

1 Original Article in Biogeography

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3 **Geographical variation in body size of a pelagic seabird,**
4 **the streaked shearwater *Calonectris leucomelas***

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44 **Short running head:** Inter-colony variation in seabird body size

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46

47 **ABSTRACT**

48 **Aim** In general, within temperate latitudes, races of endotherms tend to show larger body
49 size at higher latitudes, while smaller-bodied ones tend to be found at lower latitudes, a
50 pattern known as Bergmann's rule (or James's rule for intra-specific patterns). The adaptive
51 basis of this geographic variation in body size is explained mostly by the heat conservation
52 hypothesis. Application of Bergmann's rule has been confirmed mostly among terrestrial
53 taxa and studies of marine taxa are rare. Our aim was to examine whether the intra-specific
54 variation in body size of a pelagic seabird species (streaked shearwater *Calonectris*
55 *leucomelas*) follows Bergmann's/James's rule.

56

57 **Location** Eight different breeding colonies of the streaked shearwater, ranging from
58 24–39°N in latitude (approximately the full latitudinal range of the species) and 142–123°E
59 in longitude.

60

61 **Methods** We measured morphological traits of 454 adult streaked shearwaters in total.
62 Principal components analysis was used to create a composite body size index for each sex
63 from each colony using the measured traits, and the value of first principal component was
64 compared. The relationships between body size index and latitude, longitude and the
65 averaged mean air temperature were examined using generalized linear models.

66

67 **Results** Body size was positively correlated with latitude and longitude, and negatively
68 correlated with the mean air temperature. Latitude and longitude were highly correlated
69 with air temperature. Nonetheless, between colonies, populations that are considered to

70 forage over large areas appeared to exhibit smaller body size than those of lower latitude
71 populations.

72

73 **Main conclusion** The overall trend of the geographical variations in body size of streaked
74 shearwaters followed Bergmann's/James's rule, suggesting that this rule may be applicable
75 to seabirds. However, in addition to thermoregulatory adaptation, intra-specific differences
76 in foraging characteristic in relation to local marine environment might also affect the body
77 size in highly mobile seabirds.

78

79 **Key words**

80 Bergmann's rule, *Calonectris leucomelas*, James's rule, latitude, local adaptation, longitude,
81 marine environment, streaked shearwater, temperature

82

83 **INTRODUCTION**

84 There has been a widely supported hypothesis that mean body size of endothermic races
85 tends to be larger within temperate latitudes where conditions within the range are cooler,
86 which manifests in a cline of increasing body size with latitude: this is known as Bergman's
87 rule at the inter-specific level (Bergmann, 1847 cited in Blackburn, *et al.*, 1999) or James's
88 rule for intra-specific pattern (Rensch, 1938; James, 1970). Latitudinal gradients in body
89 size are primarily explained by the heat conservation hypothesis (James, 1970; Blackburn,
90 *et al.*, 1999; Blackburn & Hawkins, 2004). The surface area to volume ratio is lower in
91 large-bodied animals, so they are better able to conserve heat in cooler climates at higher
92 latitudes. Climate varies both latitudinally and longitudinally. Hence, body size can also

93 vary with longitude (Thurber & Peterson, 1991; Wojczulanis-Jakubas *et al.*, 2011).

94 Most evidence for a geographic pattern in body size derives from studies of
95 terrestrial taxa, including mammals (Ashton *et al.*, 2000; Meiri & Dayan, 2003; Blackburn
96 & Hawkins, 2004; Rodríguez *et al.*, 2008) and birds (Blackburn & Gaston, 1996; Ashton,
97 2002; Meiri & Dayan, 2003; Olson, *et al.*, 2009), although a few studies have also reported
98 a similar clinal trend in marine taxa (Brunner, 2002; Wojczulanis-Jakubas *et al.*, 2011).
99 Procellariiformes (albatrosses, petrels, and shearwaters) are seabirds that travel large
100 distances at sea, but return to specific locations to reproduce, usually on isolated islands
101 (Warham, 1990). Populations that are spatially disjunct may be expected to generate
102 inter-colony differences in morphological characteristic (Moen, 1991; Barrett *et al.*, 1997;
103 Waugh *et al.*, 1999; Bull, 2006; Einoder *et al.*, 2008). However, within-species
104 comparisons of body size in seabirds have often been limited to two or three populations,
105 usually due to the inaccessibility to their breeding locations (e.g. on isolated islands and/or
106 at cliffs), and therefore do not cover their full breeding range. Hence, a comprehensive
107 analysis of body size variation across a species' full geographical range has rarely been
108 performed for pelagic seabird species (Wojczulanis-Jakubas *et al.*, 2011).

109 The streaked shearwater (*Calonectris leucomelas*) breeds on isolated islands in
110 east and southeast Asia from April to early November (Yoshida, 1981; Oka, 2004).
111 Breeding colonies of this species are distributed widely from 24 °N to 42 °N in latitude and
112 from 121 °E to 142 °E in longitude, hence characteristics of the local environment differ
113 substantially between colonies (Yamamoto *et al.*, 2011, 2012). For example, Oka (2004)
114 reported that sea surface temperature in spring (average monthly mean in March during
115 1980s–1990s) vary from 1 °C to 25 °C among colonies within the breeding range. Previous

116 studies have reported body size measurements of this shearwater species in different
117 breeding colonies (on Kanmuriijima and Mikurajima, Arima & Sugawa, 2004; Ochi *et al.*,
118 2010; Arima *et al.*, 2014), indicating that there may be inter-colony differences in their
119 morphological size (Arima *et al.*, 2014), but a comprehensive analysis of their body size
120 across the full breeding range has not been performed.

121 Here, we measured the external morphology of streaked shearwaters at eight
122 different breeding colonies around Japan ranging from 24–39°N in latitude and 123–142°E
123 in longitude. Our aims were to explore the inter-colony variation in body size of this
124 pelagic seabird species, and, then, to examine if the variation follows Bergmann's/James's
125 rule. As males are larger than females in streaked shearwaters (Arima & Sugawa, 2004;
126 Arima *et al.*, 2014) sexual dimorphism may influence the pattern of inter-colony variation
127 in body size. Therefore, we analysed that issue first, and then treated males and females
128 separately in the further analyses.

129

130 MATERIALS AND METHODS

131 We measured adult streaked shearwaters during the incubation or chick-rearing period
132 (August–October) in 2006–2013 at eight islands in Japan that vary substantially in latitude:
133 Funakoshi-Ohshima (hereafter FO), which is one of the northernmost colonies for the
134 species, Sanganjima (SA), Awashima (AW), Kanmuriijima (KA), Mikurajima (MI),
135 Uwashima (UW), Danjo-gunto (DA), and Nakanokamishima (NA), which is one of the
136 southernmost colonies (see Fig. 1 for the location of each colony). The breeding
137 populations were estimated to be <1,000 birds at FO (Oka, 2004), 109,000 birds at SA
138 (Matsumoto *et al.*, 2007), 61,000 birds at AW (M. Yamamoto, unpublished data), 240,000

139 birds at KA (Yoshida, 1981; Oka, 2004), 770,000 birds at MI (Japanese Ministry of the
140 Environment, 2013), <100 birds at UW (S. Watanabe, personal communication), several
141 thousand birds at DA (Oka, 2004), and ca. 5,500 birds at NA (Yamamoto *et al.*, 2015).

142 Body mass was measured using a 1 kg spring balance to the nearest 1 g. Bill length,
143 bill depth, total head length, and tarsus length were measured using a Vernier caliper to the
144 nearest 0.1 mm (see Fig. 2 in Arima & Sugawa, 2004 for the measurement parts), and wing
145 length was measured with a ruler to the nearest 1 mm, for a total of 454 birds from eight
146 breeding colonies (see Table 1 and Appendix S1 in Supporting Information). To minimize
147 errors (Bailey & Byrnes, 1990), each measurement was repeated 2 or 3 times, and the
148 average value was used. Most measurements were undertaken by T. Yamamoto (400 out of
149 454 birds), but some were done by co-authors (34 birds at UW by S. Watanabe and 20 birds
150 at DA by K. Yoda and S. Matsumoto) following the same method previously confirmed
151 between the authors. We determined the sex of all the birds based on their vocalizations
152 during handling; the calls of males are high pitched, whereas those of females are low
153 pitched (Arima & Sugawa, 2004; Arima *et al.*, 2014). Some birds did not call voluntarily
154 during the handling, and, then, we pushed their abdomen gently once or twice in
155 accordance with breathing to produce a call.

156 We compared the sexual size difference (SSD) in streaked shearwaters using the
157 formula: $SSD = M_{ave}/F_{ave}$ (Smith, 1999), where M_{ave} and F_{ave} is the mean value of each
158 morphological trait (bill length, bill depth, total head length, wing length, and tarsus length)
159 in males and females of a given colony, respectively.

160 Principal components analysis (PCA) was used to create a composite body size
161 index for each sex from each colony. Body size index was derived by incorporating

162 measures of five parameters (bill length, bill depth, total head length, tarsus length, and
163 wing length). We excluded body mass from the PCA of individuals, because body mass can
164 vary depending on the breeding phase (i.e. shearwaters fast for up to several days during
165 the incubation duty: Yamamoto *et al.*, 2012) and the timing of capture (i.e. before/after
166 feeding a chick: Ochi *et al.*, 2010). Collectively, the first principal component (PC1)
167 explained 75.2% of the variance in body size (see Appendix S2 for the relationship between
168 PC1 and each of the input variables).

169 Differences in body size between sexes and among colonies were compared using
170 Mann-Whitney U tests and Kruskal-Wallis rank sum tests with a Bonferroni post hoc test
171 for multiple comparisons, respectively (Zar, 1999). To test Bergmann's rule, the
172 relationships between body size and latitude/longitude/air temperatures were examined
173 using generalized linear models (GLM) with a Gaussian error distribution. We also
174 examined the relationships without NA, because the outlier may affect the result of linear
175 regression and/or to confirm that the relationship still existed within a narrower range of
176 latitude (31–39°N).

177 The averaged mean air temperature in July–September (during incubation and
178 chick-rearing periods for streaked shearwaters) in 1981–2010 was obtained from the Japan
179 Meteorological Agency (available at www.jma.go.jp), and data measured at a
180 meteorological station closest to each colony were used; <30 km from the colony except
181 DA (c. 70 km).

182 The PCA were performed in Minitab (version 14.20, Minitab Inc.). Other
183 statistical analysis were conducted in R software (version 2.5.1, R Development Core Team,
184 2008). Values are presented as the mean \pm SD and statistical significance was set at <0.05.

185

186 **RESULTS**

187 Male streaked shearwaters had a significantly larger body size index than females at all the
 188 study colonies (Mann-Whitney U tests, all $Z > 3.21$, $P \leq 0.001$, Table 1, Fig. 2). Bill depth
 189 was the trait showing the largest difference between sexes, being 1.08–1.16 times larger in
 190 males than females (Table 2). Furthermore, SSD in bill depth exhibited a relatively large
 191 variation among the colonies, as standard deviation for bill depth was 0.03, compared to
 192 other traits ($SD = 0.01$) (Table 2).

193 Overall, geographical variation in body size was positively correlated with latitude
 194 [male: $Y = 1.16X + 197.5$ ($R^2 = 0.67$, $P < 0.001$), female: $Y = 1.20X + 186.6$ ($R^2 = 0.69$, $P <$
 195 0.001)] and longitude [male: $Y = 0.87X + 119.0$ ($R^2 = 0.58$, $P < 0.001$), female: $Y = 0.88X +$
 196 108.4 ($R^2 = 0.58$, $P < 0.001$)], and negatively correlated with air temperature [male: $Y =$
 197 $-2.25X + 291.6$ ($R^2 = 0.58$, $P < 0.001$), females: $Y = -2.26X + 282.9$ ($R^2 = 0.55$, $P < 0.001$)]
 198 (Fig. 2). Both latitude and longitude were highly correlated with air temperature [Pearson's
 199 correlation coefficient, latitude vs. temperature: -0.91 ($P < 0.001$), longitude vs.
 200 temperature: -0.89 ($P < 0.001$)]. The coefficient of determination (R^2) decreased, especially
 201 for the longitude, when excluding NA, which possessed birds of smaller body size than the
 202 other study colonies [latitude: $Y = 0.95X + 205.3$ ($R^2 = 0.22$, $P < 0.001$) in male and $Y =$
 203 $0.70X + 205.5$ ($R^2 = 0.16$, $P < 0.001$) in female, longitude: $Y = 0.37X + 188.4$ ($R^2 = 0.06$, P
 204 < 0.001) in male and $Y = 0.27X + 193.3$ ($R^2 = 0.05$, $P < 0.001$) in female, and air
 205 temperature: $Y = -1.20X + 268.1$ ($R^2 = 0.20$, $P < 0.001$) in male and $Y = -0.89X + 251.8$ (R^2
 206 $= 0.14$, $P < 0.001$) in female] (Fig. 2).

207 Body size index values differed among the colonies (Kruskal-Wallis rank sum test,

208 $X^2 = 133.30$, $df = 7$, $P < 0.001$ for males and $X^2 = 135.75$, $df = 7$, $P < 0.001$ for females).
209 FO males were significantly larger than MI males; SA birds larger than birds at KA, MI,
210 and DA (SA females were also larger than UW females); AW birds larger than MI birds
211 (AW females were also larger than KA females); and birds from all other colonies were
212 significantly larger than NA birds (see Table 3).

213

214 **DISCUSSION**

215 Streaked shearwaters exhibit sexual size dimorphism in their morphology (Arima &
216 Sugawa, 2004; Shirai *et al.*, 2013; Arima *et al.*, 2014), and we confirmed that males were
217 larger than females in the overall body size and each morphological trait throughout all the
218 study colonies. Bill depth was the most different trait between males and females, while the
219 degree of SSD for bill depth appeared to vary among the colonies. *Calonectris* species
220 commonly defend their nests against conspecifics by fighting (Warham, 1996), and a more
221 robust bill could be advantageous to males for physical combat (Navarro *et al.*, 2009a;
222 Shirai *et al.*, 2013). In streaked shearwaters, the competence of males for competition
223 during the breeding period should be relevant; during pre-laying period males are probably
224 responsible for nest defence against other prospecting birds, while females engage in
225 offshore foraging to accumulate resources for egg production (Yamamoto *et al.*, 2011).
226 Among the study colonies, individuals breeding in large populations (>60,000 birds: SA,
227 AW, KA and MI) appeared to show relatively larger SSD compared to birds in small
228 populations (less than several thousand birds: UW, DA, and NA, except FO) (Table 2).
229 Social interactions may affect bill morphology in streaked shearwaters through sexual
230 selection (Navarro *et al.*, 2009a).

231 We found that the body size of streaked shearwaters showed an overall increase
232 from the south to north (and also from the west to east). Such a relationship between body
233 size and latitude is in line with Bergmann's/James's rule, which describes a general pattern
234 of larger-bodied individuals living at higher (cooler) latitudes and smaller-bodied
235 individuals living at lower (warmer) latitudes (Bergmann, 1847; James, 1970; Blackburn *et*
236 *al.*, 1999). The adaptive basis of geographic variation in animals' body size has been
237 explained mostly by the heat conservation hypothesis (Blackburn *et al.*, 1999). Increased
238 body size at higher latitudes is thought to reduce heat loss owing to a lower surface area to
239 volume ratio that enables individuals to conserve heat in cooler climates. In this study,
240 latitude and longitude were highly correlated with air temperature, and air temperature
241 itself also showed a negative relationship with the body size. Hence, overall latitudinal and
242 longitudinal trends in the body size of streaked shearwaters likely reflect adaptations to
243 thermal conditions of each colony location (i.e. air temperature). Nonetheless, the
244 coefficient of determination (R^2) became smaller when excluding NA from the analysis.
245 This might suggest that there could be additional factors driving the variation in their body
246 size, such as characteristics relating to foraging behaviour (cf. the resource availability
247 hypothesis: Blackburn *et al.*, 1999).

248 Among some colonies, the body size–latitude relationship appeared to be reversed;
249 MI birds were smaller than UW and DA birds that breed at colonies of lower latitude, and
250 UW birds were larger than higher latitude colony of KA (Fig. 2a), although these
251 differences were not significant (Table 3). During the breeding period, MI shearwaters
252 travel comparatively greater distances than shearwaters from other colonies (e.g. the mean
253 maximum distance from the colony during the incubation period was 272 km for SA, 228

254 km for AW, and 645 km for MI: Yamamoto *et al.*, 2012). In contrast, UW birds forage in a
255 very small area (c. <150 km from the colony), mostly within the Seto Inland Sea (Ito *et al.*,
256 2013). Smaller body size is thought to be adaptive for travelling great distances (for
257 example as found in snow petrels *Pagodroma nivea*: Barbraud *et al.*, 1999), while possible
258 higher flight costs due to increased body size (i.e. lower surface area to volume ratio) could
259 be offset by reduced travel time (Weimerskirch, 2007; Cairns *et al.*, 2008). In this respect,
260 differences in foraging behaviour may also determine, in part, the inter-colony variations in
261 the body size, though foraging behaviour has not been examined in all of our study colonies.
262 Annual variations in marine environment may relate to foraging behaviour of parents at a
263 given colony that affects the growth rate of chicks (Weimerskirch *et al.*, 2001; Hedd *et al.*,
264 2002; Quillfeldt *et al.*, 2010) and therefore may influence the adult body size. The age was
265 not known for the individuals measured in this study, and, therefore, any annual differences
266 in fledgling size might be obscured: our body size index represents only the mean for each
267 colony.

268 One striking finding in this study was that individuals at NA were significantly
269 smaller than all other study colonies. NA is the only population breeding in tropical region
270 among the study colonies. In tropical waters, surface food abundance is generally low, and
271 resources are much less predictable due to less structured oceanographic features compared
272 to temperate or polar region (Longhurst & Pauly, 1987; Weimerskirch, 2007). Hence,
273 efficient gliders are believed to be favoured in tropical oceans due to their low flight costs
274 when searching over large areas (Ashmole & Ashmole, 1967; Ballance & Pitman, 1999;
275 Cairns *et al.* 2008). Theoretically, the surface area to volume ratio becomes larger with the
276 decrease of body size (i.e. smaller bodied individuals are supposed to have larger wing

277 relative to the volume). Hence, NA shearwaters could be specifically adapted to a tropical
278 environment. Another possibility may be a large spatial gap (>950 km) between mainland
279 populations (FO, SA, AW, KA, MI, UW and DA) and SakishimaIsland populations
280 (located at the southernmost end of the Japanese Archipelago), including NA (Fig. 1).
281 Hence, there could be a possibility that NA shearwaters are genetically different from other
282 mainland populations, potentially representing sub-species or even different species.
283 Recently, another species in the same genus (the Cory's shearwater) has been divided into
284 two different species: the larger Cory's shearwater *Calonectris borealis* and the smaller
285 Scopoli's shearwater *C. diomedea* (Gómez-Díaz *et al.* 2006, 2009), showing different
286 foraging characteristics, one of which relates to wing loading (Navarro *et al.* 2009b).

287 In streaked shearwaters breeding on islands around Japan, the overall trend of the
288 geographical variations in body size followed Bergmann's/James's rule. Our results
289 therefore show that the rule may be applied to at least some seabirds, i.e. to species that
290 forage in the marine realm. Furthermore, we propose the need for considering local
291 characteristics of foraging behaviour to understand the body size–environment relationship
292 in highly mobile seabirds in addition to the thermoregulatory adaptation: such studies may
293 provide a new insight into the field of biogeography.

294

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312

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446 **Supporting Information**

447 Additional Supporting Information may be found in the online version of this article:

448

449 **Appendix S1** Histograms of body size (PC1) for streaked shearwaters *Calonectris*
450 *leucomelas*.

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452 **Appendix S2** The relationship between PC1 and each of the input variables for streaked
453 shearwater *Calonectris leucomelas*.

454

455 **BIOSKETCH**

456 Takashi Yamamoto is a postdoctoral fellow at Graduate School of Environmental Studies,
457 Nagoya University in Japan. His dissertation research focuses on the migratory behaviour
458 and behavioural and morphological adaptations of seabirds to the local marine environment.

459 Author contributions: T.Y. conceived the study; all the authors conducted/contributed data
460 collections; T.Y. and K.Y. analysed the data; and T.Y. wrote the paper with contributions
461 from the other authors.

462

463 Editor: Michael Patten

464 Table 1. Summary of external measurement of streaked shearwaters *Calonectris leucomelas* conducted during the incubation or
 465 chick-rearing period (August–October) in 2006–2013 at eight breeding colonies in Japan. Values are presented as means \pm SD
 466 and ranges in parenthesis. Upper and lower values for each morphological trait represent males and females, respectively. For the
 467 abbreviation and location of colonies, see Fig. 1.

| Colony | FO | SA | AW | KA | MI | UW | DA | NA |
|------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|
| N | 14 males 10 females | 54 males 52 females | 47 males 40 females | 14 males 22 females | 32 males 26 females | 11 males 23 females | 7 males 13 females | 43 males 46 females |
| Body mass (g) | 589 \pm 51 (500–650) | 641 \pm 45 (573–750) | 596 \pm 58 (468–710) | 563 \pm 44 (500–638) | 543 \pm 48 (462–670) | 593 \pm 60 (495–695) | 510 \pm 29 (485–565) | 516 \pm 54 (410–632) |
| | 503 \pm 36 (450–580) | 537 \pm 39 (463–640) | 510 \pm 34 (452–592) | 482 \pm 37 (440–600) | 468 \pm 45 (390–540) | 511 \pm 45 (410–625) | 463 \pm 40 (405–522) | 443 \pm 56 (348–680) |
| Bill length (mm) | 51.7 \pm 1.6 (49.4–54.4) | 51.6 \pm 1.5 (48.7–54.2) | 51.3 \pm 1.6 (46.4–54.2) | 50.9 \pm 1.7 (48.0–54.0) | 50.3 \pm 1.8 (46.0–54.3) | 50.4 \pm 1.6 (47.1–51.8) | 49.6 \pm 1.8 (47.6–51.8) | 48.4 \pm 1.5 (44.8–52.9) |
| | 48.5 \pm 1.1 (46.9–50.5) | 48.2 \pm 1.7 (44.0–51.9) | 48.3 \pm 1.5 (45.8–51.2) | 47.4 \pm 1.3 (45.1–50.0) | 46.9 \pm 1.5 (44.5–50.0) | 47.7 \pm 2.0 (43.7–51.2) | 47.7 \pm 1.4 (45.9–49.6) | 44.4 \pm 1.4 (41.1–47.3) |
| Bill depth (mm) | 12.5 \pm 0.6 (11.6–13.5) | 13.3 \pm 0.6 (11.9–15.1) | 12.9 \pm 0.8 (11.0–15.1) | 12.6 \pm 0.6 (11.5–13.8) | 12.4 \pm 0.6 (11.1–14.0) | 12.2 \pm 1.2 (9.3–13.5) | 12.9 \pm 0.8 (11.8–14.1) | 11.9 \pm 0.6 (10.8–13.0) |
| | 11.1 \pm 0.5 (10.1–11.8) | 11.6 \pm 0.7 (10.5–13.1) | 11.5 \pm 0.6 (10.3–13.0) | 11.3 \pm 0.7 (10.0–12.9) | 10.7 \pm 1.0 (7.9–12.1) | 11.2 \pm 0.6 (9.2–12.3) | 11.9 \pm 0.6 (11.0–13.0) | 10.8 \pm 0.5 (9.5–11.8) |

| | | | | | | | | |
|---|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|
| Head length (mm) | 103.4 ± 4.4 (90.1–107.7) | 107.7 ± 2.8 (102.0–115.2) | 105.5 ± 2.7 (98.9–114.0) | 106.1 ± 2.2 (102.7–109.7) | 102.9 ± 2.6 (97.6–108.2) | 105.6 ± 3.9 (97.7–113.0) | 102.0 ± 2.7 (98.0–105.8) | 99.0 ± 2.3 (93.6–105.6) |
| | 98.2 ± 1.7 (95.7–100.4) | 100.5 ± 2.8 (90.4–106.3) | 99.9 ± 2.1 (96.3–104.0) | 99.1 ± 2.2 (95.2–103.5) | 96.4 ± 2.2 (92.6–101.0) | 100.2 ± 3.4 (92.5–106.0) | 96.3 ± 2.6 (91.1–101.3) | 92.8 ± 2.0 (87.6–97.5) |
| Wing length (mm) | 325 ± 8 (312–345) | 324 ± 7 (310–340) | 322 ± 8 (308–343) | 318 ± 7 (309–331) | 316 ± 5 (307–326) | 322 ± 9 (305–342) | 322 ± 4 (316–326) | 299 ± 8 (273–323) |
| | 313 ± 7 (301–323) | 317 ± 6 (305–331) | 315 ± 8 (300–326) | 308 ± 5 (294–318) | 311 ± 7 (297–325) | 311 ± 8 (293–329) | 314 ± 5 (305–323) | 290 ± 7 (271–303) |
| Tarsus length (mm) | 53.9 ± 1.7 (51.5–56.7) | 53.7 ± 1.2 (50.0–55.7) | 53.2 ± 1.3 (50.6–56.0) | 52.5 ± 1.2 (50.4–54.1) | 52.2 ± 1.2 (49.6–55.0) | 53.3 ± 1.5 (50.6–55.2) | 51.7 ± 2.3 (48.9–55.6) | 50.4 ± 1.4 (47.6–54.1) |
| | 51.6 ± 1.5 (49.2–53.7) | 51.6 ± 1.3 (48.3–54.3) | 51.3 ± 1.4 (47.4–54.0) | 50.6 ± 1.2 (47.5–52.4) | 50.4 ± 1.3 (48.2–53.0) | 50.9 ± 2.0 (47.0–56.9) | 50.3 ± 1.2 (47.9–53.3) | 47.3 ± 1.3 (45.4–50.1) |
| Body size index (PC1) | 241.5 ± 5.2 (227.9–252.2) | 243.3 ± 4.1 (234.0–252.3) | 240.7 ± 4.5 (228.5–250.4) | 238.7 ± 4.7 (233.4–248.2) | 235.7 ± 3.5 (227.7–244.6) | 240.0 ± 5.6 (227.3–251.3) | 237.6 ± 4.7 (231.5–243.7) | 224.9 ± 4.4 (213.7–236.9) |
| | 230.5 ± 3.8 (224.3–237.3) | 233.5 ± 3.9 (224.7–241.5) | 232.2 ± 4.4 (223.3–239.4) | 228.3 ± 3.7 (219.4–234.8) | 227.4 ± 4.2 (218.5–234.3) | 230.2 ± 5.0 (219.9–240.6) | 229.5 ± 3.2 (224.1–234.7) | 214.5 ± 3.9 (208.2–222.7) |
| Difference in body size index between sexes | Z = 3.63 P < 0.001 | Z = 8.15 P < 0.001 | Z = 6.61 P < 0.001 | Z = 4.80 P < 0.001 | Z = 5.88 P < 0.001 | Z = 3.88 P < 0.001 | Z = 3.21 P < 0.001 | Z = 7.59 P < 0.001 |

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469 Table 1.Continued.

470 Table2. Summary of sexual size difference (SSD) in streaked shearwaters *Calonectris leucomelas* in each colony. For the
 471 abbreviation and location of colonies, see Fig. 1.

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| Colony | FO | SA | AW | KA | MI | UW | DA | NA | Mean \pm SD |
|---------------|------|------|------|------|------|------|------|------|-----------------|
| Bill length | 1.07 | 1.07 | 1.06 | 1.07 | 1.07 | 1.06 | 1.04 | 1.09 | 1.07 \pm 0.01 |
| Bill depth | 1.13 | 1.15 | 1.12 | 1.12 | 1.16 | 1.09 | 1.08 | 1.10 | 1.12 \pm 0.03 |
| Head length | 1.05 | 1.07 | 1.06 | 1.07 | 1.07 | 1.05 | 1.06 | 1.07 | 1.06 \pm 0.01 |
| Wing length | 1.04 | 1.02 | 1.02 | 1.03 | 1.02 | 1.04 | 1.03 | 1.03 | 1.03 \pm 0.01 |
| Tarsus length | 1.04 | 1.04 | 1.04 | 1.04 | 1.04 | 1.05 | 1.03 | 1.07 | 1.04 \pm 0.01 |

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480 Table 3. Summary of a Bonferroni post hoc test for multiple comparisons between the colonies for streaked shearwaters
 481 *Calonectris leucomelas*. Statistical significance ($P < 0.05$) is presented in bold. For the abbreviation and location of colonies, see
 482 Fig. 1.
 483

| Colony | | Female | | | | | | | |
|--------|-----------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|
| | | FO | SA | AW | KA | MI | UW | DA | NA |
| Male | FO | – | 0.959 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | <0.001 |
| | SA | 1.00 | – | 1.00 | <0.001 | <0.001 | 0.041 | 0.047 | <0.001 |
| | AW | 1.00 | 0.087 | – | 0.010 | <0.001 | 1.00 | 0.987 | <0.001 |
| | KA | 1.00 | 0.015 | 1.00 | – | 1.00 | 1.00 | 1.00 | <0.001 |
| | MI | 0.001 | <0.001 | <0.001 | 0.847 | – | 0.497 | 1.00 | <0.001 |
| | UW | 1.00 | 0.648 | 1.00 | 1.00 | 0.136 | – | 1.00 | <0.001 |
| | DA | 1.00 | 0.039 | 1.00 | 1.00 | 1.00 | 1.00 | – | <0.001 |
| | NA | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | – |

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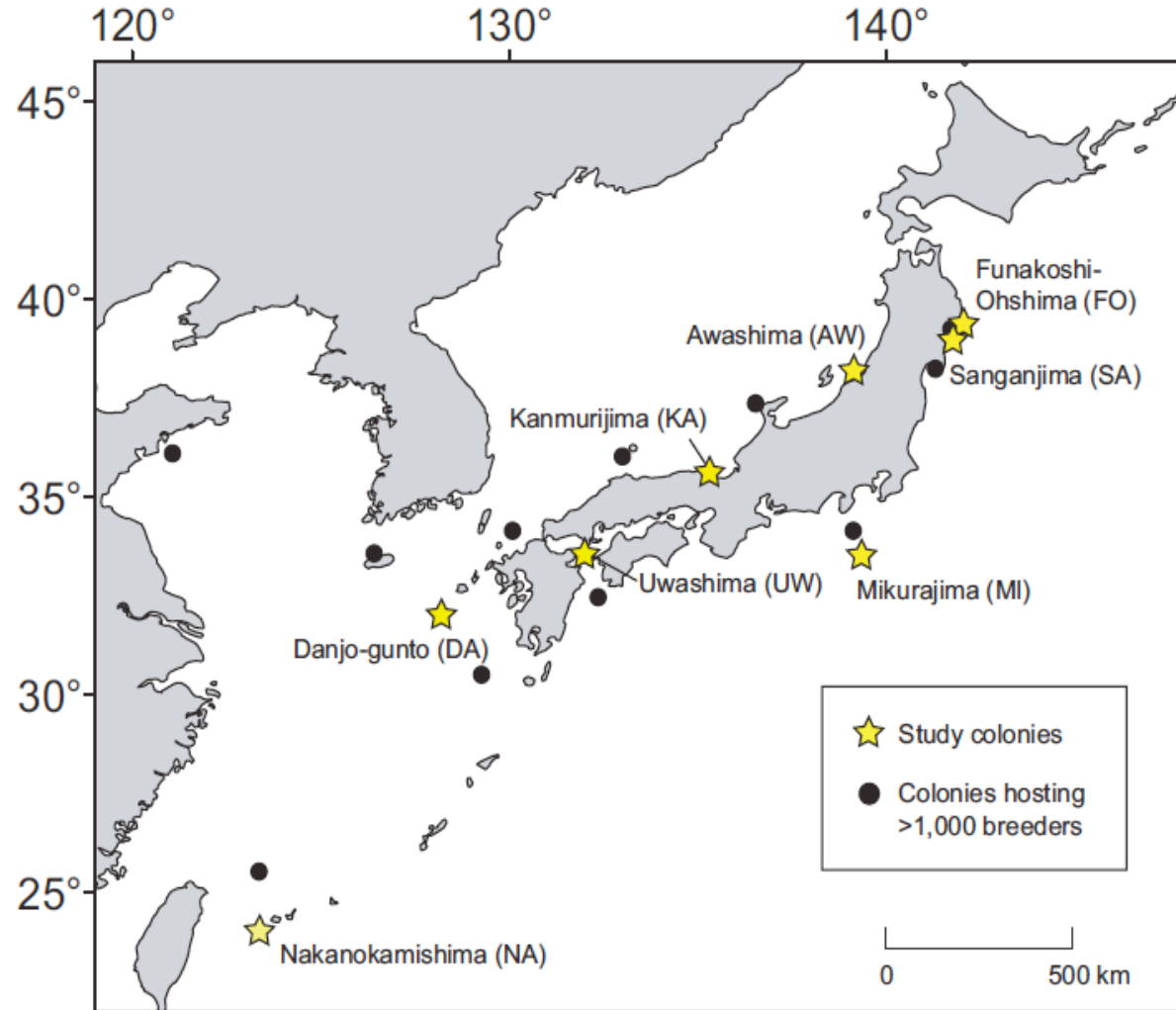
487 **FIGURE LEGENDS**

488 Figure 1. The location of study islands (stars) and colonies of streaked shearwaters
489 *Calonectris leucomelas* that host >1,000 breeding birds (black circles: in reference to Oka,
490 2004). Funakoshi-Ohshima (FO, 39°24'N, 142°00'E), Sanganjima (SA, 39°18'N, 141°58'E),
491 Awashima (AW, 38°27'N, 139°13'E), Kanmuriijima (KA, 35°40'N, 135°25'E), Mikurajima
492 (MI, 33°52'N, 139°14'E), Uwashima (UW, 33°44'N, 132°01'E), Danjo-gunto (DA, 31°59'N,
493 128°21'E), and Nakanokamishima (NA, 24°11'N, 123°34'E).

494

495 Figure 2. The relationship between the mean body size of streaked shearwaters *Calonectris*
496 *leucomelas* and (a) latitude, (b) longitude, and (c) the mean air temperature (in
497 July–September 1981–2010, representing the period between incubation and chick-rearing
498 of the species) of the study colonies. Black symbols represent males and grey symbols
499 represent females. Linear regressions estimated by generalized linear models (males: $N =$
500 222 and females: $N = 232$) are shown using solid lines and analyses without NA in dashed
501 lines. For the abbreviation of colonies, see Fig. 1.

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533 Figure 1

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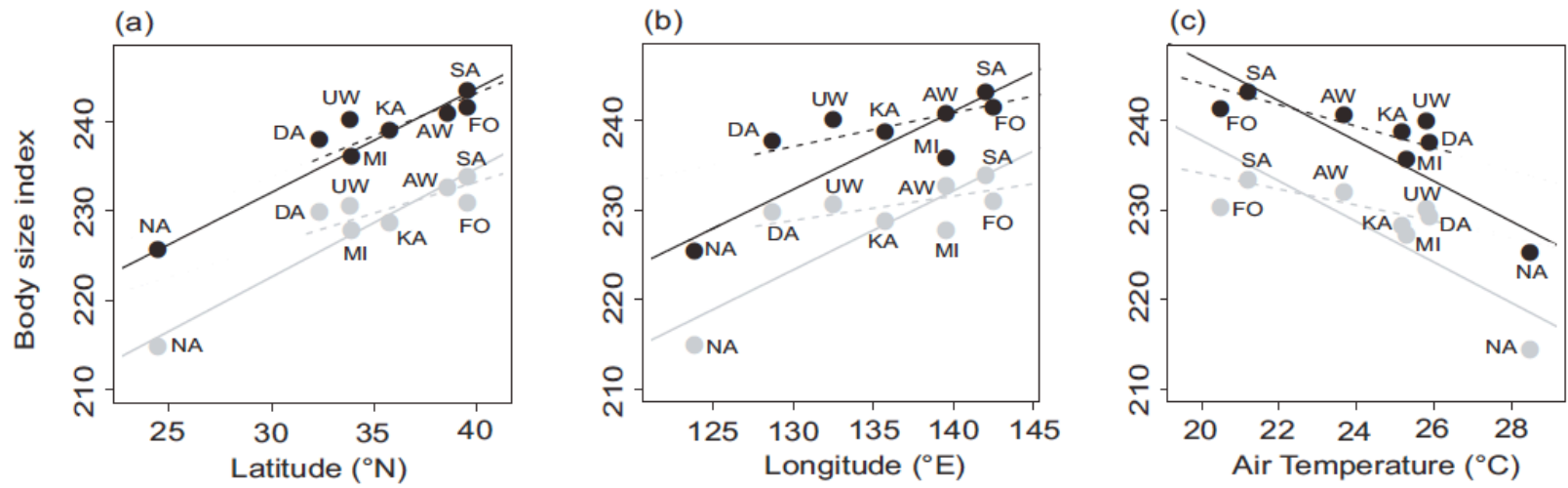


Figure 2

Journal of Biogeography

SUPPORTING INFORMATION

**Geographical variation in body size of a pelagic seabird,
the streaked shearwater *Calonectris leucomelas***

Takashi Yamamoto, Hiroyoshi Kohno, Akira Mizutani, Ken Yoda, Sakiko Matsumoto, Ryo Kawabe, Shinichi Watanabe, Nariko Oka, Katsufumi Sato, Maki Yamamoto, Hisashi Sugawa, Kiyotaka Karino, Kozue Shiomi, Yoshinari Yonehara and Akinori Takahashi

Appendix S1 Histograms of body size (PC1) for streaked shearwaters *Calonectris leucomelas*.

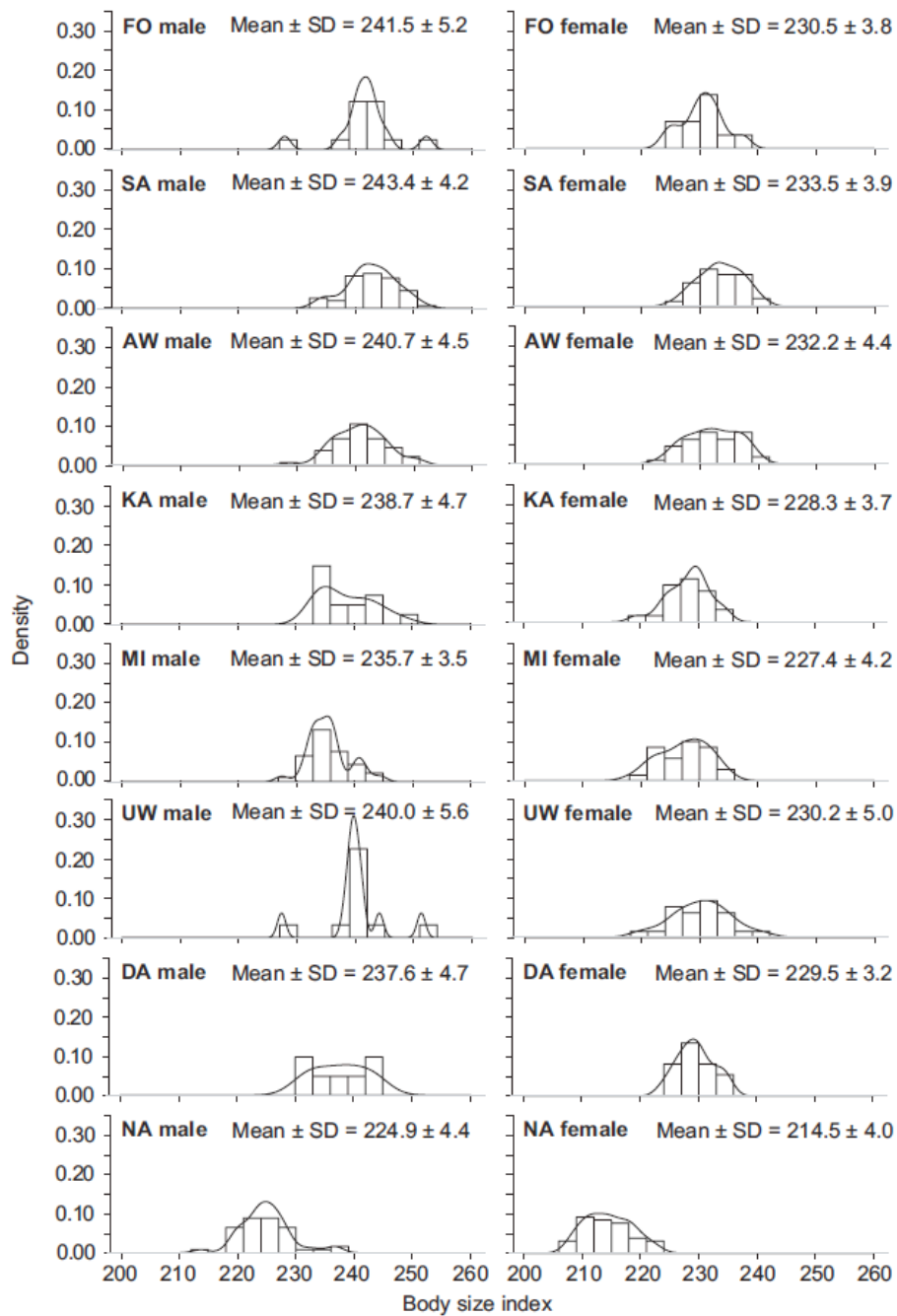


Figure S1 Histograms of body size for male and female streaked shearwaters *Calonectris leucomelas* at each breeding colony in the order of latitude from the north (top) to the south (bottom) with overlaid smoothed curves. For the abbreviation of colonies, see Fig. 1.

Appendix S2 The relationship between PC1 and each of the input variables for streaked shearwater *Calonectris leucomelas*.

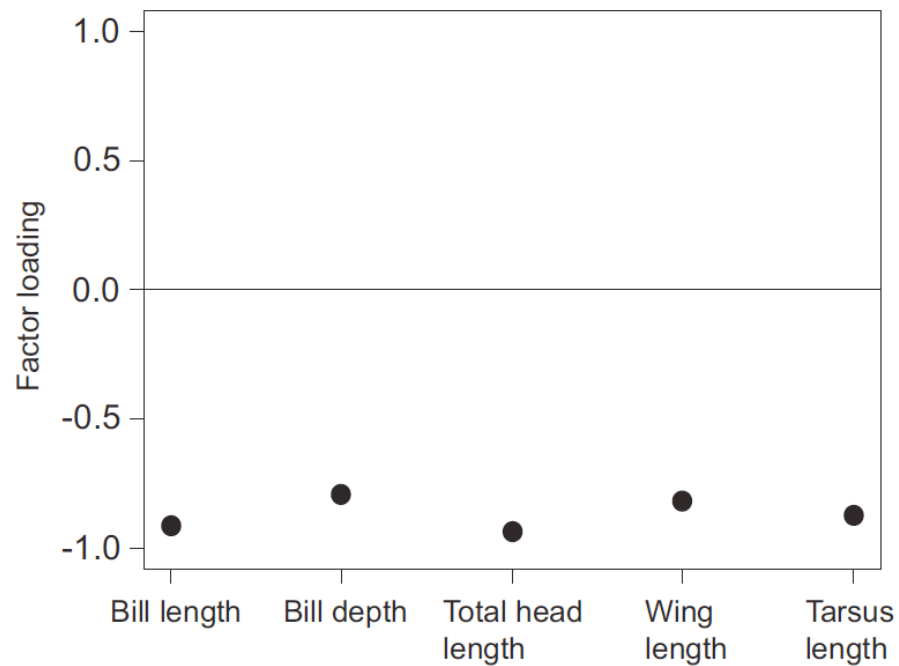


Figure S1 The relationship between the first principal component, calculated by principal components analysis, and each of the input variables (bill length, bill depth, total head length, tarsus length, and wing length) for streaked shearwaters *Calonectris leucomelas*.