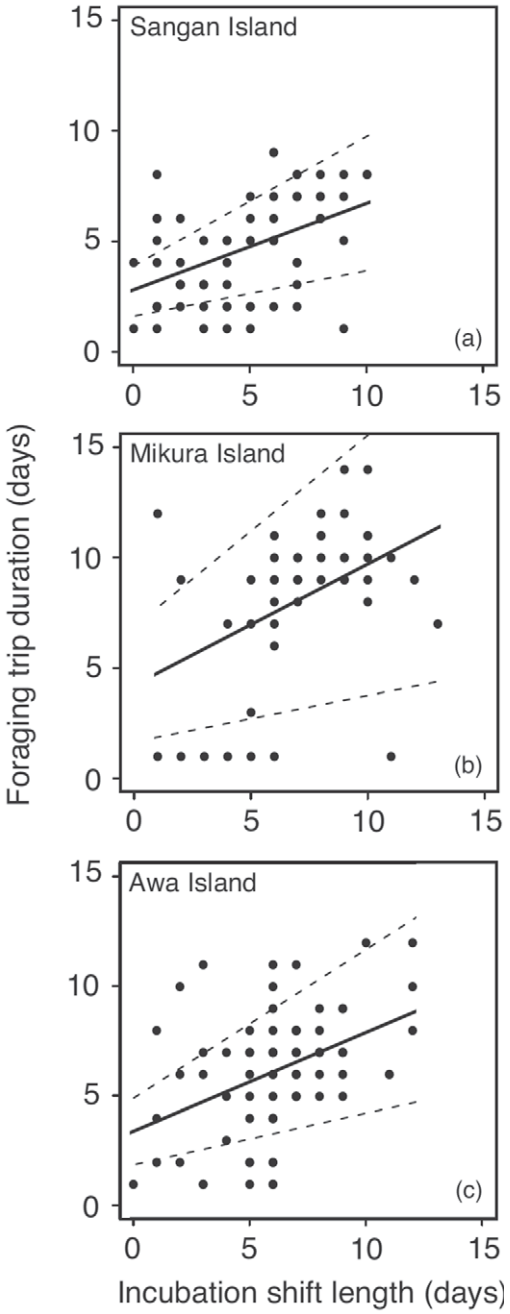


Figure 3. The relationship between the preceding incubation shift length and foraging trip duration in Streaked Shearwaters: (a) Sangan Island, (b) Mikura Island, and (c) Awa Island. The fitted regression lines from the generalized linear mixed models are shown as solid lines, and the confidence intervals of the fitted model terms are shown as dashed lines (the lower and upper lines indicate 2.5% and 97.5% confidence intervals, respectively).

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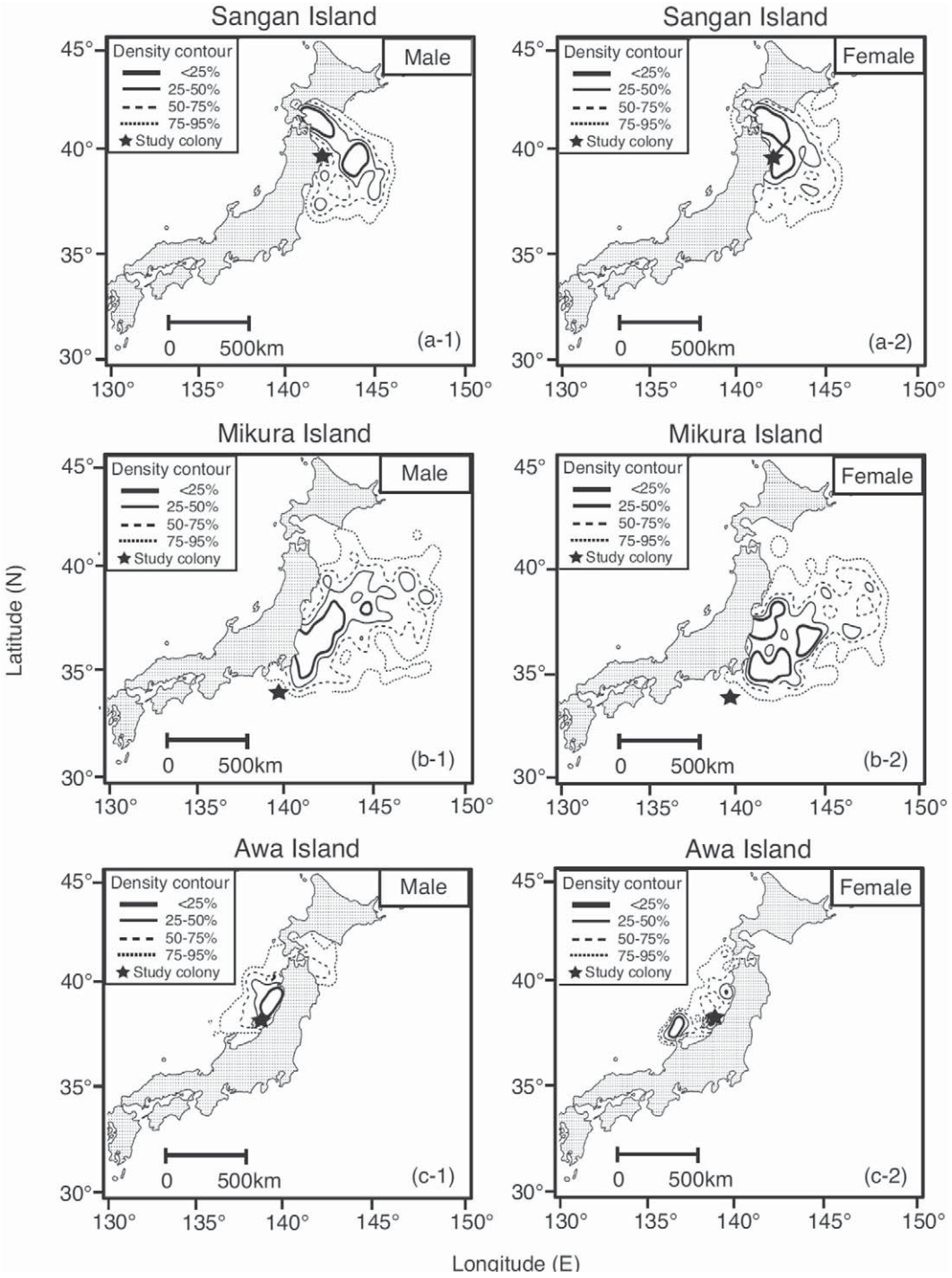


Figure 4. Density distribution (kernel contours) of Streaked Shearwaters during the incubation period: (a-1) males and (a-2) females from Sangan Island, (b-1) males and (b-2) females from Mikura Island, and (c-1) males and (c-2) females from Awa Island.

± 1.7 days at SI, 3.0 ± 3.2 days at MI, and 1.4 ± 0.9 days at AI), and stayed at the colony mostly for a single night (1.0 ± 0.1 days at SI, 1.2 ± 0.5 days at MI, and 1.0 ± 0.4 days at AI).

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Table 3. Oceanographic characteristics within foraging areas of Streaked Shearwaters. Oceanographic data (chlorophyll a concentration and sea surface temperature) in July 2007-2009 were used to characterise environmental conditions within the core foraging area (<50% kernel density) of each corresponding year; 2007 for Sangan Island, 2007 and 2008 for Mikura Island, and 2008 and 2009 for Awa Island. Chlorophyll a concentration (Chl. a concentration) and sea surface temperature (SST) were measured by Aqua-MODIS, and water depth was determined using ETOPO2 grids from the National Geophysical Data Center (see "Methods"). Values are presented as means ± SD.

Colony	Chl. a concentration (mg/m^3)	SST (°C)	Water depth (m)
Sangan Island	0.32 ± 0.11	19.0 ± 1.5	2319 ± 2208
Mikura Island	0.22 ± 0.10	22.7 ± 1.6	4237 ± 2327
Awa Island	0.23 ± 0.11	22.0 ± 2.1	818 ± 736

The core foraging areas (<50% kernel density) overlapped to a moderate degree between breeders and non-breeders at both SI and AI, while the core foraging area only overlapped a little for MI birds (Table 4).

DISCUSSION

Streaked Shearwaters conducted their pre-laying exodus in early to mid-June, with females showing a longer absence from the colony than males. The style of the pre-laying exodus for shearwaters varies depending upon species (Warham 1990). They may be: completely absent from the colony, including non-breeders (e.g. Short-tailed Shearwaters *Puffinus tenuirostris*); females may stay away longer than males (e.g. Cory's Shearwaters); or only females leave the colony (e.g. Manx Shearwaters *Puffinus puffinus*) (see review by Warham 1990). In particular, the difference in pre-laying exodus duration between sexes in Streaked Shearwaters may be related to differences in their respective reproductive roles. Males returned to the breeding colony more frequently than females before eggs were laid (Yamamoto *et al.* 2011), possibly to ensure their nests were not occupied by other prospecting birds while females foraged intensely prior to laying.

Streaked Shearwaters started their incubation routines in mid- to late June, and finished by mid-August. The incubation period of Streaked Shearwaters recorded in our study (45-58 days) was similar to the previous estimate by Yoshida (1981) (50-55 days). Incubation shift duration did not differ between sexes, but differed among the colonies. Shearwaters from Sangan Island (SI) stayed in their burrows for a shorter period and had a larger number of incubation excursions than shearwaters from Mikura (MI) and Awa Islands (AI). Incubation is energetically demanding for petrels, and one bird may lose 2-20% of its body mass during an incubation shift, while the other bird may travel long distances to find sufficient food to replenish energy stores (Chaurand and Weimerskirch 1994; Weimerskirch 1995; Tveraa *et al.* 1997). Thus, incubation shift duration may be affected not only by the physical condition of each bird and its mate, but also by the time required to search for food (Warham 1990).

Foraging trip duration for Streaked Shearwaters from SI was relatively short (4.8 ± 1.4 days), compared to trip durations made by birds from other colonies (7.9 ± 1.6 days for MI and 6.2 ± 1.3 days for AI). During the incubation period, Streaked Shearwaters from SI and MI foraged in the northwestern

Table 4. Percentages of overlap in the core foraging areas (<50% kernel density) of Streaked Shearwaters between sexes, among the colonies (Sangan, Mikura and Awa Islands), and between breeders and non-breeders in 2007-2009.

Overlap	Between sexes (%)		Between colonies (%)			Between breeders and nonbreeders (%)	
Colony	Male	Female	Sangan Is.	Mikura Is.	Awa Is.	Breeder	Nonbreeder
Sangan Island	66.9	57.5	—	1.2	0	43.6	34.7
Mikura Island	54.0	55.0	1.0	—	0	5.6	6.5
Awa Island	20.9	32.4	0	0	—	46.4	16.1

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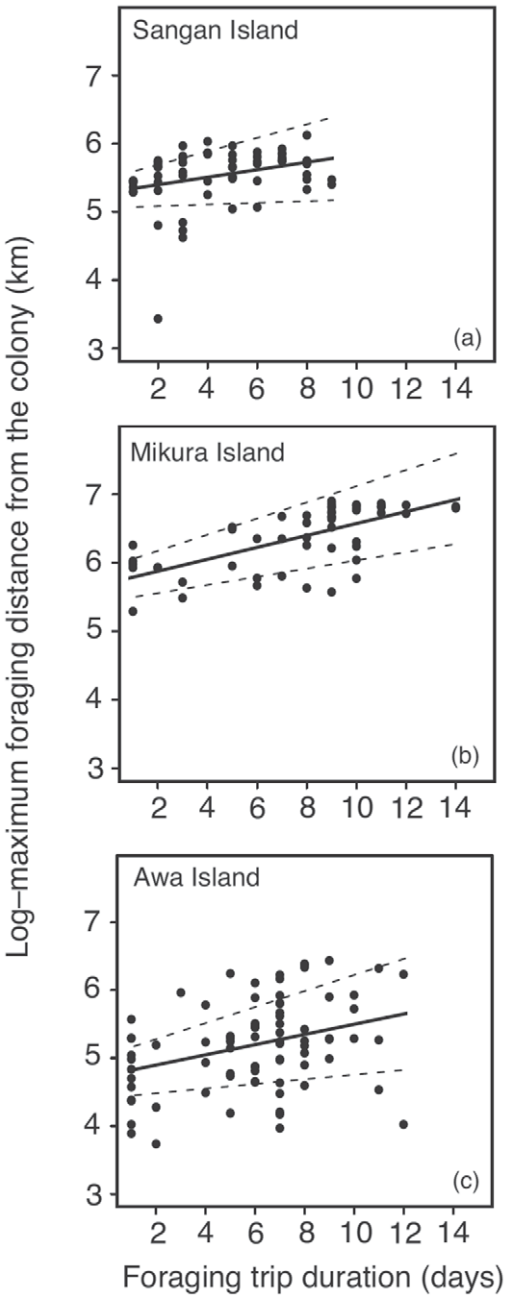


Figure 5. The relationship between foraging trip duration and maximum foraging trip distance from the colony in Streaked Shearwaters: (a) Sangan Island, (b) Mikura Island, and (c) Awa Island. The fitted regression lines from the generalized linear mixed models are shown as solid lines, and the confidence intervals of the fitted model terms are shown as dashed lines (the lower and upper lines indicate 2.5% and 97.5% confidence intervals, respectively).

Pacific, while shearwaters from AI mostly foraged in the Japan Sea. In the northwestern Pacific, the warm Kuroshio water and cold Oyashio water converge and generate a variety of complex hydrographic features. These features help maintain one of the highest zones of productivity in the world's oceans (Olson 2001; Yasuda 2003). Differences in food availability or foraging efficiency are likely to affect foraging trip duration for seabirds (Tveraa *et al.* 1997; Mallory *et al.* 2008), with those foraging in productive waters showing shorter durations (Peck and Congdon 2005). Although we were not able to present direct evidence about the differences in prey availability and distribution between the Pacific Ocean and Japan Sea, we might reasonably assume that shearwaters from SI foraged in more productive waters closer to the colony, based on chlorophyll a concentrations in foraging area, and that foraging efficiency in such areas is higher, leading to shorter foraging excursions. Nonetheless, shearwaters from MI also foraged in similar areas to shearwaters from SI in the northwestern Pacific, but showed significantly longer foraging trip durations. In the northwestern Pacific, many fish species show a northward migration towards productive Oyashio water in spring and summer (Odate 1994), including the principal prey of Streaked Shearwaters (Japanese anchovy *Engraulis japonicas*; Matsumoto 2008; M. Yamamoto unpublished data). The colonies of SI and MI are located to the north and south of the transition area between the Kuroshio and Oyashio regions respectively (see Fig. 1 in Yamamoto *et al.* 2011); therefore, the preferred foraging habitat of Streaked Shearwaters potentially moves farther from MI, while it moves closer to SI during the incubation period (Yamamoto *et al.* 2011). Shearwaters from MI conducted longer foraging trips to reach more distant foraging areas. Consequently, when compared to SI birds, MI birds probably needed to fast for longer until their partner returned to the colony. In addition, like their partners, they would need to travel long distances, after long periods on the nest, to reach profitable foraging destinations.

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The mean incubation shift length was similar between members within a pair. Poor coordination of incubation shift length with a partner is likely to increase the rate of breeding failure in seabirds (Tveraa *et al.* 1997). Although we were not able to present comparative data on incubation routines of failed pairs, such the concordance in incubation shift length within a pair may have resulted in successful hatching in Streaked Shearwaters.

Our results provided some unexpected findings, in that non-breeding birds undertook much shorter foraging trips and foraged in areas closer to the colony than did breeding birds. This was surprising, as their foraging activities would not be constrained by incubation duties. We can find no obvious explanation for such patterns in non-breeding birds, but one possibility could be that non-breeding birds do not need to forage to replace resources or build up reserves to withstand a period of fasting. Both activities would lead to high energetic demands for breeding birds, as would engaging in nesting activities or mating activities necessary to ensure their future reproductive success as suggested by previous studies (Vanderkist 1999; Hébert and Golightly 2008).

In conclusion, the incubation shift duration in Streaked Shearwaters did not differ between sexes, but differed among the colonies. The inter-colony differences in incubation shift length appeared to be related to differences in foraging distance and foraging conditions in the areas around the breeding colonies.

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