



Humans preserve non-human primate pattern of climatic adaptation

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ABSTRACT

There is evidence for early Pleistocene *Homo* in northern Europe, a novel hominin habitat. Adaptations enabling this colonisation are intriguing given suggestions that *Homo* exhibits physiological and behavioural malleability associated with a 'colonising niche'. Differences in body size/shape between conspecifics from different climates are well-known in mammals, could relatively flexible size/shape have been important to *Homo* adapting to cold habitats? If so, at what point did this evolutionary strategy arise? To address these questions a base-line for adaptation to climate must be established by comparison with outgroups. We compare skeletons of Japanese macaques from four latitudes and find inter-group differences in postcranial and cranial size and shape. Very small body mass and cranial size in the Southern-most (island) population are most likely affected by insularity as well as ecogeographic scaling. Limb lengths and body breadths show group differences that accord with the expectations of thermoregulation across the whole range of latitudes. Postcranial size appears to vary more than shape, yet there is also evidence that limb segments follow Allen's rule in the forelimb at least, suggesting differing climatic signals in different regions of the skeleton. In contrast to other intraspecific studies of catarrhine ecogeography, the results presented here demonstrate non-allometric latitudinal patterns in craniofacial shape in Japanese macaques, which align closely with what is seen in cold-adapted humans. These insights begin to provide a comparison for hominin adaptation to similar habitat diversity and the role of biological adaptation in shaping the evolution and dispersal of *Homo* species.

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1. Introduction

1.1. Hominins in Northern Europe

Footprints found in 2013 at Happisburgh, Norfolk, provide evidence of hominins in northern Europe as early as ~850 ka (Ashton et al., 2014). This cool, continental and very seasonal climate (Parfitt et al., 2010; Ashton and Lewis, 2012) would have presented a novel set of challenges to hominins adapted to tropical Africa, including key stressors such as very low temperatures, increased seasonality, snow cover/precipitation, a shorter growing season and shorter day length (Ashton and Lewis, 2012; Hosfield, 2016).

How northern European Early Pleistocene populations would

have adapted to this environment is an open question. As hominins, with inherently flexible cognition and behaviour, behavioural and technological coping mechanisms would be expected, yet there is no evidence for great technological sophistication at this time and in this place. The oldest technology at Happisburgh is Mode 1, simple flake tools, and there is no evidence of structures (Ashton et al., 2014). Furthermore, despite continuing debate, it seems likely that control of fire was not mastered in Europe until the middle Pleistocene, at about 4–300 ka (Roebroeks et al., 2011). In terms of mitigating behaviour, migration on a scale large enough to avoid the cold seems unlikely, especially for the entire group, including the young, old, and pregnant females (Hosfield, 2016). Range expansion is possible, however, as are changes in diet either through dietary expansion (Buck and Stringer, 2014; Buck et al., 2016; Hosfield, 2016) or the consumption of greater amounts of meat and fatty tissues (Cordain et al., 2000). The extent of clothing in the middle Pleistocene is unknown, and the technology for tailored clothing is absent from the archaeological record (Gilligan,

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2010), but coverings of some kind seem likely, as for the later Neanderthals (Wales, 2012). If earlier hominins had similar thermoregulatory systems to present day *Homo sapiens*, it seems doubtful that with such a simple suite of technologies, behavioural adaptation would have buffered environmental stress sufficiently. If this is the case, biological adaptations would also have been required to allow the colonisation of this new climatic niche.

1.2. Biological adaptation to climate in hominins

Adaptation to climate is one of the key determinants of animal form and some of the most well-known and robust thermoregulatory patterns in morphology throughout the mammal class are Bergmann's (Bergmann, 1847) and Allen's (Allen, 1877) rules (Ashton et al., 2000; Meiri and Dayan, 2003). Bergmann's rule states that, within a species, individuals from higher latitudes will be larger (Bergmann, 1847) and Allen's states that those same cold-adapted individuals will have shorter appendages, including limbs and tail (Allen, 1877). The relationship between surface area and heat loss underpins these rules; endothermic animals produce their own heat internally and heat loss is directly proportional to surface area. Depending on surrounding temperatures, it is beneficial to either conserve or lose internally-generated heat and animal body proportions correspond accordingly. As with many other mammal species (Katzmarzyk and Leonard, 1998; Ashton et al., 2000; Meiri and Dayan, 2003), obedience to Bergmann's and Allen's rules can be seen in differing body proportions between populations of recent *H. sapiens* from different climates. Brachial and crural indices, bi-iliac breadth and rib cage shape have a close relationship with mean annual temperatures and populations living in cooler areas tend to have more barrel-shaped chests and broader hips (Ruff, 1994, 2002; Ruff et al., 1997; Franciscus and Churchill, 2002; Stock, 2006).

Climate is also an important selective pressure on human cranial shape; in fact, adaptation to extreme cold stress is thought by some to be the only non-neutral signal in recent *H. sapiens* craniofacial morphology (Roseman, 2004; Roseman and Weaver, 2004). *H. sapiens*, neurocranial shape and size seem to vary with climate in accordance with Allen's and Bergmann's Rules; crania are larger and more brachycephalic in cold climates (Beals, 1972; Beals et al., 1984; Nowaczewska et al., 2011). Cold-adaptation has also been inferred in greater facial breadth and reduced facial projection (Hubbe et al., 2009; Betti et al., 2010; Evteev et al., 2014, 2017), in accordance with Allen's rule, and in the shape of the nasal apparatus (Carey and Steegmann, 1981; Franciscus and Long, 1991; Betti et al., 2010; Noback et al., 2011). In cold climates the nasal aperture is generally narrower in relative terms (Weiner, 1954; Franciscus and Long, 1991; Hubbe et al., 2009; Evteev et al., 2014) and the internal nasal cavity is configured to increase contact time between the air and highly-vascularised nasal mucosa (Noback et al., 2011; Evteev et al., 2014, 2017). This morphology is thought to be an adaptation to optimise air conditioning. A close relationship between climate and nasal morphology is to be expected, as inspired air must be warmed to body temperature to avoid damaging respiratory tissues and to enable the proper functioning of the nasal cilia and mucosa, whilst expired air can be an important source of heat and moisture loss (Negus, 1957; Carey and Steegmann, 1981). For each of these cranial regions, the majority of differences seem to be driven by populations from very cold climates, and the signal becomes weaker or disappears if those samples are removed (Roseman, 2004; Harvati and Weaver, 2006; Hubbe et al., 2009; Betti et al., 2010; Relethford, 2010; Foster and Collard, 2013).

Climatic effects on hominin skeletal morphology have also been inferred in the fossil record, particularly with regards to Neanderthals in glacial Eurasia (Coon, 1962; Brose, 1967; Churchill, 1998;

Wolpoff, 1999; Steegmann et al., 2002). In the cranium, increased mid-facial prognathism was historically seen as an adaptation to increase the distance between the respiratory apparatus and arteries serving the brain, thus reducing the cooling effect of inspired air on the cranial blood and delicate cerebral tissues (Coon, 1962; Brose and Wolpoff, 1971; Wolpoff, 1999), whilst the large nasal aperture has been attributed to the need to warm and condition air (Coon, 1962; Churchill, 1998; Wolpoff, 1999). The relationship between greater prognathism and cold-adaptation is dubious, since it is the exact opposite of the trends described above for *H. sapiens* and also for other mammals, such as experimentally cold-adapted rats (Steegmann and Platner, 1968; Rae et al., 2006, 2011). The evidence of whether the Neanderthal nose is cold-adapted is still debated (see Churchill [2014] for a review), some elements of Neanderthal nasal morphology appear to optimise inspired air passage for more efficient warming, as in cold-adapted *H. sapiens* (de Azevedo et al., 2017; Wroe et al., 2018). The great breadth of Neanderthal noses, however, is still puzzling when compared to narrower noses in cold-adapted recent humans, macaques, and rats (Steegmann and Platner, 1968; Rae et al., 2003, 2006, 2011), and may be due to constraint and integration with other cranial structures.

In contrast to the debate over Neanderthal cranial morphology, there is substantial agreement that many of distinctive Neanderthal postcranial traits are climatic adaptations (Trinkaus, 1981; Holliday, 1997; Churchill, 2014). Holliday has shown Neanderthals to have body proportions similar to those of modern humans from very high latitudes, but even more 'hyperpolar' (Holliday, 1997). Neanderthals have short limbs and especially short distal limb segments relative to trunk height or proximal limb segment length, following Allen's rule. They have long trunks and high body mass also obeying Allen's and Bergmann's rules (Holliday, 1997). The extreme postcranial robusticity and larger joint diameters seen in Neanderthals compared to *H. sapiens* are likely linked to colder temperatures via their relationships with body mass and proportions (Ruff, 1994).

1.3. The relative importance of biological adaptation in hominins

The above evidence demonstrates that hominins adapt physically to the climate as other mammals do, following ecogeographic rules such as Bergmann's and Allen's. What is unknown is the extent which this adaptation is of the same magnitude and follows the same patterns as in other primates and whether the hominin pattern of climatic adaptation is conserved or derived. Though humans display considerable phenotypic diversity, we are remarkably genetically homogenous compared to other primate species (Kaessmann et al., 2001; Bowden et al., 2012) and from what we know of genetic variation in other hominin species, it appears they were even more so (Meyer et al., 2012; Castellano et al., 2014). It has been suggested that this dichotomy between variation in phenotype and genotype arises from a human evolutionary strategy characterised by flexibility and adaptability, making humans consummate generalists (Wells and Stock, 2007; Stock, 2008; Antón et al., 2016). This hyperadaptability, varying physically and behaviourally whilst largely buffering the genotype, would have facilitated dispersal into novel habitats and has thus been described as constituting a "colonising" niche (Wells and Stock, 2007).

If the exploitation of a colonising niche is a human trait, when did it begin? Is it a trait of the primate order, a trait of the tribe hominini, a trait of the genus *Homo*, or a trait of the species *H. sapiens*? Adaptability would have been particularly important during periods of climatic instability (Vrba, 1985, 2015; Foley, 1987; Potts, 1998, 2013). Regional variation in *Homo* during one such

period, the Plio-Pleistocene, suggests environmental variation could have led to local adaptation and plasticity (Will et al., 2017; Will and Stock, 2015). If this is the case, the hominins inhabiting Northern Britain in the Early Pleistocene may have benefitted from this heritage of selection for adaptability.

1.4. A suitable base-line

In order to discern whether human skeletal morphology follows a conserved ecogeographic pattern it is necessary to compare covariation between climate and morphology to those in a non-human outgroup. Here we investigate ecogeographic patterns in Japanese macaque (*Macaca fuscata*) skeletal morphology to determine a non-human primate base-line against which to compare hominin climatic adaptation. *M. fuscata* is one of the most northerly wild-living non-human primates, with groups in the Shimokita peninsula of Honshu living at > 41°N (Fooden and Aimi, 2005). The species shows a wide latitudinal spread throughout the Japanese Archipelago (with the exception of Hokkaido and its surrounding islets), from temperate regions experiencing high snowfall in winter to subtropical islands (Fooden and Aimi, 2005). The Primate Research Institute (PRI), part of Kyoto University, houses very large collections of wild-shot, complete, well-documented specimens from all over Japan allowing the assemblage of an excellent sample. To the best of our knowledge, this is not only the first study to investigate intraspecific primate ecogeography throughout the skeleton, but also the first to do so with the express purpose of using it as a base-line against which to compare the human pattern of adaptation. Shared ecogeographic patterning between humans and macaques could suggest that human climatic adaptation is conserved. If this is the case, it would emphasise the importance of technological and behavioural adaptation to climate in our lineage. A lack of covariation between climate and morphology in macaques, or a different pattern of covariation to that seen in humans, could suggest that the human propensity for phenotypic variation is an evolutionary novelty that could have been key in our successful global colonisation.

1.5. Non-human primate ecogeography

There is a considerable body of literature on the subject of non-human primate ecogeography (e.g., Frost et al., 2003; Cardini and Elton, 2008, 2009a, 2009b; Weinstein, 2008; Ito et al., 2011, 2014; Dunn et al., 2013; Meloro et al., 2013; Cáceres et al., 2014), but the focus of such studies has not generally been a systematic characterisation of patterns of adaptation throughout the skeleton in a single, widely distributed species. This is in part, no doubt, because few species have ranges comparable with *M. fuscata*. Here we examine cranial and postcranial ecogeographic patterns in groups of *M. fuscata* covering their entire distribution to provide a future comparison for human data analysed using the same methods.

Across the macaque genus there is an ecogeographic cline in craniofacial morphology related to allometry whereby, as cranial size increases faces are more elongated (Ito et al., 2011, 2014a). This pattern is disrupted by the most cold-adapted species, including *M. fuscata*, where faces are rounder and cranial size greater than expected, following thermoregulatory predictions of Bergmann's and Allen's rules (Ito et al., 2011, 2014a). Once size is accounted for however, the relationship between shape and phylogeny is stronger than with any other variable and if phylogeny is controlled for, there is no relationship between shape and climate (Ito et al., 2014a). These results are consistent with studies of species and genera that are more geographically-restricted than the macaques, such as red colobus monkeys (Cardini and Elton, 2009a, 2009b), guenons (Cardini and Elton, 2008) and papionins (Frost et al., 2003;

Dunn et al., 2013), where size has been found to be more labile than shape in ecogeographic patterning and phylogeny is generally the most important determinant of non-allometric shape.

Across the macaques as a genus, there is also evidence that postcranial morphology conforms to Bergmann's and Allen's rules (Weinstein, 2011). In addition to variation linked to locomotion and phylogeny, species experiencing colder temperatures have comparably shorter limbs and larger body sizes and joint surfaces, the latter reflecting greater body masses (Weinstein, 2011). Paterson (1996), in studying groups of *M. fuscata* transplanted from Arashima (central Japan) to both Texas and Oregon demonstrated that in the transplanted monkey's adherence to Bergmann's rule, macaque postcrania is plastic over a small number of generations (20 years and 27 years respectively). *M. fuscata* differ throughout their range in coat colour, body composition and size (Hamada, 1996; Fooden and Aimi, 2005; Hamada and Yamamoto, 2010). In many respects these differences can be interpreted as ecogeographic patterns; for example, thicker, paler coats in colder regions provide greater insulation and camouflage against the snow (Inagaki and Hamada, 1985; Hamada et al., 1992; Hamada and Yamamoto, 2010) and body mass and trunk length generally follow Bergmann's rule (Hamada, 1996; Hamada and Yamamoto, 2010). The evidence regarding specific body measurements is equivocal, however. There is no consistent cline throughout Japan in greater head and body lengths, sitting height or anterior trunk length (Hamada, 1996; Fooden and Aimi, 2005).

The results from previous research show some evidence for skeletal adaptation to climate in *M. fuscata*. The current study builds on this work by systematically studying differences in cranial and postcranial morphology between groups from different latitudes throughout the species' range. This will clarify the nature of ecogeographic patterns in this species and provide a base-line pattern of non-human primate adaptation in a wide range of latitudes against which to compare human variation.

2. Materials and methods

2.1. Materials

2.1.1. Sample

The sample (Table 1) consisted of 82 adult *M. fuscata* skeletons from the collections housed at the Primate Research Institute, Kyoto University (PRI). Adulthood was judged by the eruption of the 3rd molar to occlusion and the fusion of the basioccipital synchondrosis. Only specimens without visible pathology in the regions of interest were used.

The sample comes from locations at four different latitudes ranges within Japan: Shimokita in North Honshu; Nagano in mid Honshu; Shimane, Wakayama, Takasakiyama and Yamanashi in

Table 1

Macaque sample. F: female, M: male. Latitude: degrees north for central point of prefecture.

| Group | Prefecture | Sex | n | Latitude |
|-------------------------|------------|--------------|----|----------|
| N. Honshu | Shimokita | F | 10 | 41.31 |
| | | M | 10 | |
| M. Honshu | Nagano | F | 10 | 36.64 |
| | | M | 10 | |
| S. Honshu/ N. Kyushu | Shimane | F | 10 | 35.02 |
| | | M | 5 | |
| | Wakayama | M | 1 | 33.78 |
| | | Takasakiyama | M | 2 |
| Kyushu | Yamanashi | M | 3 | 35.66 |
| | Yakushima | F | 11 | 30.34 |
| | | M | 10 | |

South Honshu/North Kyushu; and Yakushima island off the Southern coast of Kyushu (Table 1). This includes both the most northerly (Shimokita) and most southerly (Yakushima) populations of *M. fuscata* in the wild. These groups are geographically well separated and most populations of Japanese macaques are isolated from one another due to human-induced habitat fragmentation, making gene flow between groups unlikely (Marmi et al., 2004). For the South Honshu/North Kyushu sample, there were ten complete female skeletons available, but only five complete male skeletons available from a single site, Shimane, thus the sample also includes six male individuals from latitudinally close groups (Wakayama, Takasakiyama and Yamanashi). The effect of combining these specimens from different sites, in a group named Shimane et al. is examined below.

2.1.2. Analyses of variation in sample composition – combination of sites in shimane et al

2.1.2.1. Sample variation in postcranial measurements.

Coefficients of variation for traditional morphometric postcranial measurements, adjusted for small sample sizes (V^* : Sokal and Rohlf, 1995), were calculated to investigate the potential effect of combining males from several different sites in the Shimane et al. group (Fig. 1). The mixed site Shimane et al. male group has higher levels of variation than the females from Shimane et al. (which are all from Shimane itself), and higher than most of the other male samples. However, the Shimane et al. males' level of variation is comparable to that of the male sample from Yakushima, which is also considerably higher than variation in the female Yakushima sample. This suggests the level of variation introduced into the sample by combining different South Honshu/North Kyushu sites is acceptable, given the need to preserve sample size.

2.1.2.2. Sample variation in cranial analyses.

To quantify the amount of variation in craniofacial shape within samples the mean Procrustes distance from each group member to the group centroid was calculated (Table 2) (Gunz et al., 2009; Webster and Sheets, 2010). Shimane et al. fits well within the mean variation for the other groups and has, in fact the second lowest level of within group shape variation. This suggests grouping South Honshu/North Kyushu males from several sites is not unacceptably inflating the levels of variation in the Shimane et al. group and that this sample may reasonably be compared with other, single-site groups.

Table 2

Within group shape variation as measured by the mean of Procrustes distances from each group member to the mean shape for that group.

| Group | Mean Procrustes distance |
|----------------|--------------------------|
| Shimokita | 0.053 |
| Nagano | 0.060 |
| Shimane et al. | 0.058 |
| Yakushima | 0.062 |

2.2. Methods

Crania were CT scanned by LTB on the Asteion Premium 4 helical scanner (Toshiba Medical Systems, Otawara, Japan) housed at the PRI. Voxel sizes vary slightly between individuals due to differences in cranial size, but all are approximately $0.3 \times 0.3 \times 0.5$ mm. Humeri, radii, ulnae, femora, tibia, first metacarpals/tarsals, clavicles, 2nd ribs, os coxae, and sacra were measured using callipers and an osteometric board (Table 3).

Latitude was used as a simple univariate proxy for climate, as is common in ecogeographic studies (e.g., Bergmann, 1847; Allen, 1877; Ashton et al., 2000; Meiri et al., 2007; Meloro et al., 2013; Roseman and Auerbach, 2015). Across the study sites latitude shows a strong relationship with mean annual temperature (Reduced Major Axis Regression: mean annual temperature = $-1.008 + 48.3 * \text{latitude}$, $r^2 = 0.8$, $p < 0.0001$) and annual precipitation (RMA regression: annual precipitation = $-214.1 + 9637.1 * \text{latitude}$, $r^2 = 0.7$, $p < 0.0001$), showing the suitability of the proxy.

2.2.1. Traditional morphometric analyses of postcrania

To investigate postcranial size, measurements of the maximum lengths of humeri, radii, ulnae, femora and tibiae were taken. To investigate body breadth, the chord of second rib, maximum clavicle length, bi-iliac breadth, and anterior breadth of the sacrum were measured (Table 3). To preserve sample sizes, sexes were pooled and male values corrected to female mean following Rogers Ackermann et al. (2006). The few missing values were replaced by group and sex appropriate means (see Table 4 for details of missing data). To investigate postcranial shape, crural and brachial indices of limb measurements were calculated. An ordinal variable (latitude) was used to analyse the macaque data as it best describes the sample, which comes from several, distinct

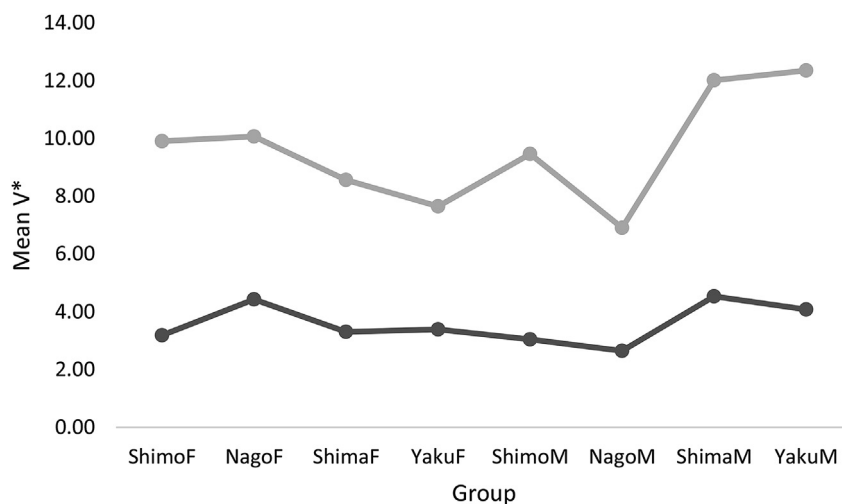


Fig. 1. Means of sample size-adjusted coefficients of variation for maximum lengths (dark grey) and body breadths (light grey) across males and females for each group. ShimoF: Shimokita females, NagoF: Nagano females, ShimaF: Shimane females, YakuF: Yakushima females, ShimoM: Shimokita males, NagoM: Nagano males, ShimaM: mixed group of South Honshu/North Kyushu males, YakuM: Yakushima males.

Table 3

Traditional morphometric measurements used to characterise postcranial size and shape. Except where indicated, all measurements are taken from Buikstra and Ubelaker (1994).

| Measurement | Definition |
|---------------------------|--|
| Humeral maximum length | Distance from superiormost point on humeral head to inferiormost point on trochlea |
| Radial maximum length | Distance from most proximal point on radial head to tip of styloid process |
| Ulnar maximum length | Distance from superiormost point on olecranon to inferiormost point on styloid process |
| Femoral maximum length | Distance from superiormost point on femoral head to inferiormost point on distal condyles |
| Tibial maximum length | Distance from superior articular surface of lateral condyle to tip of medial malleolus |
| 2nd rib | Tuberculoventral chord (Franciscus and Churchill, 2002) |
| Clavicular maximum length | Maximum distance between most extreme ends of clavicle |
| Bi-iliac breadth | Maximum breadth of iliac crests when both os coxae are held in anatomical position with sacrum |
| Sacral anterior breadth | Maximum transverse breadth of sacrum at level of anterior projection of auricular surface |

Table 4

Missing data in traditional morphometric measurements per sample for each site, sexes combined. Hum = humerus, Rad = radius, Uln = ulna, MC1 = first metacarpal, Fem = femur, Tib = tibia, MT1 = first metatarsal, Bi-il Br = bi-iliac breadth, Sac Ant = anterior breadth of sacrum, Clav = clavicle, Max = maximum length, 2nd Rib = chord of the 2nd rib.

| Group | Site | N of individuals with missing data per measurement/n for site per measurement | | | | | | | | |
|---------------------|----------------|---|---------|---------|---------|---------|----------|---------|----------|---------|
| | | Hum Max | Rad Max | Uln Max | Fem Max | Tib Max | Bi-il Br | Sac Ant | Clav Max | 2nd Rib |
| N. Honshu | Shimokita | 0/20 | 0/20 | 1/20 | 0/20 | 0/20 | 0/20 | 1/20 | 0/20 | 0/20 |
| M. Honshu | Nagano | 0/20 | 0/20 | 0/20 | 0/20 | 0/20 | 1/20 | 0/20 | 0/20 | 2/20 |
| S. Honshu/N. Kyushu | Shimane et al. | 1/20 | 1/20 | 2/20 | 1/20 | 1/20 | 1/20 | 1/20 | 1/20 | 4/20 |
| Kyushu | Yakushima | 0/20 | 2/20 | 1/20 | 0/20 | 0/20 | 1/20 | 1/20 | 1/20 | 2/20 |

sites rather than representing a continuous distribution from throughout Japan. Analyses of Variance (ANOVA) were performed in PAST (Hammer et al., 2001) to test for significant differences in the normally distributed individual variables between groups from different latitudes. In the variable that was not normally distributed (anterior sacral breadth), a Kruskal Wallis analysis was used as a non-parametric equivalent of an ANOVA (Hammer et al., 2001). Canonical Variates Analysis (CVA) and Multivariate ANOVA (MANOVA), also in PAST, were used to ascertain group separation and its significance when analysing multiple variables. CVA was used as it enables investigation of the variables contributing most to differences between groups and allowed consistency between analyses of craniofacial (see below) and postcranial morphology, despite the different landmark and traditional morphometric approaches used respectively.

2.2.2. Measurement of body mass

Weight at death was available for most specimens, taken from PRI records. No weight at death was given for any male Yakushima individuals used in the sample, nor for eight of ten female Yakushima individuals used. For these Yakushima individuals a value was used based on captive Yakushima *M. fuscata* held at the PRI (Males = 9.97 kg [standard deviation = 2.24, n = 47], Females: 7.57 kg [standard deviation = 1.67, n = 60]). As these values are taken from captive individuals (in the case of the females, a mean was calculated with the captive data and the two weight at deaths from the specimens used in the study) they will be an over-estimation of actual weight in this group (see below). Due to the use of a captive mean, the distribution of body mass in the Yakushima sample was unknown and thus non-parametric permutation tests, ANOSIMS (analysis of similarity), were performed using PAST (Hammer et al., 2001) on all the body mass analyses. An ANOSIM is analogous to an ANOVA in that it compares differences within and between groups. Distances are converted to ranks and the test statistic R gives a measure of relative within group dissimilarity, with more positive numbers showing greater difference. R is interpreted like a correlation coefficient and is a measure of size effect (Hammer et al., 2001).

2.2.3. Geometric morphometric analyses of crania

In Avizo 9.1 Lite (FEI, Hillsboro, USA) 63 3D landmarks (Table 5, Fig. 2) were digitised onto virtual cranial surfaces produced from CT data by a single observer (LTB). Landmarks were chosen from published non-human primate ecogeographic studies (Singleton, 2002; Frost et al., 2003; Cardini and Elton, 2008; Ito et al., 2011) and aimed to capture neurocranial globularity, facial projection, nasal aperture size/shape and orbit size/shape.

Five repetitions of the landmarks on the same cranium (not included in the sample) showed an error of <1 mm in accuracy for each, with a range of 0.07 mm (incisivism) - 0.90 mm (pterion pos.). Generalised Procrustes superimposition (GPA) of the five repetitions of the cranium used for the error testing and the entire sample showed that none of the sample had equal or smaller Procrustes Distances to one another as the largest distance between the error test repetitions (see SI). The landmarks were thus judged to be of sufficient precision and accuracy to accurately capture shape.

Landmark coordinates were exported to MorphoJ (Klingenberg, 2011) and subjected to GPA to remove translation, rotation and (non-allometric) size differences. Superimposition was followed by principle components analysis (PCA) to summarise major axes of shape variation and visualise groupings. Warps of mean shape along PCs allowed visualisation of differences, aided by wireframes (Fig. 3, Table 6). As for the individual traditional morphometric variables, ANOVA of centroid sizes in PAST was used to investigate group differences in cranial size. CVA in MorphoJ was used to examine whether the morphological differences between groups were related to latitude. CVA decomposes variation between groups and produces new variables that are uncorrelated within and between groups and each explain successively less intergroup variation. This method was chosen because it provides ordination of the differentiation between groups, allows for the testing of the significance of the morphological differences between groups and allows visualisation of these differences by warping the mean shape. Distances in CVA space are in Mahalanobis distances and a concurrent MANOVA was used to test for significant differences in Mahalanobis distances between groups.

3. Results

3.1. Body mass results

Due to the non-parametric distribution of the Yakushima estimates caused by the use of captive mean weights (see above), one-way ANOSIM tests were used to determine significant differences between groups. Females: mean rank within: 239.8, mean rank between: 436, $R: 0.503$, $p < 0.001$. Males: mean rank within: 238.3, mean rank between: 462.4, $R: 0.547$, $p < 0.001$. Both male and female Yakushima macaques are significantly smaller than members of the same sex of other groups (Tables 7 and 8, Fig. 4). There are no other significant differences between groups. Since the values used for the Yakushima samples are from captive individuals, which are greater than wild animal's weights, the real difference between wild Yakushima *M. fuscata* and other groups would be greater.

3.1.1. Postcranial results - limb lengths

The pooled sex Yakushima sample has highly significantly shorter measurements than all other groups for each limb measurement (see SI for results of all comparisons). There are also smaller, but still significant, differences between Shimokita and Shimane et al. in femoral and tibial lengths and this difference is border-line significant in humeral length (Table 9). In each bone measurement, Shimokita is the larger. There are no significant differences between groups (discounting Yakushima) in radial or ulnar lengths.

A canonical variates analysis (CVA, Fig. 5) shows that the groups can be separated with an accuracy of 72% using combined maximum limb bone lengths. Yakushima in particular is well-separated from all the other groups on CV1, the axis with the greatest discriminatory power. Maximum femoral and tibial length contribute most to CV1 (89.87% variance), radius and ulna to CV2 (9.46% variance) and tibial length to CV3 (0.67% variance) (Table 10). Thus, hindlimb length contributes most to group separation between Yakushima and the other groups and distal forelimb length contributes most to the separation between Shimokita and the other groups, despite differences in radial and ulnar length not reaching significance alone.

A MANOVA shows that there are significant differences in combined lengths between all groups except Nagano and Shimane et al. ($F [15, 204.7] = 20.76$, $p < 0.0001$). The Mahalanobis distances between groups (Table 11) reflect the latitudinal origins of groups, such that groups closer together in latitude are closer together in size as measured by limb length.

3.1.2. Postcranial results - body breadth

The pattern in body breadth measurements is more complex than in limb lengths, but there is a general decrease in body breadth from Nagano to Shimokita to Shimane et al. to Yakushima. Yakushima is always the narrowest group, although not all differences are significant (see SI).

The Yakushima group have significantly shorter clavicle lengths than all others and there are no other significant differences (ANOVA: $F [3, 78] = 24.97$, $p < 0.001$). In the chord of the second rib Shimokita/Nagano are significantly broader than Shimane et al./Yakushima (ANOVA: $F [3, 78] = 21.30$, $p < 0.001$). In bi-iliac breadth Yakushima is significantly narrower than all other groups and Nagano is significantly broader than Shimane et al. (ANOVA: $F [3, 78] = 19.25$, $p < 0.001$). In anterior sacral breadth there are significant differences between all groups except Shimokita and Shimane et al. (Kruskal Wallis: $\chi^2 = 27.41$ (3), $p < 0.001$); Nagano is the broadest and Yakushima the narrowest (for statistical details of pairwise comparisons, see SI).

A CVA shows that the groups can be separated with an accuracy

of 70.73% using all four measurements of body breadth (Fig. 6). As with the maximum limb lengths, Yakushima is the most distinctive group, but it is less so in body breadth than in limb lengths. When the measurements are combined, Nagano and Shimokita overlap almost completely, whilst Shimane et al. is lower on CV2 and slightly lower on CV1. Bi-iliac breadth contributes most to CV1 (86.79% variance), maximum clavicle length to CV2 (13.11% variance) and anterior sacral breadth to CV3 (0.10% variance) (Table 12). Thus bi-iliac breadth contributes most to the difference between Yakushima and the other groups, whilst clavicular length and sacral breadth contribute most to the differences between Shimane et al. and the other groups.

Using combined body breadth measurements, there are significant differences between Yakushima and all groups and also between Shimane et al. and Nagano. (MANOVA: $F [12, 198.7] = 7.09$, $p < 0.0001$) (Table 13).

3.1.3. Postcranial results - limb indices

To investigate postcranial shape, differences in limb proportions between groups were examined.

3.1.3.1. Brachial indices. Shimokita has significantly lower brachial indices than all the other groups (ANOVA: $F = 4.82$, $p < 0.005$, $\sigma^2 = 0.12$, Fig. 7, Table 14), demonstrating relatively shorter distal forelimb segments.

3.1.3.2. Crural indices. Crural indices in the Shimane et al. group are significantly lower than Yakushima (ANOVA: $F = 3.26$, $p < 0.05$, $\sigma^2 = 0.08$, Fig. 8 and Table 15), likely due to the low outlier in Shimane et al. There are no other significant differences between groups. Despite the lack of significant differences, Yakushima has slightly higher crural indices than Shimokita and Nagano as well as Shimane et al. showing that this sample have slightly longer relative distal hindlimb segments.

3.2. Cranial shape results

3.2.1. Allometry in cranial shape

Centroid size generated using the cranial landmark set (Fig. 9) reflects the same patterns as body mass (Fig. 4). Males are significantly larger than females for each group and Yakushima macaques are significantly smaller than members of the other groups of their respective sex (ANOVA: $F = 69.58$, $p < 0.0001$, $\sigma^2 = 0.86$, for Tukey's pairwise comparisons of individual groups, see SI). There are no other significant differences between groups, there is, however, a trend for centroid size to decrease as latitude increases in males (excluding Yakushima), contra to what would be expected given Bergmann's rule.

Following PCA, which suggested the major source of variation (represented by PC1, which explains 10% of variation in the sample, see Fig. 10) between specimens was due to sex and sex-related size, a multiple multivariate regression analysis was performed in MorphoJ of the Procrustes aligned shape coordinates on sex (coded as a dummy variable: 1 or 0) and size (the natural log of centroid size) to produce sex/size-free residuals (Ito et al., 2014a). These residuals were used in subsequent canonical variates analysis (CVA) and permutation tests of significance.

3.2.2. Allometry-free cranial shape results

A CVA of sex- and allometry-free shape variables (see above) separates groups on CV1 (Fig. 11). This CV (60% variance) separates Shimokita/Nagano at the lower end, from Shimane et al. in the middle, from Yakushima at the highest end. Using all three axes there are significant differences between all groups (permutation test with 1000 rounds [Klingenberg, 2011]), and the sizes of

Table 5
Landmarks used in this study.

| Number in this study | Landmark | Definition |
|----------------------|---|--|
| 1 | Glabella | Most anterior midline point on frontal |
| 2 | Nasion | Meeting point of nasals and frontal |
| 3 | Rhinion | Most inferior point on nasals |
| 4 | Nasal/premaxilla | Meeting point of nasal and pre-maxilla on the border of the piriform aperture |
| 5 | Premaxillary suture inf. | Most inferior point on premaxillary suture |
| 6 | Premaxillary suture sup. | Most superior point on premaxillary suture |
| 7 | Optic foramen | Top middle of optic foramen |
| 8 | Supraorbital notch | Most lateral point on supraorbital notch/foramen |
| 9 | Midtorus inf. | Point on inferior margin of supraorbital torus (superior margin of orbit) roughly at middle of orbit |
| 10 | Midtorus sup. | Point superior to midtorus inferior on superior most point of supraorbital torus when viewed in Frankfurt horizontal |
| 11 | Frontomalare orbitale | Meeting point of frontozygomatic suture and orbital margin |
| 12 | Zygoorbitale | Meeting point of zygomatic suture and orbital margin |
| 13 | Zygomaxillare | Most inferior point on zygomatic suture |
| 14 | Alare | Most lateral point on nasal margin |
| 15 | Nasiospinale | Most antero-inferior point of piriform aperture |
| 16 | Prosthion | Most inferior point on alveolar bone between central incisors |
| 17 | Prosthion 2 | Most inferior point on alveolar bone between central and lateral incisors |
| 18 | Canine alveolus ant. | Anteriormost point of canine alveolus |
| 19 | Mesial P3 | Most mesial point on P3 alveolus, projected onto alveolar margin |
| 20 | Dacyron | meeting point of frontal, maxilla and lacrimal |
| 21 | Frontomalare temporale | Most lateral point on frontozygomatic suture |
| 22 | Zygomatic arch/alisphenoid/ frontal | Meeting point of zygomatic arch, alisphenoid and frontal bone |
| 23 | Pterion pos. | Meeting point of frontal, parietal and sphenoid |
| 24 | Zygomatic arch/alisphenoid | Meeting point zygomatic arch & alisphenoid on sup margin of pterygomaxillary fissure |
| 25 | Zygomatic arch ant. | Maximum curvature of anterior upper margin of zygomatic arch |
| 26 | Zygotemporale sup. | Most superior point on zygotemporal suture |
| 27 | Zygotemporale inf. | Most inferior point on zygotemporal suture |
| 28 | Maxilla sup. | Uppermost posterior point of maxilla (visible through pterygomaxillary fissure) |
| 29 | Porion | Most superior point on external auditory meatus |
| 30 | Asterion | Meeting point of lambdoid, parietomastoid, and occipitomastoid sutures |
| 31 | Inion | Meeting point of superior nuchal lines |
| 32 | Lambda | Meeting point of lambdoid and sagittal sutures |
| 33 | Bregma | Meeting point of sagittal and frontal sutures |
| 34 | Frontotemporale | Most medial point on temporal line on frontal |
| 35 | Zygomatic process pos. | Posteriormost point of zygomatic process of temporal bone |
| 36 | Opisthion | Midline point on posterior margin of foramen magnum |
| 37 | Basion | Midline point on anterior margin of foramen magnum |
| 38 | Occipital condyle med. | Medial extremity of occipital condyle projected onto margin of foramen magnum |
| 39 | Occipital condyle lat. | Lateral extremity of occipital condyle projected onto margin of foramen magnum |
| 40 | Stylomastoid foramen | Most post point on stylomastoid foramen |
| 41 | Hypoglossal canal | Most posteriolateral point on hypoglossal canal |
| 42 | Jugular foramen lat. | Most lateral point on jugular foramen |
| 43 | Jugular foramen med. | Most medial point on jugular foramen |
| 44 | Carotid foramen | Anteriormost point on carotid foramen |
| 45 | Articular tubercule | Most inferior post on articular tubercule |
| 46 | Condylar fossa | Centre of condylar fossa |
| 47 | Post-glenoid process | Distal most point on post-glenoid process |
| 48 | Temporal zygomatic curve pos. | Posteriormost point on curvature of anterior margin of zygomatic process of temporal |
| 49 | Petrous/alisphenoid/zygomatic | Meeting point petrous temporal, alisphenoid & base of zygomatic process of temporal |
| 50 | Foramen lacerum | Most medial point of the foramen lacerum |
| 51 | Basisphenoid/basioccipital | Meeting point between the basisphenoid and basioccipital along midline |
| 52 | Basisphenoid/basioccipital/ temporal | Meeting point of basisphenoid, basioccipital and temporal |
| 53 | Foramen ovale | Most posteriolateral point on foramen ovale |
| 54 | Hormion | Most posterior midline point on vomer |
| 55 | Palatine incurvature | Point of maximum curvature on the posterior edge of the palatine |
| 56 | Greater palatine foramen | Most posterior point |
| 57 | Molars posterior | Posterior midpoint onto alveolar margin of M3 |
| 58 | Maxilla/palatine | Meeting point of maxilla and palatine along midline |
| 59 | Incisvion | Most posterior midline point of incisive foramen |
| 60 | P3/4 | Contact point between P3/4 projected onto alveolar margin |
| 61 | P4/M1 | Contact point between P4/M1 projected onto alveolar margin |
| 62 | M1/2 | Contact point between M1/2 projected onto alveolar margin |
| 63 | M2/3 | Contact point between M2/3 projected onto alveolar margin |

Mahalanobis distances reflects the difference in latitude (Table 16).

Fig. 12 uses wireframes to model the shape differences represented by CV1. Compared to higher scoring individuals, low scoring configurations (those from Shimokita and Nagano) have taller,

narrower nasal apertures, broader more anteriorly placed midfaces, slightly taller and broader neurocrania, and more orthogonal faces, with an inferosuperiorly taller supranasal region and the subnasal region retracted more posteriorly.

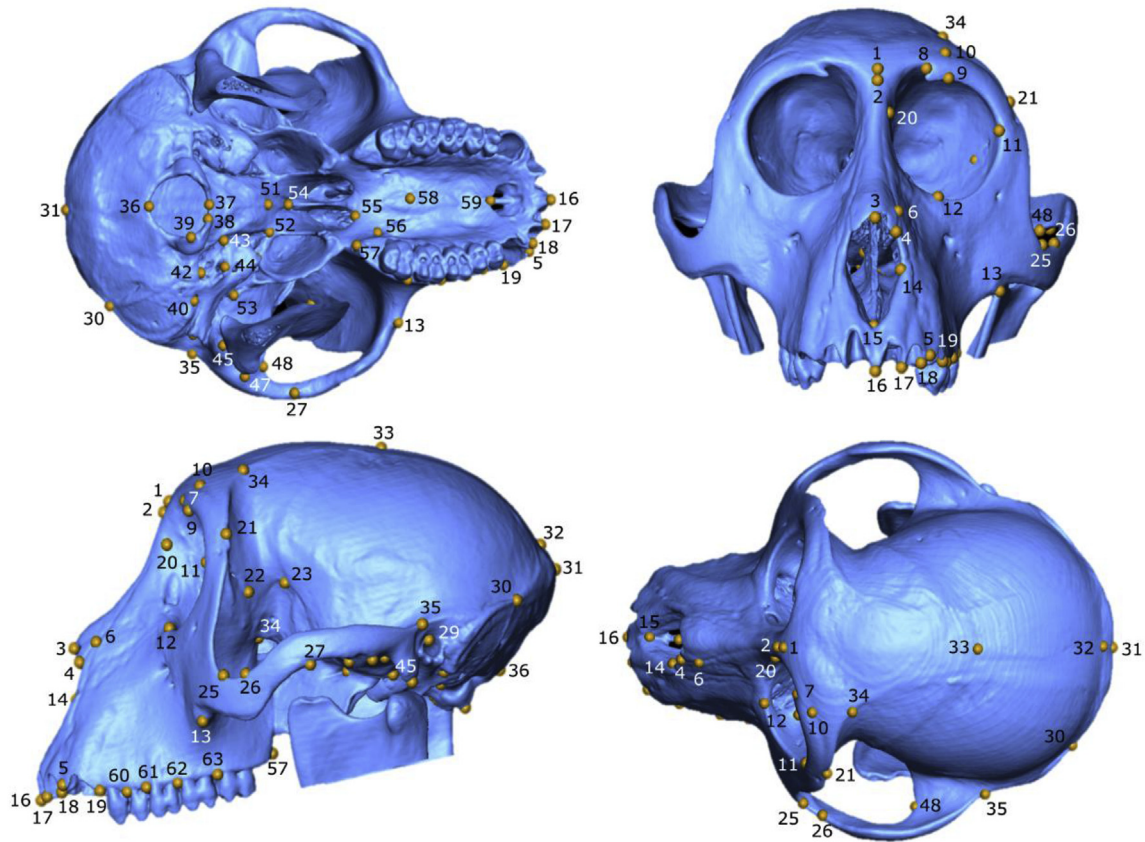


Fig. 2. Landmarks used in geometric morphometric analyses, for numbers and definitions, see Table 5.

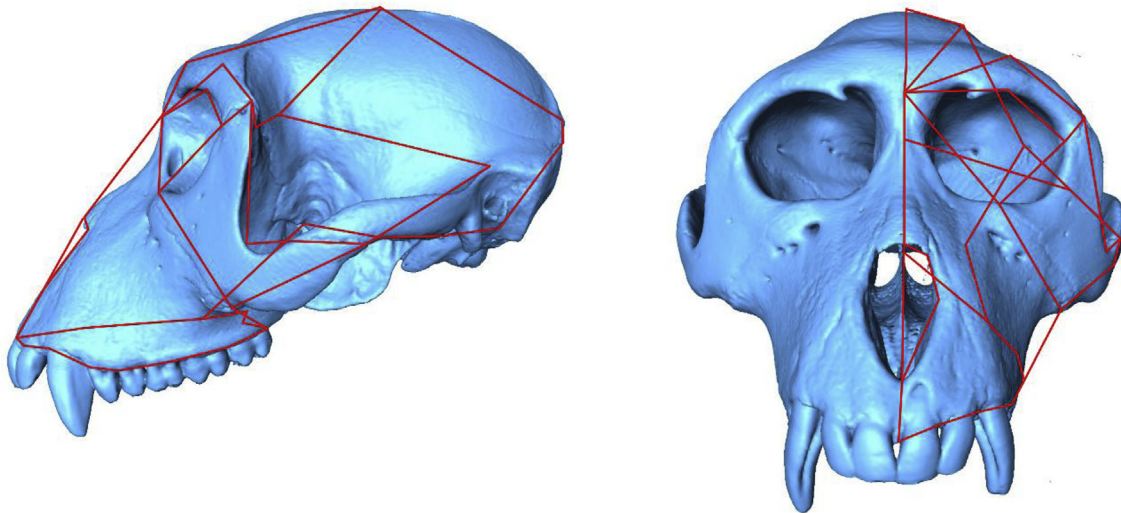


Fig. 3. Wireframe used to visualise shape differences superimposed onto *M. fuscata* cranium. Left: norma lateralis, right: norma frontalis.

4. Discussion

4.1. Size in Yakushima macaques

The Yakushima macaques are far smaller than all the other groups in postcranial bone measurements, body mass and cranial size. This fits with the results of previous studies, which have found a positive relationship between size and latitude from Kyushu

(Yakushima is just off the southern tip of Kyushu) to Honshu, but not consistently within Honshu (Hamada, 1996; Fooden and Aimi, 2005). In the current study, however, the difference in size between Yakushima macaques and those from the rest of Japan is far greater than those between the other groups, even where such differences exist between the Honshu macaques as well, such as in lower limb length. This suggests that small size in Yakushima is not solely due to thermoregulation.

Table 6
Landmarks connected to form wireframe (see Fig. 3).

| From | To |
|------------------------------------|------------------------------------|
| Bregma | Glabella |
| Nasion | Rhinion |
| Glabella | Nasion |
| Rhinion | Nasal/Premaxilla |
| Nasal/Premaxilla | Nasiospinale |
| Prosthion | Nasiospinale |
| Prosthion | Prosthion 2 |
| Prosthion 2 | Canine alveolus ant. |
| Canine alveolus ant. | P3 mes. |
| P3 mes. | P3/4 |
| P3/4 | P4/M1 |
| P4/M1 | M1/2 |
| M1/2 | M2/3 |
| M2/3 | M3 pos. |
| Bregma | Lambda |
| Lambda | Inion |
| Inion | Opisthion |
| Opisthion | Occipital condyle lat. |
| Occipital condyle lat. | Occipital condyle med. |
| Occipital condyle med. | Basion |
| Opisthion | Basion |
| Basion | Basisphenoid/basioccipital |
| Basisphenoid/basioccipital | Hormion |
| Hormion | Maxilla/palatine |
| Maxilla/palatine | Incisivion |
| Incisivion | Prosthion |
| Maxilla/palatine | Palatine incurvature |
| Palatine incurvature | Greater palatine foramen |
| Greater palatine foramen | M3 pos. |
| Glabella | Midtorus sup. |
| Glabella | Midtorus inf. |
| Midtorus inf. | Frontomalare orbitale |
| Frontomalare orbitale | Frontomalare temporale |
| Frontomalare orbitale | Zygoorbitale |
| Zygoorbitale | Dacryon |
| Dacryon | Glabella |
| Zygoorbitale | Zygomaxillare |
| Nasion | Dacryon |
| Zygotemporale sup. | Zygotemporale inf. |
| Zygomaxillare | Zygotemporale inf. |
| Zygomatic arch ant. | Zygotemporale sup. |
| Frontomalare temporale | Zygomatic arch ant. |
| Zygotemporale sup. | Porion |
| Zygotemporale inf. | Porion |
| Frontomalare temporale | Zygomatic arch/alisphenoid/frontal |
| Zygomatic arch/alisphenoid/frontal | Pterion pos. |
| Porion | Asterion |
| Bregma | Pterion pos. |
| Pterion pos. | Asterion |
| Rhinion | Nasiospinale |
| Midtorus sup. | Frontomalare temporale |
| M3 pos. | Zygomaxillare |

Table 7
Mean body mass (kg) for each group. Yakushima means are based on captive data (see above).

| Group | Male | Female |
|----------------|------|--------|
| Shimokita | 12.4 | 10.0 |
| Nagano | 13.2 | 9.6 |
| Shimane et al. | 12.5 | 10.0 |
| Yakushima | 9.0 | 6.7 |

The Yakushima macaques' (small) island habitat may be another contributor to their reduced size. There is a general trend for smaller animals tend to diminish on islands, whilst the reverse is true of large animals, although this is trend is governed by interplay between different selective pressures on species of different sizes in different insular environments and, as such, there are numerous exceptions (Foster, 1964; Heaney, 1978; Lomolino, 1985, 2005). In

Table 8
Results of one-way ANOSIM analyses on body weights. Tables are symmetrical, above trace: R values, below trace: p values with sequential Bonferroni correction. Significant differences in bold.

| Females | Shimokita | Nagano | Shimane et al. | Yakushima |
|----------------|---------------|---------------|----------------|---------------|
| Shimokita | | −0.0618 | −0.0683 | 0.9509 |
| Nagano | 0.8891 | | −0.0848 | 0.8236 |
| Shimane et al. | 0.8561 | 0.9893 | | 0.8907 |
| Yakushima | 0.0001 | 0.0001 | 0.0001 | |
| Males | Shimokita | Nagano | Shimane et al. | Yakushima |
| Shimokita | | 0.1087 | −0.0266 | 0.9578 |
| Nagano | 0.0590 | | 0.0186 | 0.8922 |
| Shimane et al. | 0.6500 | 0.2780 | | 0.8473 |
| Yakushima | 0.0001 | 0.0001 | 0.0001 | |

accordance with this trend, many island primate species seem to decrease in size compared to their closest non-island relatives (Albrecht, 1980). There are several potential reasons for this diminution, including lower predation pressure, lower resource availability and a reduced genepool potentially leading to greater impact of stochastic phenomena such as founder's effects (Foster, 1964). Interestingly, Sika deer sympatric with Japanese macaques also show a reduction in body size between those on large islands (such as Honshu and Kyushu) and small islands (including Yakushima) in addition to a general Bergmannian trend with latitude (Terada et al., 2012; Kubo and Takatsuki, 2015).

It is possible that lack of predation pressure plays a part in the reduction of body size in Yakushima macaques, since there have been no predators on the island during the Quaternary period (Majolo et al., 2009). Rare, but potential, predation risk exists from hawk eagles and racoon dogs in other parts of Japan (Fooden and Aimi, 2005), and on Honshu there were wolves until the late nineteenth century (Enari and Sakamaki, 2012).

As an argument against the idea of resource scarcity affecting body size, Yakushima has been described as the richest of all habitats for Japanese macaques, due to its evergreen forest and mild temperatures (Maruhashi, 1980). It is not only the resources that exist on the island which are important, however, it is their availability to individual macaques, which is in part a function of population density. There is evidence that macaque density is high on Yakushima (Hanya et al., 2006), leading to increased levels of intragroup competition and fission, and of intergroup aggression at home range boundaries, potentially due to patchy food distribution (Nakagawa, 1998). Whilst high levels of competition might in general favour larger individuals (Foster, 1964), this may not be possible if the population density is near the carrying capacity of the island.

Yakushima macaques are more distinct from other groups in limb lengths than in body breadths, showing that they have disproportionately short limbs. This is counter to a purely thermoregulatory explanation, which would lead to an expectation of proportionally longer limbs at lower latitudes, following Allen's rule (Allen, 1877). This is seen in macaques from the southern island of Koshima, which are small like those from Yakushima, but also show the relatively long limbs expected of low latitude macaques (Hamada et al., 1986). Different regions of the skeleton may adapt differentially to stressors such as climate or resource scarcity depending on the balance of selective pressures and constraints acting upon them (Buck et al., 2010). As the breadth of the trunk and pelvis is determined at least in part by obstetric requirements, restricting their growth may severely affect an individual's fitness. In contrast, the limbs continue to function, if less efficiently, at shorter lengths, thus the trunk may be preferentially buffered against stunting in lower resource environments (Pomeroy et al., 2012). This suggestion is supported by the consistently lower

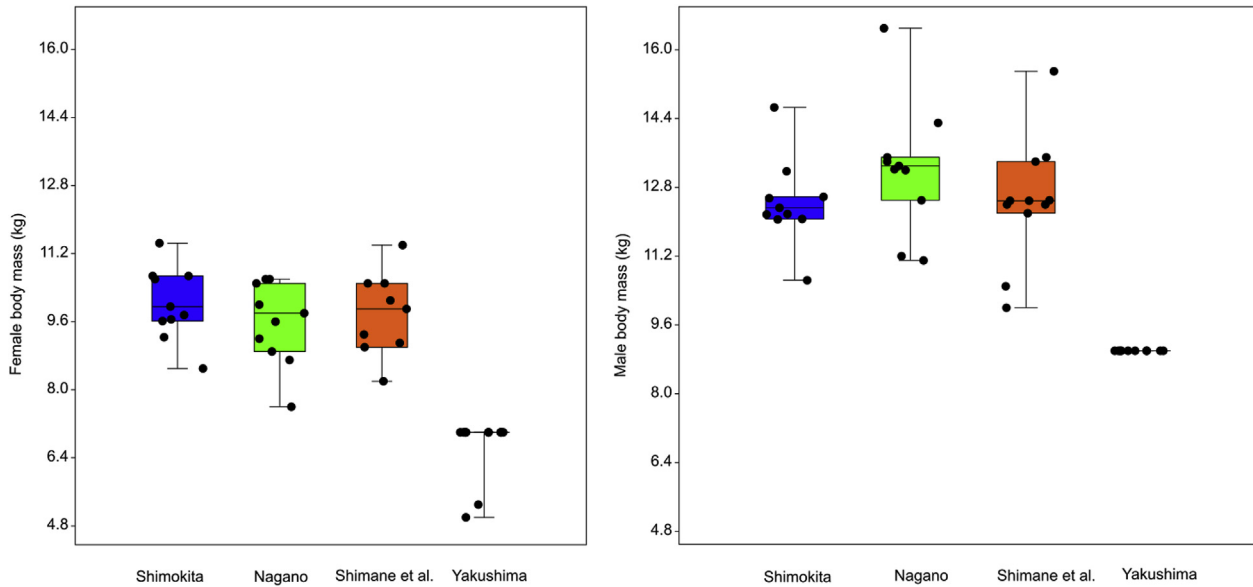


Fig. 4. Box and jitter plots of body mass (kg) in females (left) and males (right). Mean weight of captive Yakushima macaques used for all missing male Yakushima specimens and eight out of ten female Yakushima specimens (see above). This is an overestimate for wild monkeys.

Table 9

Tukey's pairwise comparison, posthoc tests from ANOVAs of maximum humeral, femoral and tibial length showing significant (borderline in the case of the humerus) differences between the Shimokita and Shimane et al. samples.

| | Tukey's Q | p value |
|---------|-----------|---------|
| Humerus | 3.63 | 0.05 |
| Femur | 4.36 | 0.01 |
| Tibia | 4.49 | 0.01 |

Table 10

Loadings for each maximum limb bone measurement on canonical variates axes. Percent of variation in the group explained by each CV is given in brackets.

| Maximum length | CV1 (89.87%) | CV2 (9.46%) | CV3 (0.67%) |
|----------------|--------------|-------------|-------------|
| Humerus | 3.884 | -0.452 | 1.398 |
| Radius | 3.691 | 1.607 | 2.008 |
| Ulna | 3.440 | 1.571 | 2.159 |
| Femur | 4.822 | -1.083 | 0.441 |
| Tibia | 4.152 | -0.860 | 3.229 |

Table 11

Posthoc comparisons from MANOVA of group differences in maximum limb length. Below the trace: p values, above the trace: squared Mahalanobis distances. Significant differences in **bold**.

| | Shimokita | Nagano | Shimane et al. | Yakushima |
|----------------|-----------------|-----------------|-----------------|----------------|
| Shimokita | | 4.5667 | 3.8180 | 36.3870 |
| Nagano | < 0.0001 | | 0.7197 | 33.4640 |
| Shimane et al. | 0.0001 | 0.2771 | | 27.4840 |
| Yakushima | < 0.0001 | < 0.0001 | < 0.0001 | |

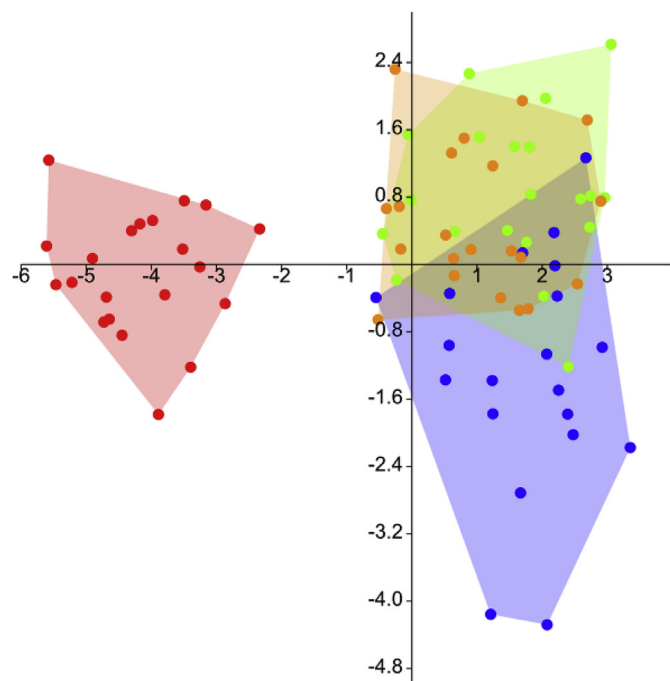


Fig. 5. CVA of maximum long bone lengths. CV1 (89.87% variance): x axis, CV2 (9.46% variance): y axis. Red: Yakushima, orange: Shimane et al. green: Nagano, blue: Shimokita (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

levels of variation between individuals in body breadth measurements than in limb length measurements, suggesting that body breadths are constrained (Fig. 1).

Having been separated from the larger island of Kyushu for an estimated 178 ka (Hayaishi and Kawamoto, 2006), one would expect Yakushima macaques to be somewhat distinct from their closest neighbours. In fact, Yakushima macaques are designated by some as a separate sub-species, *Macaca fuscata yakui* (Kuroda, 1940) on morphological grounds including coat colour and small size (e.g., Fooden and Aimi, 2005). They were not separated for the current study because molecular evidence does not support the designation (Hayasaka et al., 1987; Nozawa et al., 1991; Marmi et al., 2004; Kawamoto et al., 2007). In contrast to mtDNA analysis (Kawamoto et al., 2007), there is evidence from microsatellite markers and blood protein genes that there are several peripheral groups of macaques throughout Japan, such as those in Shimokita, the Boso Peninsula, Kinkazan and Yakushima, that are genetically divergent from those in central Honshu and Kyushu (Hayasaka

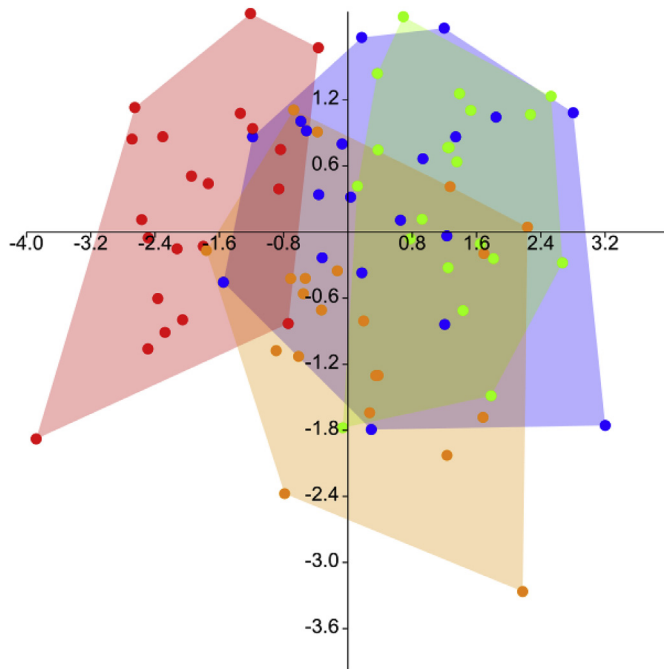


Fig. 6. CVA of body breadth measurements. CV1 (86.79% variance): x axis, CV2 (13.11% variance): y axis. Red: Yakushima, orange: Shimane et al. green: Nagano, blue: Shimokita. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 12

Loadings for each body breadth measurement on canonical variates axes. Percent of variation in the group explained by each CV is given in brackets. Clav. Max.: maximum length of clavicle, 2nd Rib: chord of second rib, Bi-iliac Br.: bi-iliac breadth, Ant. Sac.: anterior sacral breadth.

| Measurement | CV1 (86.79%) | CV2 (13.11%) | CV3 (0.10%) |
|--------------|--------------|--------------|-------------|
| Clav. Max. | 2.715 | −2.113 | −0.044 |
| 2nd Rib | 2.082 | 1.994 | −0.196 |
| Bi-iliac Br. | 4.335 | 0.836 | −0.877 |
| Ant. Sac. | 1.384 | 0.709 | 1.689 |

Table 13

Posthoc comparisons from MANOVA of group differences in body breadth. Tables are symmetrical, below the trace: p values, above the trace: squared Mahalanobis distances. Significant differences in **bold**.

| | Shimokita | Nagano | Shimane et al. | Yakushima |
|-----------------------|--------------------|--------------------|--------------------|----------------|
| Shimokita | | 0.4877 | 1.4620 | 6.6700 |
| Nagano | 2.1684 | | 2.4473 | 10.6820 |
| Shimane et al. | 0.1036 | 0.0063 | | 5.7381 |
| Yakushima | < 0.0001 | < 0.0001 | < 0.0001 | |

et al., 1987; Nozawa et al., 1991; Marmi et al., 2004; Kawamoto, 2010). This is of importance to the question of size because several of these peripheral populations (with the notable exception of Shimokita) are noted for being small (Hamada, 1996; Kawamoto, 2010). In addition to Yakushima, there are also the small-bodied populations from Koshima (Hamada et al., 1986) and Kinkazan (Hamada, 1996), which are small islands, perhaps suggesting an additional role of resource competition (whether from over-all scarcity, or competition). There is also the population on the Boso Peninsula (Hamada, 1996), however, which is isolated, yet part of the mainland. Divergent genetic markers and low heterogeneity in these peripheral regions could have resulted from a bottleneck after the last glaciation, leading to smaller size by stochastic gene

sorting (Kawamoto, 2010). A similar explanation could be invoked for Yakushima, genetic homogeneity of the populations on the island could be due to a severe bottle neck resulting from a natural disaster around 8000 ya (Hayaishi and Kawamoto, 2006; Kawamoto, 2010).

These different lines of evidence suggest that small size in Yakushima macaques is complex and determined by a range of factors. These may include absence of predators, resource scarcity due to high levels of competition in an island environment, and stochastic genetic sorting due to isolation and past bottlenecks. Greater investigation into the population density and carrying capacities associated with the habitats of all the groups in the sample could help clarify these results. The investigation of the trend for diminution in small island-living macaque populations could also be another area where this genus could provide a useful model for investigating hominin evolution, given the still unanswered questions regarding the phylogeny of the small-bodied, insular *Homo floresiensis*.

There is no ecogeographic pattern in body mass or cranial size within the sample, with the exception of the extremely small size of the most southerly group, Yakushima. The three macaque groups from Honshu have statistically indistinguishable mean masses, but they differ in the lengths of their limbs and the breadths of their trunks. This suggests that climate is acting on relative body proportions, rather than raw body mass, as seen in recent and fossil humans (Ruff, 1994, 2002; Holliday, 1997). This may explain why previous studies measuring variables such as anterior trunk length, cranial length, or body mass (Hamada, 1996; Fooden and Aimi, 2005) have found an incomplete ecogeographic cline, with differences between Kyushu and Honshu, but not within Honshu.

4.2. Latitudinal patterns in size and shape in the postcrania

There appear to be ecogeographic patterns in limb lengths, limb proportions and body breadths across *M. fuscata* groups, but the relationship is strongest in the limb lengths. This may reflect the different priorities of the appendicular and axial regions of the skeleton, as discussed above. It is also the pattern seen in recent and fossil human populations; Ruff (1994) noted that body breadth seemed to adapt to climate more slowly than limb length, perhaps due to differences in canalization in the two regions. In addition to the distinctively short limb bones of Yakushima, Shimokita macaques have shorter limbs than those from lower latitudes, yet they are of comparative mass to the other Honshu groups. They also have relatively shorter distal segments in their forelimbs. Mahalanobis distances between groups, showing differences in combined limb bone lengths, reflect geographical ordering of groups showing that groups closer to one another have limbs of more similar lengths. Those in the south are longer than those in the north. These results fit findings from Weinstein (2011) and Paterson (1996), which suggested both macaques as a genus and Japanese macaques as a species conform to Allen's law. In this relationship it seems that recent humans (Ruff, 1994; Holliday, 1997; Stock, 2006) fit into the wider primate pattern.

The general trend in body breadth measurements in this study shows a pattern of wider individuals at higher latitudes and narrower ones at lower latitudes according with Allen's rule and corresponding to the trend seen in human populations (Ruff, 1994; Holliday, 1997; Stock, 2006). When all breadth measurements are analysed together, Shimokita and Nagano inhabit almost the same space, yet individual breadth measurements from monkeys from Nagano are often wider than those from Shimokita, despite the former being from lower latitudes. In this study, as in many other investigating ecogeographic patterns, latitude was used as a proxy for climate (see above). However, these broad comparisons may

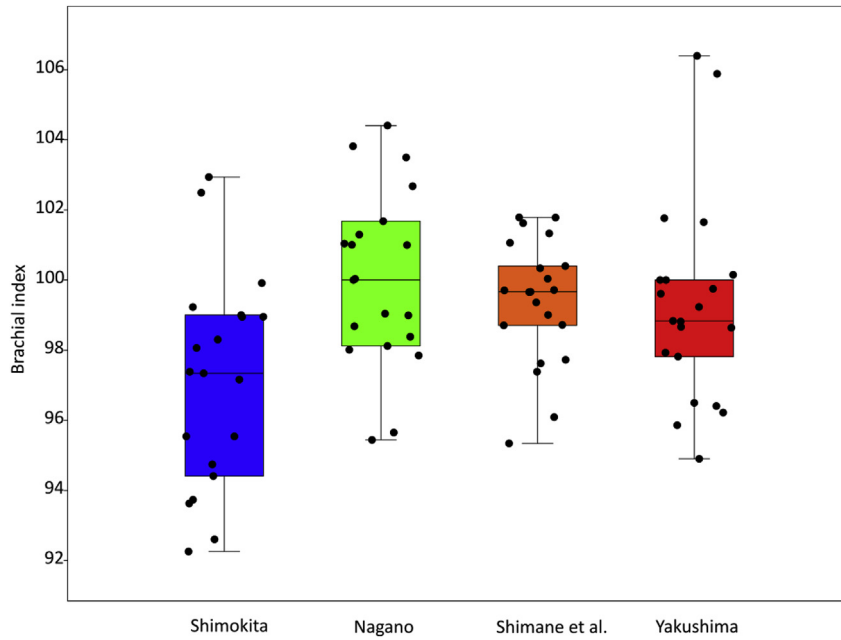


Fig. 7. Box and jitter plot of brachial indices.

mask more complex interactions in the monkeys' experience of their environment. Although it is further south, Nagano is as cold or colder as Shimokita in the mean temperature of the coldest month

(Nagano: $-1.7-0.96\text{ }^{\circ}\text{C}$, Shimokita: $-0.37-0.96\text{ }^{\circ}\text{C}$) (Ito et al., 2015). If crude temperatures are comparable between groups, the importance of other climatic variables such as snow-fall, elevation,

Table 14

Tukey's pairwise comparisons of brachial indices. Tables are symmetrical, below trace: Tukey's Q, above trace: p values. Significant values in **bold**.

| | Shimokita | Nagano | Shimane et al. | Yakushima |
|-----------------------|---------------|---------------|----------------|---------------|
| Shimokita | | 0.0032 | 0.0318 | 0.0432 |
| Nagano | 5.0930 | | 0.8552 | 0.7958 |
| Shimane et al. | 3.9650 | 1.1280 | | 0.9995 |
| Yakushima | 3.7960 | 1.2970 | 4.0620 | |

Table 15

Tukey's pairwise comparisons of crural indices. Tables are symmetrical, below trace: Tukey's Q, above trace: p values. Significant values in **bold**.

| | Shimokita | Nagano | Shimane et al. | Yakushima |
|-----------------------|-----------|--------|----------------|---------------|
| Shimokita | | 0.7010 | 0.9307 | 0.1143 |
| Nagano | 1.5310 | | 0.3378 | 0.6375 |
| Shimane et al. | 0.8536 | 2.3850 | | 0.0265 |
| Yakushima | 3.2090 | 1.6770 | 4.0620 | |

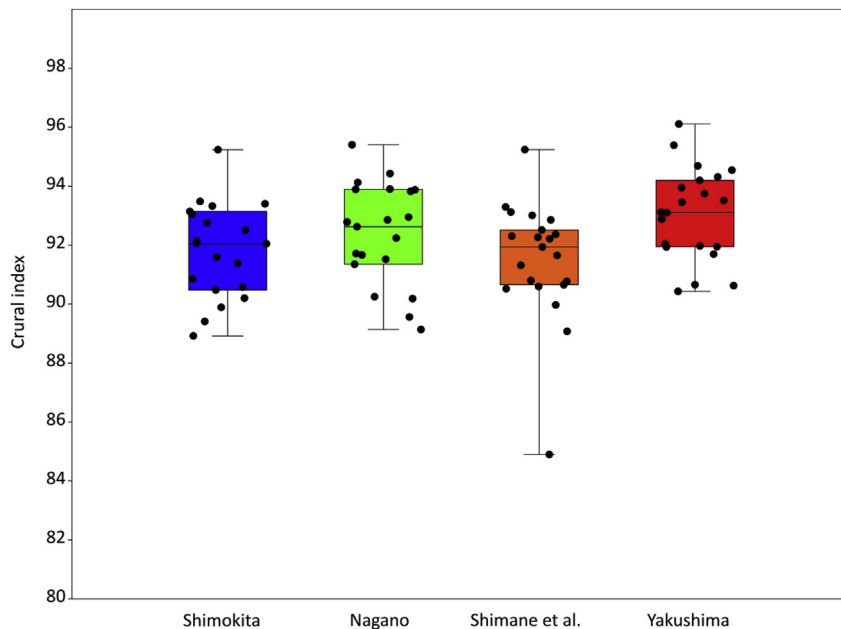


Fig. 8. Box and jitter plot of crural indices.

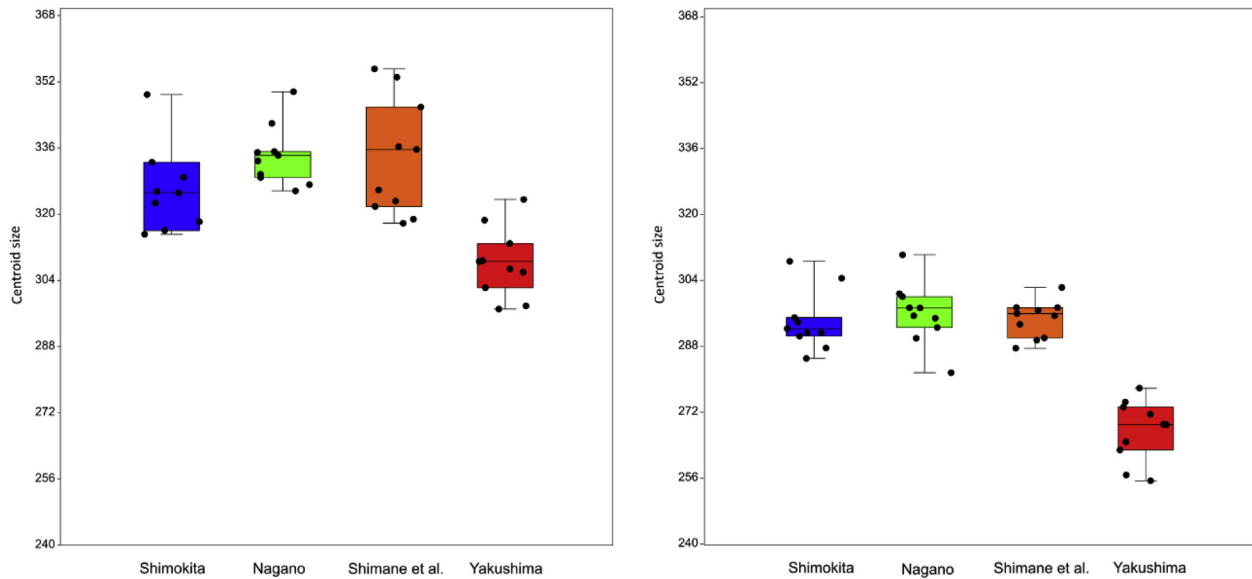


Fig. 9. Box and jitter plot showing centroid size (CS) of macaque cranial landmark configurations. Left: males, right: females.

seasonality and resource availability, which may differentially affect different parts of the skeleton, may be relevant. More detailed analyses of climate in future investigations will enable a better comparison between Japanese macaque and human patterns of climatic adaptation, but from the data presented here, it seems that both conform to Allen's rule in similar ways.

4.3. Craniofacial shape

When corrected for sex and size, the shape differences best differentiating macaque groups separate them in latitude order (with overlap between Nagano and Shimokita), suggesting an ecogeographic cline in craniofacial shape. This vector of shape differences shows differences in nasal, midfacial and neurocranial shape that appear similar to morphology described as cold-adaptation in humans. The over-all (not just on CV1) sex- and sex-corrected Mahanobis differences between the groups correspond to their latitudinal order, as with limb lengths, supporting the idea of an ecogeographic cline in shape.

4.3.1. The role of climate

Modelling differences in shape that distinguish latitude groups shows that macaques from Shimokita and Nagano have taller, narrower nasal apertures than those from the lower latitudes of Shimane et al. and Yakushima, with the former also taller and narrower than the latter. Previous studies have shown that nasal morphology in Japanese macaques varies with climate, with the internal nasal cavity showing a positive relationship with latitude relative nasal cavity volume in *M. fuscata* increases with latitude (Rae et al., 2003; Ito et al., 2014b). In recent humans there is a wealth of evidence that the nasal aperture (Betti et al., 2010; Carey and Steegmann, 1981; Evteev et al., 2014; Franciscus and Long, 1991; Hubbe et al., 2009; Roseman, 2004; Roseman and Weaver, 2004; Weiner, 1954; Wolpoff, 1968) and nasal cavity (Holton et al., 2013; Noback et al., 2011) differ with climate. In humans, relatively narrower nasal apertures in cold climates condition cold air to protect delicate internal tissues and to prevent heat and moisture (Weiner, 1954; Negus, 1957; Franciscus and Long, 1991; Hubbe et al., 2009; Evteev et al., 2014). It seems plausible that the taller, narrower nasal aperture in Northern Japanese macaques serves the same function.

In the current sample, macaques from Shimokita and Nagano have flatter, broader faces than those from Shimane et al. which in turn have flatter, broader faces than those from Yakushima. In recent humans, facial flatness and breadth are associated with extremely cold climates and very high latitudes (Roseman and Weaver, 2004; Hubbe et al., 2009; Betti et al., 2010; Evteev et al., 2014). This may be to reduce heat loss in accordance with Allen's rule, and/or may result from reorganisation of the midface in response to optimisation of the nasal apparatus for air conditioning, as described above (Harvati and Weaver, 2006). Both the need to minimise heat loss and the adaptation of the nasal apparatus would be critical stressors for Japanese macaques in Northern regions and it seems likely their morphology adapts accordingly, mirroring the patterns seen in recent humans.

The shape differences between the macaque groups show that neurocranial shape changes subtly with latitude; with increasing latitude there is a slight superoinferior and mediolateral vault expansion. Within recent *H. sapiens*, the evidence for a climatic effect on the shape of the neurocranial vault is well established: populations living in colder climates tend to have larger, more spherical, brachycephalic neurocrania, which has been interpreted as conformation to Allen's rule (Beals, 1972; Beals et al., 1984). The most robust expression of this difference in neurocranial shape at different temperatures appears to be in measures of cranial breadth (Roseman, 2004; Hubbe et al., 2009; Betti et al., 2010; Nowaczewska et al., 2011). The data presented here appear to show that Japanese macaques also follow Allen's rule in the shape of their neurocranial, presumably to reduce heat loss by minimising surface area.

Previous non-human primate ecogeographic studies focussing on cranial morphology have found that size is more plastic than shape and that little or no relationship between shape and climate remains once allometric effects are accounted for (Frost et al., 2003; Cardini and Elton, 2008, 2009b; Dunn et al., 2013; Meloro et al., 2013). In general these studies have focussed on species/genera with a narrower latitudinal range than Japanese macaques (papionins, guenons, red colobus monkeys, howler monkeys respectively), and which therefore experience less climatic variation. Perhaps particularly relevant, since these studies have used field sites in the tropics, none of these species experiences considerable cold stress as do the Japanese macaques. In northern

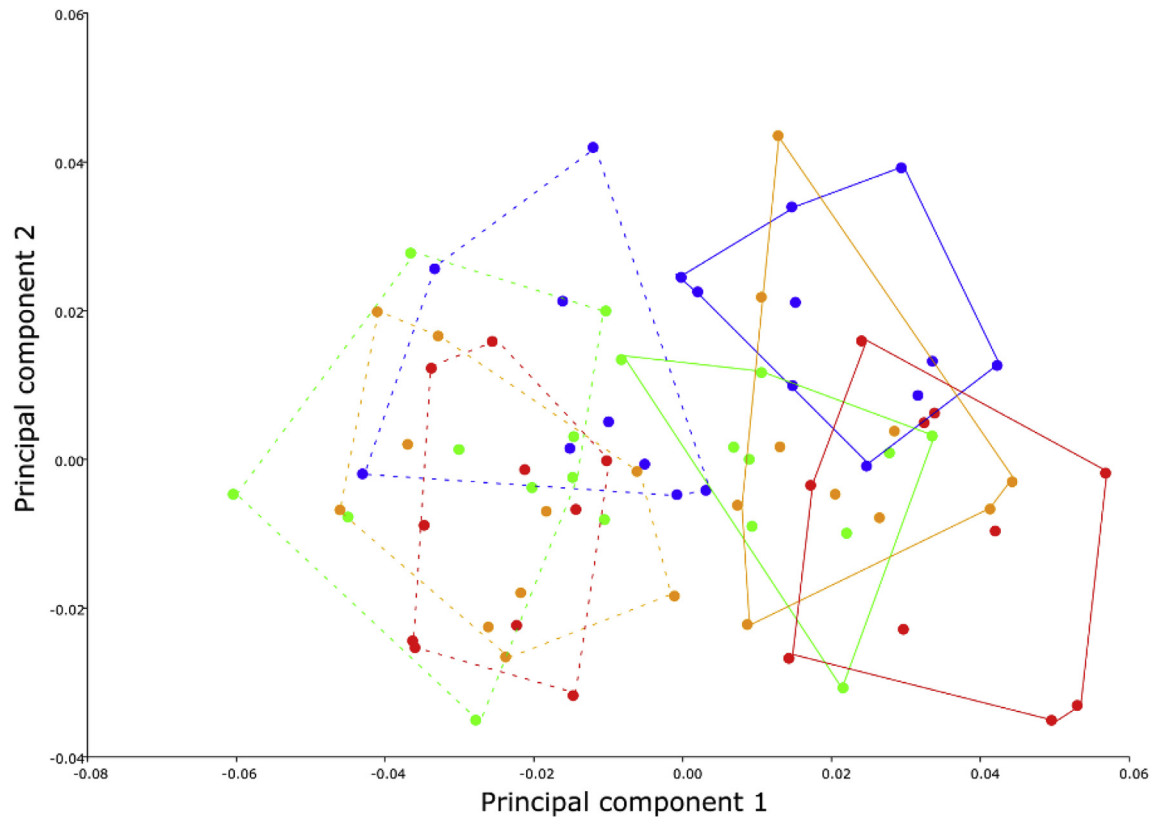


Fig. 10. PCA of shape variation. Blue: Shimokita, green: Nagano, orange: Shimane et al. red: Yakushima. Dashed lines: females, solid lines: males. PC1 explains 10% of variation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

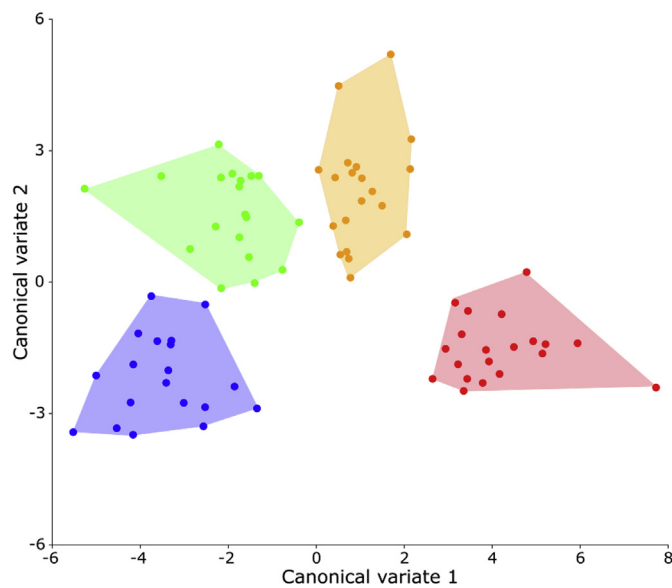


Fig. 11. CVA of sex- and allometry-free cranial shape variables. CV1: 60% variance, CV2: 24% variance.

Table 16

Differences between groups. Tables are symmetrical, Mahalanobis distances below trace, p values above trace. Significant values in **bold**.

| | Shimokita | Nagano | Shimane et al. | Yakushima |
|-----------------------|---------------|-----------------|-----------------|-----------------|
| Shimokita | | < 0.0001 | < 0.0001 | < 0.0001 |
| Nagano | 4.9958 | | < 0.0001 | < 0.0001 |
| Shimane et al. | 6.2880 | 4.9217 | | < 0.0001 |
| Yakushima | 7.8508 | 7.0407 | 5.4359 | |

of non-human primates. Ito et al. (2014a) did include Japanese macaques in their intrageneric comparison of macaque craniofacial morphology, and found no climatic signal in the non-allometric component of their results, which suggests perhaps that the more subtle signature of non-allometric, intraspecific craniofacial adaptation is swamped by the greater variation in inter-specific comparisons.

Shape variation associated with climate in recent humans is reported to occur only at very high latitudes/in very extreme cold (e.g., Roseman and Weaver, 2004; Harvati and Weaver, 2006; Betti et al., 2010; Foster and Collard, 2013), more extreme than the Japanese climate. The appearance of latitudinal patterns in macaque cranial and postcranial morphology where it might not be expected to exist in comparable human populations may be due to a difference in the threshold required to effect adaptation, or to the monkeys' lack of cultural buffering, including the protection of fire, houses and clothes. If this is the case, it would emphasise the importance of hominin culture and technology in facilitating northwards dispersal and alleviating the need for biological adaptation until a more extreme climatic cut-off than in non-human primates. There is some evidence for ecogeographic patterns in cranial and postcranial morphology of prehistoric Japanese

Japan monkeys inhabit regions with mean coldest month temperatures of $-1.70 \sim -0.37^\circ\text{C}$ (Ito et al., 2014b) and substantial snow cover (Enari and Sakamaki-Enari, 2013). In recent humans, climate only affects cranial morphology under extreme cold stress (e.g., Roseman and Weaver, 2004; Harvati and Weaver, 2006; Betti et al., 2010; Foster and Collard, 2013) and it seems likely the same is true

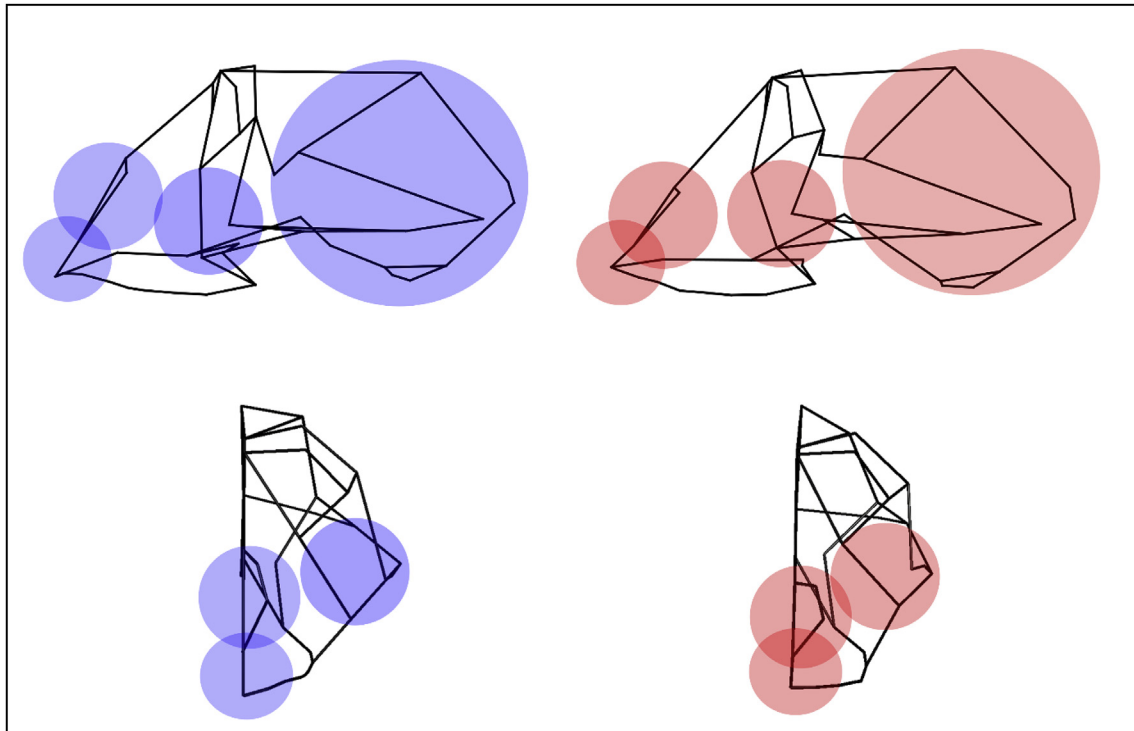


Fig. 12. Wireframes (see Table 6, Fig. 3) of mean shapes warped to -10 (left) and $+10$ (right) (Mahalanobis distances) along CV1. Shaded circles indicate regions of interest in shape change referred to in the text. Red = positive, where Yakushima falls, Blue = negative scores, where Nagano and Shimokita fall. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

foragers, the Jomon (e.g., Temple and Matsumura, 2011; Fukase et al., 2012), but a systematic study throughout the skeleton is currently lacking. Here we describe similarities in the pattern of adaptation between high latitude humans and Japanese macaques, in research in progress (Buck et al. in prep) we compare both patterns and magnitudes of ecogeographic variation between monkeys and humans from matched latitudes to elucidate whether the same level of stressor leads to the same level and pattern of adaptation in both species.

4.3.2. The role of diet

One of the key factors influencing primate cranial shape is diet (e.g., Antón, 1996; Singleton, 2005; Koyabu and Endo, 2009). Dietary hardness, rather than climate, could be invoked to explain the more retracted, wider face seen in more northerly *M. fuscata* in this study; Antón (1996) and Ito et al. (2014) have suggested that similar shape differences in *M. fuscata* compared to other macaques are, at least in part, related to mechanical efficiency and harder diet. However, Antón's (1996) dismissal of the effects of climate on this morphology seems premature, as it is almost entirely based on analogy with Hylander's (1975) argument that reduced facial projection in Inuit crania is related to high occlusal forces. She also mentions that Steegmanns, (1970, 1972) work has rejected the explanation of Allen's rule for flatter faces in cold-adapted humans, but as Ito et al. (2014) point out, the impact of cold stress on macaques, with more projecting rostra, may be very different to that seen in the Inuit and other human groups. Whilst Japanese macaque morphology is shaped, at least in part, by their consumption of harder foods than their congeners (Antón, 1996; Ito et al., 2014a), it is not clear whether there is sufficient within-species dietary variation to lead to morphological differences.

Japanese macaques as a species eat foliage, fruits and seeds, bark and leaf buds, flowers, fungi, and animal matter in varying amounts

throughout their entire range (Tsuji et al., 2015). The main difference in the diets of Japanese macaques from different regions is between those inhabiting evergreen and deciduous forests (Tsuji et al., 2015). This divide largely corresponds with a floral North/South divide, but altitude also affects the type of vegetation able to grow (Enari and Sakamaki, 2012). In the current study, the groups from the two lower latitudes (Shimane et al. and Yakushima) inhabit evergreen forests and the two more northerly groups (Nagano and Shimokita) inhabit deciduous forests (Tsuji et al., 2015). Bark and buds form a greater proportion of diet in deciduous forests, where there is greater seasonality. This is particularly during winter, when snow may cover preferred foods for many months (Tsuji et al., 2013, 2015). Tsuji et al. (2015) found no other significant differences between Japanese macaques in dietary components or any relationship between dietary composition and latitude, elevation or productivity.

Observations of feeding in the wild show that bark is sometimes peeled off by hand and then ingested, and at other times is gnawed straight from the tree (Suzuki, 1965). Bark gouging for exudates is thought to shape cranial morphology in other primate species (e.g., Dumont, 1997), but this is likely to be far more biomechanically demanding than consuming peeled bark, or even stripping the outer layer of bark and cambium, as seen in Japanese macaques. Nonetheless, if bark consumption is a major cause of craniofacial variation between the groups it should lead to greater craniofacial similarity between macaques from Shimane et al. and Yakushima, which both inhabit temperate, evergreen forests and should have low levels of bark consumption. However, Shimane et al. are as distinct from Yakushima as they are from Nagano. Furthermore, although it is biomechanically plausible that diet could contribute to the greater facial flatness and breadth in more northerly macaques seen in this study, it would not explain the nasal and neurocranial shape differences seen between groups, as described

above. Thus, though a role of diet cannot be ruled out, and there is certainly interplay between climate and available diet, the results in this study do not fit expectations of morphological patterns driven mainly by dietary hardness.

4.3.3. The role of phylogeny

In recent humans it is thought that the majority of regional variation in craniofacial morphology is due to neutral accumulation of differences via population history (e.g., Roseman, 2004; Weaver et al., 2007; Betti et al., 2009, 2010). This could suggest that the pattern observed in the macaque data reported here, with closer populations more similar to one-another, also reflects isolation by distance. However, as described above, the current molecular evidence suggests that isolation by distance is a poor model of Japanese macaque phylogeny (Hayasaka et al., 1987; Nozawa et al., 1991; Kawamoto et al., 2007; Kawamoto, 2010). There are to date no whole genome analyses of Japanese macaque phylogeny and investigations into different regions of the nuclear genome and into regions of the mitochondrial DNA provide different results. Autosomal nuclear markers show a major division between central and peripheral regions, with Shimokita the most divergent, followed by Yakushima and the Boso Peninsula, which form a cluster with Shodoshima and Koshima islands. All the other populations are part of the remaining, central cluster (Hayasaka et al., 1987; Nozawa et al., 1991; Kawamoto, 2010). This clearly does not fit an isolation by distance pattern, nor the morphological patterns of seen in either the crania or postcranial skeletons in this study. Mitochondrial DNA analyses in contrast show an East/West divide in macaque haplogroups. Low levels of variation in the East have led to the hypothesis that this pattern resulted from extinction and repopulation of Northern and Eastern during the last glaciation (Kawamoto et al., 2007; Kawamoto, 2010). The differences between these two models are due to degree of resolution and means of inheritance in a species with male dispersal and female philopatry (Kawamoto, 2010); however, neither would account for the results reported here, which are instead consistent with the influence of climate.

5. Conclusions

These analyses of differences in cranial and postcranial skeletal morphology between groups of Japanese macaques from different latitudes demonstrate ecogeographic patterns corresponding to common mammalian and hominin thermoregulatory rules. That non-human primates show patterns of adaptation similar to what is reported both for recent humans and fossil hominins may suggest that the hominin lineage does not show a distinct pattern of adaptation when compared with other primates. To date, it remains unclear whether the level of adaptation in humans and monkeys is correspondingly similar. Even if further work continues to show no heightened adaptability in humans, this does not preclude distinctive biological adaptation in many other aspects of physiology and immune function that have yet to be tested. However, if it is assumed that Pleistocene *Homo* lacked the thick fur (Rogers et al., 2004) that is so important in insulating Japanese macaques (Inagaki and Hamada, 1985), their conserved primate pattern of skeletal plasticity might emphasise the importance of behavioural and technological adaptation in hominin dispersals into novel cold habitats, such as the colonisation of Northern Europe in the early Pleistocene.

Contributions

LTB, IDG and JTS designed the study, YH allowed and enabled access to the sample and CT scanner, LTB collected and analysed the

data, LTB, IDG, JTS and YH contributed to writing the paper.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.quascirev.2018.05.032>.

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