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What makes a long tail short? Testing Allen's rule in the toque macaques of Sri Lanka

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Abstract

Allen's rule (1877) predicts ecogeographical anatomical variation in appendage proportions as a function of body temperature regulation. This phenomenon has been tested in a variety of animal species. In macaques, relative tail length (RTL) is one of the most frequently measured appendages to test Allen's rule. These studies have relied on museum specimens or the invasive and time-consuming capturing of free-ranging individuals. To augment sample size and lessen these logistical limitations, we designed and validated a novel noninvasive technique using digitalized photographs processed using LibreCAD, an open-source 2D-computer-aided design (CAD) application. This was used to generate pixelated measurements to calculate an RTL equivalent, the Tail to Trunk Index (TTI) = (tail [tail base to anterior tip] pixel count/trunk [neck to tail base] pixel count). The TTI of 259 adult free-ranging toque macaques (*Macaca sinica*) from 36 locations between 7 and 2,087 m above sea level (m.a.s.l.) was used in the analysis. Samples were collected from all three putative subspecies (*M. s. sinica*, *aurifrons*, and *opisthomelas*), at locations representing all altitudinal climatic zones where they are naturally distributed. These data were used to test whether toque macaque tail length variation across elevation follows Allen's rule, predicting that RTL decreases with increasing elevation and lower temperature. Our results strongly supported this prediction. There was also a statistically significant, negative correlation between elevation and annual average temperature. The best predictor for the TTI index was elevation. Significant subspecies differences in RTL are linked in part to their ecological and altitudinal niche separation, but overall the variation is seen as the species' adaptation to climate. The method developed for the quick morphometric assessment of relative body proportions, applicable for use on unhabituated free-ranging animals, widens the range of materials available for research studying morphological characteristics and their evolution in primates.

KEYWORDS

Allen's rule, elevation, morphometrics, Sri Lanka, tail length, toque macaque

1 | INTRODUCTION

Allen's (1877) and Bergmann's (1847) rules of ecogeographical anatomical variation in body size and appendage proportions state that warm-blooded animals with distinct geographical and climatic distributions will regulate body temperature by either minimizing exposed surface area to conserve heat loss in cold climates or maximizing exposed surface area to help cool down in hot climates. These rules predict that populations or species from hot climates will be smaller (Bergmann) and have extremities (ears, tails, limbs, snouts, etc.) that are long and thin (Allen), whereas equivalent populations from cold climates will have thicker and shorter versions of those body parts. Since the introduction of these ideas almost 200 years ago, these hypotheses have received wide attention, looking at a variety of avian and mammalian species around the world (Brown & Lee, 1969; Danner & Greenberg, 2015; Gohli & Voje, 2016; Gutiérrez-Pinto et al., 2014; Meiri, Yom-Tov, & Geffen, 2007; Oswald & Arnold, 2012; Symonds & Tattersall, 2010; Yom-Tov & Geffen, 2010; Yom-Tov, Yom-Tov, Wright, Thorne, & du Feu, 2006).

A growing number of nonhuman primate (NHP) studies have looked at Allen's and Bergmann's rules as they apply to the evolution and phylogeography of extant species, in particular on interspecies variation as an aspect of phylogeography in the genus *Macaca*. The majority of these studies are based on detailed, systematic analysis of such factors as external morphology, cranial morphology, and relative tail length (RTL: the ratio of tail length and body length), using museum skeletal specimens (Fooden, 1979, 1988, 1997, 2006; Fooden & Albrecht, 1999; Fooden, Guoqian, Zongren, & Yingxiang, 1985; Weinstein, 2011), and somatometric measurements of live captive and translocated groups or habituated free-ranging populations (Clarke & O'Neil, 1999; Hamada, Urasopon, Hadi, & Malaivijitnond, 2006; Hamada, Watanabe, & Iwamoto, 1996; Paterson, 1996; Zhang et al., 2016). A few studies have also addressed intraspecific variation in tail length of a few *Macaca* spp. distributed across a wide range of habitats (e.g., Fooden, 1988, 1995, 1997; Fooden & Albrecht, 1999).

Macaques are a good NHP model for testing these rules given their wide and highly successful distribution, ranging from coastal tropical forests to temperate alpine habitats (Fleagle, 2013; Richard, Goldstein, & Dewar, 1989). Currently, the genus *Macaca* consists of 23 species, divided into five taxonomic subgroups; *sylvanus*, *silenus*, *fascicularis*, *sinica*, and *arctoides* (Li, Zhao, & Fan, 2015; Mittermeier, Rylands, & Wilson, 2013).

From a morphological perspective, Wakamori and Hamada (2019) looked at the skeletal determinants of tail length in macaques, that is, proximal vertebrae, longest vertebra, distal vertebrae, and a total number of vertebrae, and found distinct variation in these determinants across species groups. They concluded that tail length was caused by different mechanisms in different species, reflective of the evolutionary history of the genus. In the *silenus* and *sinica* groups, vertebral length was found to be the major skeletal determinant of tail length, while in the *fascicularis* group, vertebral number was the

determinant of tail length. Fooden's analysis of macaque morphological variation and Allen's or Bergmann's rule in species members of the *fascicularis*-, *sinica*-, *silenus*-, and *arctoides* groups, remain one of the most comprehensive bodies of work on this topic in a NHP genus (Fooden, 1975, 1979, 1982, 1988, 1995, 1997, 2006; Fooden & Albrecht, 1999; Fooden et al., 1985). Interspecies competition has been implicated as a factor responsible for the ecogeographic segregation of the genus *Macaca* (Fooden, 1982), which partly helps to explain the interspecies differences in tail length. Within the *fascicularis* group, dramatic tail length variation occurs primarily at the interspecies level, with the longest tail length found in the most southerly distributed (warmer climate) species, the appropriately named long-tailed macaque (*M. fascicularis*). Also, within the wide distribution of *M. fascicularis*, tail length decreases with latitude (Fooden, 1995, 1997, 2006). In accordance with Allen's rule, an interspecies tail length of the other three members (rhesus macaque *M. mulatta*, Taiwanese macaque *M. cyclops*, and Japanese macaque *M. fuscata*), becomes markedly shorter with the increasing northerly, nonoverlapping habitats of these three species (Fooden, 1997, 2006). *M. fuscata*, the northerly most distributed species of the *fascicularis* group, and notably of all NHP, predictably has the shortest tail.

In contrast, within the *silenus* group (lion-tailed macaque *M. silenus*, northern pig-tailed macaque *M. leonina*, Sunda pig-tailed macaque *M. nemistrina*, and the Pagai macaque *M. pagensis*) this pattern is not so clear. While *M. silenus* of southwestern India has by far the longest tail, the trend in tail lengths of the other three species does not strictly become shorter with increasing latitude; the trend in fact is slightly reversed (Fooden, 1975). Intraspecific variation in *M. mulatta* populations also shows exceptions to Allen's rule, attributed to postglacial-advancement-induced movement by shorter tailed *M. mulatta* populations from the north, displacing the now extinct longer tailed *M. mulatta* populations further south (Fooden & Albrecht, 1999; Zhang et al., 2016). Nonetheless, *M. mulatta* tail length remains approximately the same across latitude (Fooden, 1997). A recent study on *M. fuscata* by Buck, De Groot, Hamada, and Stock (2018) did find evidence in support of Allen's rule in this shorter tailed species using other morphological characteristics. They reported morphological variation in limb length and body breadth across latitude and nonallometric latitudinal patterns in craniofacial shape closely resembling cold-adaptations recognized in humans.

Similar to the *fascicularis* group, the southern-most distributed species in the *sinica* group, Sri Lanka's toque macaque (*M. sinica*) and the bonnet macaque (*M. radiata*) of southern India have the longest tails. Intraspecific tail length becomes progressively shorter among the western and eastern Assamese macaques (*M. assamesnsis pelops* and *M. a. assamensis*, respectively), and the Tibetan macaque (*M. thibetana*), with increasing, basically nonoverlapping, northerly latitudinal distribution (Fooden, 1988).

In this respect, the stumptail macaque *M. arctoides*, whose average tail length is shorter than *M. thibetana* (Fooden et al., 1985), and which is distributed among northern India, Burma, and southern China, down south to the top of West Malaysia, at elevations

between 0 and 2,800 m above sea level (m.a.s.l.), has a very short tail, which does not change significantly in length with latitude or elevation (Fooden, 1990; Fooden et al., 1985). In fact, the shortest tailed specimens were found in southern Vietnam and peninsular Thailand (Fooden, 1990), the southern-most latitude of this species' distribution. Fooden (1990) notes that *M. arctoides* and those Sulawesi macaques with stumped tails are exceptions to Allen's rule for tail reduction as an adaptation to cool climates. He further points out that both are distributed at mainly low latitudes and low altitudes south of the Tropic of Cancer. He goes on to infer from subfossil evidence that, perhaps sometime during the Late Pleistocene, local environmental factors may have triggered development in the ancestral stock of *M. arctoides* leading to the distinctive reproductive anatomy and degeneration of the tail. This suggests that phylogenetic factors may be more important here. *M. arctoides* is proposed to have speciated by the process of hybridization between the *mulatta* subgroup and the common ancestor of *assamensis/thibetana* (Tosi, Morales, & Melnick, 2003), all relatively shorter tailed macaques. Wakamori and Hamada (2019) also suggest that in some cases, phylogenetic signals may be stronger than climatic factors.

The tendency for the interspecies difference in tail length based on latitudinal distribution within the *fascicularis*, *sinica*, and *silenus* groups generally follow Allen's rule, with notable exceptions related to migration and habitat displacement, as described above. However, detailed analyses of the effect of Allen's rule on intraspecific variation have received less attention. Fooden (1979) investigated the intraspecific variation of cranial, head and body, and tail dimensions in *M. sinica* across latitude, but found none. However, he could not address elevational variation due to limited sample availability, restricted to lower elevations. Ideally, a macaque species living within a relatively limited latitudinal distribution across a wide range of elevation and eco-climatic zones would provide a useful means of detecting species-level concordance to Allen's rule. For this purpose, we chose to revisit Sri Lanka's endemic *M. sinica*, because of the small latitudinal range of their habitat (N 09° 50'–N 05° 55') and a dramatic contiguous vertical distribution between 0 and 2,400 m.a.s.l. (MAH, RK, unpublished data), across an impressive ecologically and climatically diverse landscape (Beenaerts et al., 2010; Crusz, 1986; Vitanage, 1970). Moreover, the species consists of three putative subspecies (*M. s. sinica*, *aurifrons*, and *opisthomelas*; Roos et al., 2014). Based largely on museum specimens, subspecies designation for toque macaques has been based on eco-climatic zone of habitation and a few phenotypic traits (pelage color, crown hair pattern, body size, and hair length), altitudinal climatic zone, and elevation (following Fooden, 1979; Mittermeier et al., 2013; Roos et al., 2014). However, to date our observations on free-ranging toque macaques suggest greater phenotypic variation in these traits across the island. This phenotypic variation attributed to subspecies differences appears to be strongly influenced by adaptations following Allen's and Bergmann's rule in response to eco-climatic differences, rather than clear-cut toque macaque genotypic subspecies differences. Looking at tail length variation may further shine light onto this discrepancy.

For many years, the golden standard of morphometric studies was the measurement of museum specimens collected in the days when the hunting of specimens from wild populations was accepted scientific practice. Capture and release of free ranging, often provisioned, well-habituated individuals later replaced this method and is still in practice today in some countries. While the benefits of precise measurements cannot be overstated, it is becoming increasingly difficult to obtain permission to capture wild NHPs in source countries, and scientists are becoming more sensitive about the reduction of stress on study subjects, as well as the risk of infectious disease transmission associated with close physical contact (e.g., Conly & Johnston, 2008; National Research Council Committee on Occupational Health and Safety in the Care of Nonhuman Primates, 2003; Pedersen & Davies, 2009). These factors have stimulated the development of less invasive research methods. Recently, the use of photogrammetric techniques have allowed for the reasonable assessment of such attributes as weight, body size, relative trunk length, hybrid status, and coat color (e.g., Breuer, Robbins, & Boesch, 2007; Jadejaroen, Hamada, Kawamoto, & Malaivijitnond, 2015; Kurita, Suzumura, Kanchi, & Hamada, 2012; Rothman et al., 2008).

To reassess whether *M. sinica* variation in tail length follows Allen's rule, we validated a new technique to generate a RTL index using digital photographic samples collected from live, often unhabituated, individuals in wild populations of all three subspecies in their representative elevational, climatic, and ecological habitats where they are found today. According to Allen's rule, we predict that elevation and temperature affect tail length, with tail length decreasing with increasing elevation and associated lower temperatures.

2 | MATERIALS AND METHODS

2.1 | Ethical statement

This study complied with all relevant Sri Lankan governmental policies and regulations of the University of Sri Jayawardenepura, with the Guideline for field research on nonhuman primates established by the Primate Research Institute of Kyoto University, and with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

2.2 | Study subjects

We began an extensive island-wide survey of toque macaque distribution in 2006. When macaque groups were found, GPS location and elevation were recorded using a Garmin hand-held unit (GPSmap® 62s). Climatic information (temperature and rainfall) was obtained from the Department of Meteorology, Sri Lanka, using available data from the closest meteorological monitoring station of each collection site (Table 1). Photographs of individuals were

TABLE 1 Distribution of TTI measurements collected across location, elevation, climatic, and subspecies variables

No.	Location (N)	Average TTI	Elevation (m.a.s.l.)	Latitude degree	Longitude degree	Mean annual temperature °C	Mean annual Rainfall (mm)	Altitudinal climatic zone	Subspecies
1	Kilinochchi (1)	1.3806	7	09.3735361	080.3805083	27	1,330	Dry lowland	<i>M. s. sinica</i>
2	Yala (2)	1.5165	11	06.4271694	081.3081528	27.2	1,823	Dry lowland	<i>M. s. sinica</i>
3	Thabowwa (2)	1.7764	20	08.0861194	079.9263611	27	1,950	Dry lowland	<i>M. s. sinica</i>
4	Madu (26)	1.6418	56	08.8561389	080.2042694	27.2	1,200	Dry lowland	<i>M. s. sinica</i>
5	Polonnaruwa (11)	1.8714	71	07.9326361	081.0036833	27.3	1,678	Dry lowland	<i>M. s. sinica</i>
6	Kaudulla (2)	1.7815	74	08.1566972	080.9173139	24	1,750	Dry lowland	<i>M. s. sinica</i>
7	Anuradhapura (5)	1.9067	90	08.3113528	080.4036500	28	1,368	Dry lowland	<i>M. s. sinica</i>
8	Girtale (7)	1.8440	93	08.0023556	080.9249222	27.3	1,678	Dry lowland	<i>M. s. sinica</i>
9	Nachchimale (4)	1.3019	96	06.8866250	080.0964111	26	2,550	Wet lowland	<i>M. s. aurifrons</i>
10	Wagamuwa (2)	1.8880	98	07.7532417	080.9207722	27	1,750	Dry lowland	<i>M. s. sinica</i>
11	Mihintale (20)	1.7111	122	08.3552500	080.5135700	27	1,364	Dry lowland	<i>M. s. sinica</i>
12	Kurunagala (20)	1.6083	127	07.4319278	080.3431528	27.2	1,993	Dry lowland	<i>M. s. sinica</i>
13	Dambulla (5)	1.5382	140	07.9688667	080.4036500	26	1,557	Dry lowland	<i>M. s. sinica</i>
14	Yapahuwa (1)	1.9341	154	07.8140861	080.3124694	27	2,000	Dry lowland	<i>M. s. sinica</i>
15	Sigiriya (6)	1.7734	198	07.9551528	080.7598028	26.8	1,700	Dry lowland	<i>M. s. sinica</i>
16	Gurulupotha (1)	1.5317	254	07.3437306	080.9259639	25	1,678	Dry lowland	<i>M. s. sinica</i>
17	Balangoda (16)	1.9878	294	06.6244750	080.6568750	24.1	2,581	Dry upland	<i>M. s. sinica</i>
18	Welange (6)	1.7466	294	07.2833389	080.7948639	25	1,900	Dry upland	<i>M. s. sinica</i>
19	Kandy (8)	1.5854	456	07.2905889	080.6337278	24.5	2,083	Wet upland	<i>M. s. aurifrons</i>
20	Peradeniya (13)	1.3899	496	07.2678500	080.5966600	24.6	2,900	Wet upland	<i>M. s. aurifrons</i>
21	Wegala Kandy Magiyangana Rd. (6)	1.6048	530	07.3483028	080.9142722	23	2,450	Wet upland	<i>M. s. aurifrons</i>
22	Hirikatuoya (13)	1.6941	627	06.7252250	080.7746333	22	2,581	Dry upland	<i>M. s. aurifrons</i>
23	Rawana Ella Rd. (2)	1.4785	650	06.8504306	080.9789417	15.9	2,100	Wet highland	<i>M. s. sinica</i>
24	Rawana Ella (2)	1.4588	650	06.8401167	081.0524472	21	1,945	Dry upland	<i>M. s. sinica</i>
25	Hunnasgiriya (15)	1.5203	774	07.2833500	080.7940200	22.1	2,400	Wet highland	<i>M. s. opisthomelas</i>
26	Kandy Mahiyangana Rd. (5)	1.3071	775	07.3239111	080.8863972	22	2,400	Wet upland	<i>M. s. aurifrons</i>
27	Beragala (4)	1.8211	1,064	06.7634444	080.9180083	21.3	1,981	Wet highland	<i>M. s. opisthomelas</i>

TABLE 1 (Continued)

No.	Location (N)	Average TTI	Elevation (m.a.s.l.)	Latitude degree	Longitude degree	Mean annual temperature °C	Mean annual Rainfall (mm)	Altitudinal climatic zone	Subspecies
28	Knuckles Information Center (9)	1.1110	1,112	07.3287806	080.8612972	19	2,540	Wet highland	<i>M. s. opisthomelas</i>
29	Pathana Kovil (6)	1.3632	1,134	07.4766667	081.1283333	18	2,900	Wet highland	<i>M. s. opisthomelas</i>
30	Ella Nuwara Eliya Rd. (8)	1.5485	1,160	06.8504306	080.9789417	15.9	2,100	Wet highland	<i>M. s. opisthomelas</i>
31	Edition Pathana (2)	1.0763	1,450	06.9622194	080.8601667	16	1,900	Wet highland	<i>M. s. opisthomelas</i>
32	Knuckles Range (2)	0.8496	1,505	07.3663972	080.8171667	18	2,540	Wet highland	<i>M. s. opisthomelas</i>
33	Hakgala (7)	1.4104	1,715	06.9249028	080.8218528	18	2,300	Wet highland	<i>M. s. opisthomelas</i>
34	Seetha Eliya (11)	1.2334	1,764	06.9753250	080.7844917	18	2,100	Wet highland	<i>M. s. opisthomelas</i>
35	Ohiya (7)	1.3122	1,785	06.8190111	080.8446972	13	3,000	Wet highland	<i>M. s. opisthomelas</i>
36	Hortan plains (2)	1.0140	2,087	06.8190111	080.8074056	13	3,000	Wet highland	<i>M. s. opisthomelas</i>

Note: There are 36 sites (259 samples).
Abbreviations: *M. s.*, *Macaca sinica*; m.a.s.l., m above sea level; TTI, Tail to Trunk Index.

routinely taken with hand-held cameras when groups were encountered. The photos used in this study were collected between 2013 and 2017. In total, 259 photos from one or more neighboring groups at 36 sampling locations were selected and used in the analysis (Table 1).

All individuals selected for analysis were adults. Adults were readily discernable by relative body size and facial characteristics (blemishes, scars, and wrinkles). When visible, genitalia development indicative of sexual maturity was also a reliable feature. However, sex could not always be determined from photos with certainty when being selected later for analysis, so we did not consider the sex of the subject as a variable. We did not consider this to be problematic, since Fooden's (1979) analysis of *M. sinica* found that head and trunk and tail body proportions increased at the same rate among males and females from the juvenile period up to adulthood. However, this may not hold true for shorter tailed macaque species, as Fooden noted that this relationship did not hold for macaques like *M. mulatta* and *M. nemestrina*, for which he found RTL decreased in later stages of development (Fooden, 1975, 1979).

The subjects photographed represent individuals from all altitudinal climatic zones where the subspecies are found; *M. s. sinica*: dry lowland, dry upland ($n = 20$ sites, 137 individuals), *M. s. aurifrons*: wet lowland, wet upland ($n = 6, 73$), and *M. s. opisthomelas*: wet highland ($n = 11, 49$), ranging in elevation from 7 to 2,087 m.a.s.l. (Table 1; Figure 1). We assigned subspecies classifications based on a combination of diagnostic morphological characteristics (pelage color, crown hair pattern, body size, and hair length), altitudinal climatic zone, and elevation (following Fooden, 1979; Mittermeier et al., 2013; Roos et al., 2014). Climatic zone classification follows Crusz (1986) and Beenaerts et al. (2010). With the exception of a few contact zone sites, subspecies did not appear to overlap in distribution.

2.3 | Photographic data collection protocol

Various attempts have been made in the past to use photographs for noninvasive morphometric measurements. Two important conditions should be considered when using photographic data for the estimation of body dimensions: (a) perpendicular orientation of the camera to the subject and (b) the use of easily determinable, low error identification of anatomical landmarks (Kurita et al., 2012). Rothman et al. (2008) developed a sophisticated parallel laser-based photogrammetry technique to collect body measurements but found that sometimes it was difficult to obtain adequate perpendicular orientation, especially for animals up in trees. Kurita et al. (2012) had success in meeting both conditions, using the corneal vertex of the eye and the upper edge of the ischial callosity, but this was dependent upon the monkeys being well-habituated and willing to walk across a pre-fixed horizontal bar with a camera set in front of it. Their method was an improvement upon that of Mori (1979), who measured the occipital end of the head and the upper end of the ischial callosity. Kurita et al. (2012) modified Mori's (1979) method and validated the suitability of their method comparing their measurements with adult female crown-rump length

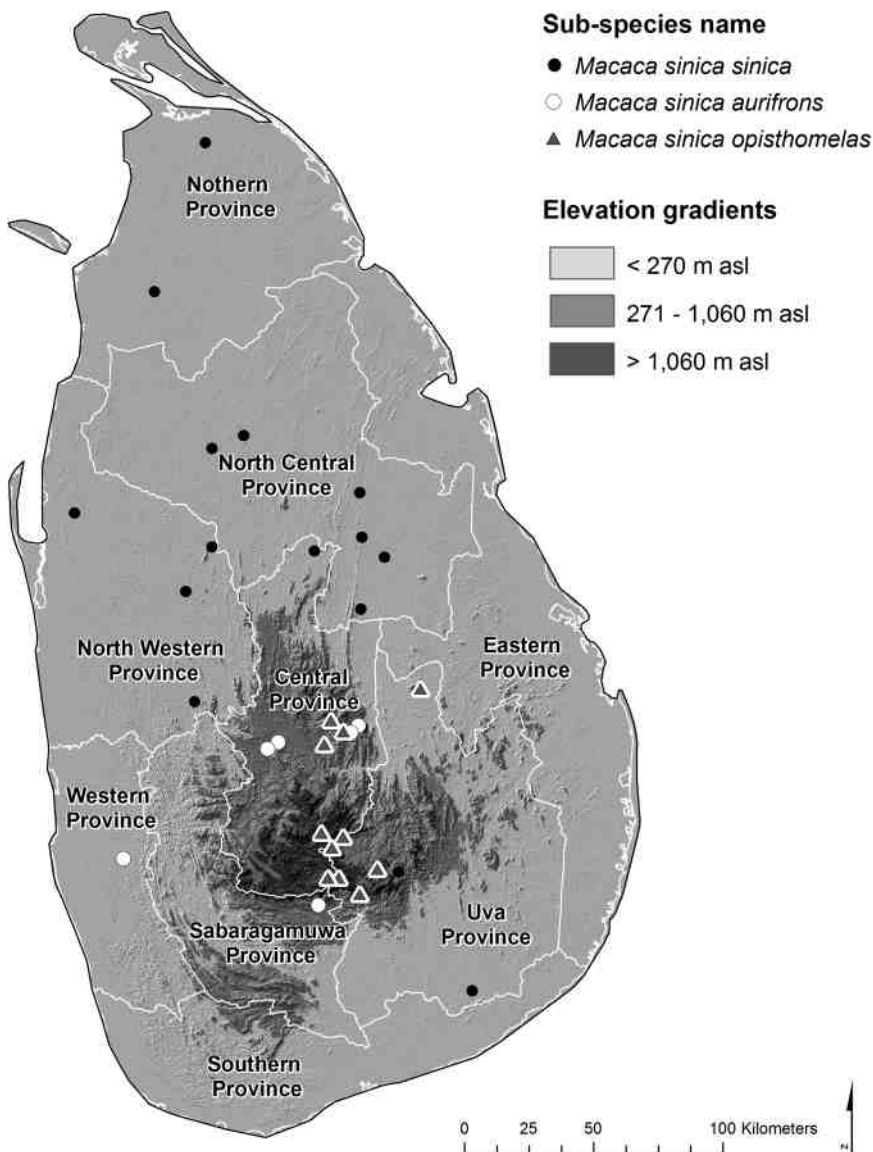


FIGURE 1 Distribution of sample collection locations across geophysical and climatic areas of Sri Lanka. m.a.s.l., m above sea level

and anterior trunk length in adult female, habituated, free-ranging Japanese macaques.

In our study, photographs with tail, trunk, and head fully visible, were taken when a troop or single individual was seen crossing a road or open field, moving across a cliff, along tree branches, fallen trees, or telephone wires parallel to the observer. Distance from the subject, camera lens magnification, and tail curvature are not problematic for our protocol if photos were perpendicular views of the subject to avoid possible distortion of the relative body proportions. Care was taken to avoid sampling bias in three ways, (a) by using only one photo of the same individual in a group, (b) when traveling in a vehicle, by not using photos from any group encountered along the road within <1 km of the group just encountered, and (c) by not using photographs taken from the same location during different years of the study. When a group was encountered, we targeted and followed specific individuals with easily recognizable facial and bodily features, until several clear photos were taken. To obtain the necessary perpendicular orientation

with the target individual, we waited for it to cross in front of us, or when possible, we shifted our position. We then took as many photos of that individual as possible. For analysis, M. A. H. and R. K. selected only the best photo from each target individual meeting these requirements. In the second case, M. A. H. and R. K. participated in all survey trips, assuring that no photographs taken from the same group or immediate vicinity were used in the analysis. In the third case, with the exception of Mihintale, Pollanaruwa, Kandy, and Dambulla (Table 1), photographs of individuals from each location were taken during a single survey of that location. At these limited locations from which photographs collected in different years were used in the analysis, photographs were selected from different identified groups within the Mihintale Archeological site under study by R. K., or from different sites within the city, archaeological sites or surrounding urban areas of Pollanaruwa, Kandy, and Dambulla, separated by enough distance to reasonably exclude the likelihood of them being the same group.

2.4 | Pixelization of trunk and tail proportions for calculation of RTL

Photos were loaded into LibreCAD, an open-source 2D-computer-aided design (CAD) application for Windows, Apple, and Linux (<http://librecad.org/cms/home.html>). Using a computer mouse, pixel distances were measured by clicking once and tracing along the contour of the animal's back from the base of the tail to the base of the neck and clicking again (Figure 2). The process was repeated, clicking from the same point at the base of the tail, following the contour of the tail to its distal end and clicking once more. From each trace, a pixel count was registered on the program's control panel (Figure 2), and this was recorded into an Excel file along with site location information for analysis (Table 1).

Traditionally, the calculation of RTL in primates is based on the distance from the crown of the head to the rump (CRL), or the snout to anus with head stretched out in line with the back, and from the tail base to the tail's distal end (Groves & Harding, 2003). Previous photometric studies, conducted under more controlled conditions, used a modification of the CRL method (Jadejaroen et al., 2015) or the corneal vortex of the eye to the rump method (Kurita et al., 2012). For our purposes, we did not add head size in the trunk measurement, in part because proper head orientation is one more uncontrollable factor when photographing animals in the wild that can hinder obtaining

appropriate photos for analysis. To validate this method, we compared our data with that of data on *M. sinica* measured by Fooden (1979) from skeletal specimens. The slope of the relationship between tail length and head and body length calculated from Fooden (1979) was not significantly different from the slope of the correlation between tail length and trunk length calculated in pixels from our data (Fooden: $r_a = .893$, $n_a = 33$; our data: $r_b = .907$, $n_b = 259$; $p = .826$, not significant [ns]). It is worth mentioning again that tail length and head and body length of immature and adults of both sexes, increase at approximately the same rate (Fooden, 1979; Figure 3, p. 113); that is, RTL is not confounded by differences in body size.

To test the precision of our method, a subsample of five individuals was selected and measures for tail length, trunk length, and Tail to Trunk Index (TTI) were taken five times each. A repeated measure analysis was run to test the hypothesis that these different measures were not significantly different, thus validating the measurements. This analysis showed that all three measurements were not significantly different across time (tail length: $F(4, 16) = 0.77$, $p = .56$; trunk length: $F(4, 16) = 1.99$, $p = .23$; TTI: $F(4, 16) = 1.35$, $p = .31$). Based on these confirmatory analyses, we proceeded to calculate RTL from our photographic samples.

The relative TTI was calculated, where $TTI = \text{tail pixel count} / \text{trunk pixel count}$. For interpretive purposes, the smaller the index value, the smaller the relative tail size is.

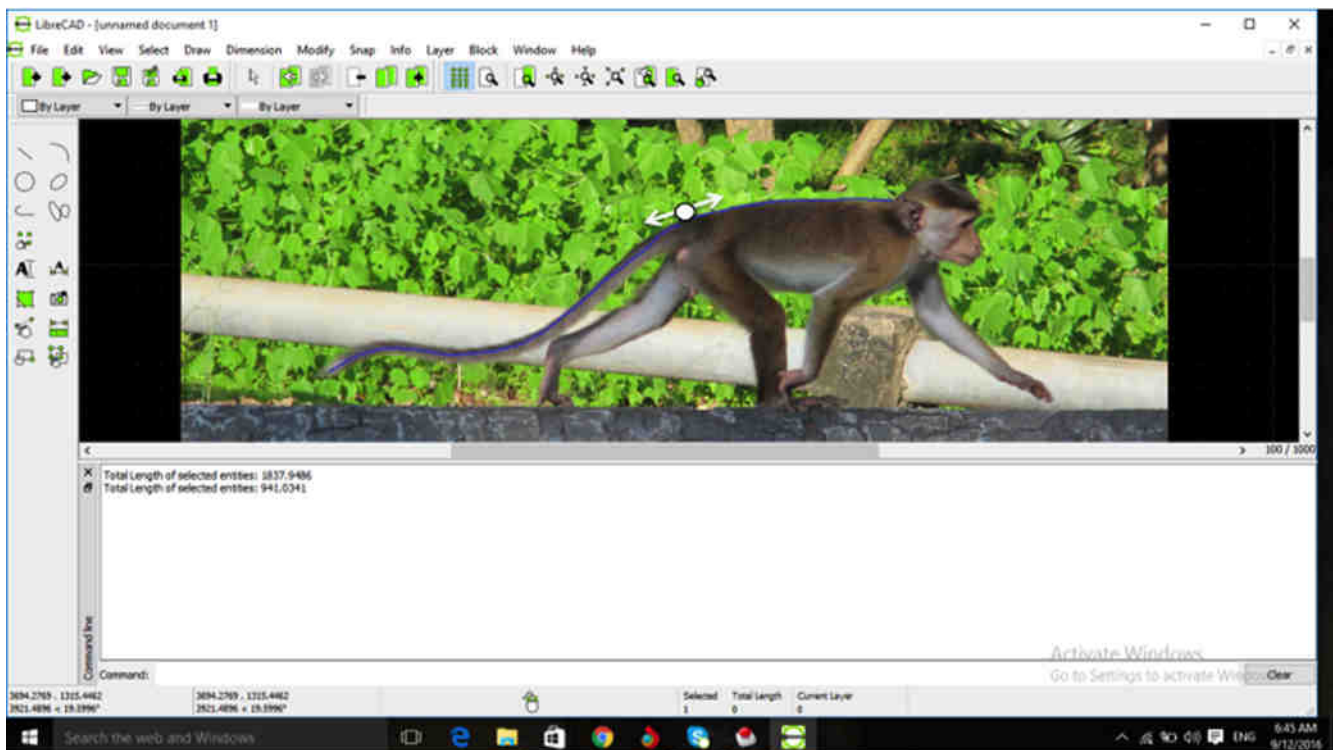


FIGURE 2 Screen shot of the LibreCAD program while measuring TTI from an uploaded digital photo of a toque monkey. The three white dots and arrows were added on to illustrate starting and ending points of measurements. The two measurements taken are displayed at the bottom of the screen. CAD, computer-aided design; TTI, Tail to Trunk Index

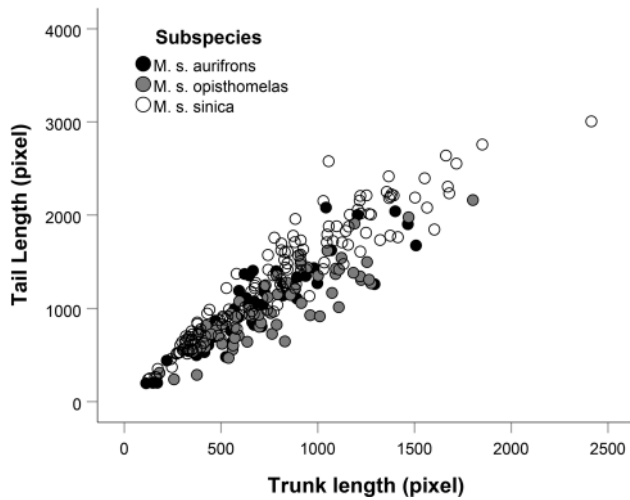


FIGURE 3 Correlation between tail length and trunk length (measured in pixels) in all three subspecies of toque macaques ($N = 259$ individuals). *M. s.*, *Macaca sinica*

2.5 | Statistical analysis

Correlation among variables was assessed using Pearson's r product-moment coefficients. The strength of the relationship was assessed by r^2 . We used the Fisher r -to- z transformation to compare the slope of our data with Fooden's data (Fooden, 1979). A stepwise regression analysis was used to identify the best predictors of the TTI among the metric independent variables (elevation, longitude, latitude, rainfall, and temperature). Several general linear models (GLM) were used to assess the effects of subspecies and climatic zone on the TTI. The α value for statistical significance was set at $p = .05$; when several analyses were performed on the same data set, we used Bonferroni's correction to adjust the significance threshold ($\alpha = .016$ after the correction). Tukey post hoc tests were used to assess the pairwise differences with factors including more than two groups. Where significant, we used partial eta squared (η_p^2) and Cohen's d to provide measures of effect size. The η_p^2 indicates the percentage of variance in the dependent variable (DV) that is attributable to a particular independent variable (IV). Cohen's d indicates the size of the difference (effect size) between two means in standard deviation (SD) units for each pairwise comparison of interest, using the formula $\delta = \mu_2 - \mu_1 / \sigma$, where δ is the population parameter of Cohen's d , and

where it is assumed that $\sigma_1 = \sigma_2 = \sigma$, that is, homogeneous population variances, and μ_1 is the mean of the respective population. Differences in sample size among groups were adjusted by the GLM models. All significance tests were two-tailed. All statistical analyses were conducted using the SPSS computer program (IBM SPSS Statistics 23.0).

3 | RESULTS

3.1 | Tail to Trunk Index

We found a statistically significant positive correlation between relative tail length and trunk length in toque macaques ($r = .91$, $n = 259$, $p < .001$; $r^2 = .82$, Figure 3). This relationship remained very strong in all three subspecies analyzed separately (*M. s. sinica*: $r = .94$, $n = 137$; *M. s. aurifrons*: $r = .90$, $n = 49$; *M. s. opisthomelas*: $r = .87$, $n = 73$, all $p < .001$), and when we separated samples by climatic zones (dry: $r = .941$, $n = 148$; wet: $r = .892$, $n = 111$).

3.2 | TTI predictors

All metric predictors of the TTI were strongly correlated (Table 2). In particular, there was a very strong negative correlation between elevation and annual average temperature ($r^2 = .941$, $n = 259$, $p < .001$; $r^2 = .882$). A stepwise regression analysis revealed that the best predictor for the TTI was elevation ($F_{1,257} = 76.16$, $p < .001$; $R^2 = .478$, Table 3). Latitude and longitude were also significant predictors, although their contribution to the model was marginal ($F_{3,253} = 31.99$, $p < .001$; $R^2 = .523$, % R^2 increase = 8%). Rainfall and temperature were not significant predictors of the TTI. Given their high correlation, the predictive effect of temperature was included in the elevation variable. Figure 4 shows the negative correlation between TTI and elevation. With every 100 m of elevation increase, TTI decreased by 0.028 units \pm 0.006 SD.

TTI was significantly different by subspecies ($F_{2,256} = 38.76$, $p < .001$; $\eta_p^2 = 0.23$, Figure 4). Post hoc tests revealed that all three subspecies were significantly different from each other (all p values $< .015$; Cohen's $d = .65$). *M. s. sinica* had the highest TTI ($M = 1.72 \pm 0.28$ SD), whereas *M. s. opisthomelas* had the lowest ($M = 1.36 \pm 0.29$ SD). Since elevation was the most important

TABLE 2 Correlations among the geographical predictors of relative tail length (RTL)

	Longitude	Latitude	Temperature	Rainfall
Elevation	-0.574 ($p < .001$)	0.512 ($p < .001$)	-0.941 ($p < .001$)	0.572 ($p < .001$)
Longitude		-0.545 ($p < .001$)	0.627 ($p < .001$)	-0.817 ($p < .001$)
Latitude			-0.570 ($p < .001$)	0.451 ($p < .001$)
Temperature				-0.628 ($p < .001$)

Note: Correlations included all animals ($n = 259$).

TABLE 3 Stepwise regression models predicting relative tail length (RTL) using elevation, latitude, longitude, average rainfall, and temperature of the locations where the animals lived

Scores	R	Adj. R ²	b	SE	β	t test	p value
<i>Model 1</i>							
(Constant)	.478	.229	1.733	0.025		69.787	<.001
Elevation			<.001	<0.001	-.478	-8.727	<.001
<i>Model 2</i>							
(Constant)	.512	.262	-18.561	5.942		-3.124	.002
Elevation			<.001	<0.001	-.587	-9.399	<.001
Latitude			.252	0.074	.213	3.415	.001
<i>Model 3</i>							
(Constant)	.523	.273	-13.557	6.423		-2.111	.036
Elevation			<.001	<0.001	-.643	-9.439	<.001
Latitude			.196	0.079	.166	2.499	.013
Longitude			-.065	0.033	-.139	-1.986	.048

Note: The models included all animals ($n = 259$). Average rainfall and temperature did not contribute significantly to explain RTL, and therefore were not included in any models.

Abbreviations: Adj. R², adjusted coefficient of determination; β , unstandardized coefficient; R², % of variable explained; R, correlation coefficient for multiple regression (equivalent of R for bivariate correlation); SE, standard error; t, t test.

predictor for the TTI and one of the subspecies (*M. s. opisthomelas*) only lives at high elevations, we included elevation as a covariate on the GLM: we still found a significant effect of subspecies on the TTI ($F_{2,255} = 3.41$, $p = .035$), although the strength of the relationship was lower ($\eta_p^2 = 0.11$). To further confirm these results, we ran a follow-up analysis including only the two subspecies, both living at overlapping lower elevation in different climatic zones, *M. s. sinica* and *M. s. aurifrons*. We found that the TTI was significantly higher in *M. s. sinica* ($F_{1,184} = 19.74$, $p < .001$, $\eta_p^2 = 0.10$), the subspecies limited to the dry and arid zones of the country.

The TTI was also significantly different by dry and wet climate zones, even when elevation was included in the GLM model as a

covariate ($F_{1,256} = 7.88$, $p = .005$; $\eta_p^2 = 0.06$). Wet areas had lower TTI values than dry areas. We also investigated the effects of temperature in the two climatic zones, again including elevation in the GLM as a covariate, and we did not find a significant difference on average temperatures between wet and dry areas ($F_{1,256} = 2.13$, $p = .15$, *ns*).

Finally, we assessed the effect of the lowland, upland, and highland altitudinal zones on the TTI, including the main predictor, elevation, as a covariate. We did not find a significant effect of these altitudinal zones on the TTI ($F_{2,255} = 2.64$, $p = .08$, *ns*).

4 | DISCUSSION

4.1 | Tail length variation as environmental adaptation

This study evaluated whether tail length in *M. sinica* follows Allen's rule by testing two predictions: (a) tail length decreases with increasing elevation and (b) tail length decreases with mean annual temperature, according to the habitat in which they live. Both of these predictions were strongly supported by the data.

While only RTL was considered, the populations of *M. sinica* living in lower elevations in the dry and arid zones were visually of slighter build, with longer, slimmer limbs, and shorter body and head hair, while higher elevation populations had thicker tails, longer body and head hair, and seemingly stockier builds. These observations support the predictions of both Allen's and Bergman's rules and can be seen as an overall adaptation for the regulation of body heat based on the external climate.

Therefore, we interpret the consistent decrease in the TTI with elevation and overlap of TTI values between subspecies along elevational lines as further evidence that this is an adaptation to

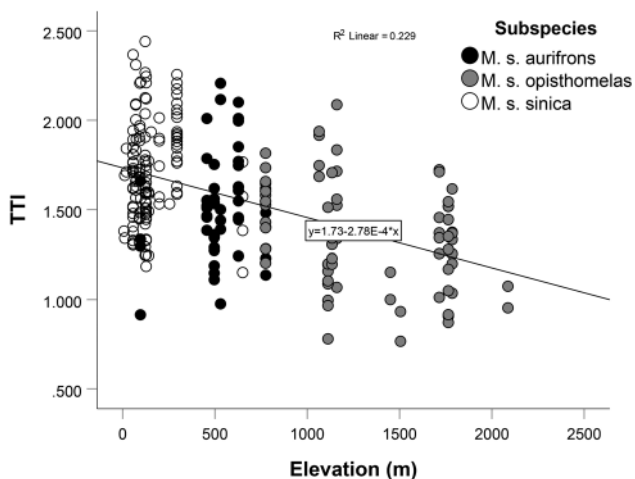


FIGURE 4 Correlation between the TTI and elevation. The three subspecies of toque macaques are indicated by different symbols. With every 100 m of elevation increase, TTI decreased by 0.028 units \pm 0.006 SD, $N = 259$ individuals. *M. s.*, *Macaca sinica*; SD, standard deviation; TTI, Tail to Trunk Index

climatic factors (temperature), and not necessarily subspecies variation per se. The analysis previously conducted on the D-loop molecular variation of mitochondrial DNA (mtDNA) in the three putative subspecies of *M. sinica* (Huffman, Nahallage, Kawamoto, Kawamoto, & Shotake, 2012) further support of our conclusions for evidence of environmental adaptation. Based on samples collected from a total of 24 sites collected widely across Sri Lanka, consisting of blood samples (17 groups, 13 sites collected by Shotake between 1981 and 1984, see Shotake, Nozawa, & Santiapilai, 1991) and fecal samples (11 sites; Huffman et al., 2012), sequence data were obtained from two regions in mtDNA: 339 bp of the D-loop region and 393 bp of the 16S ribosomal RNA region. Two distinctive groups of mtDNA haplotypes were recognized; one cluster was distributed ubiquitously in the upland/highland zone and the other in the lowland zone. From this, it was revealed that phenotypical traits of the three putative subspecies of *M. sinica* were incongruent with the two recognized mtDNA haplotypes A and B. All three subspecies were distributed between these two haplotypes. It was concluded that the phenotypical variation observed among populations in distinct ecogeographical regions were not reflected in their mtDNA haplotypes (Huffman et al., 2012).

For regional differentiation of nuclear genes in *M. sinica*, Shotake et al. (1991) report the results of a population genetics study investigating 32 blood protein gene loci from 256 samples from 20 groups across Sri Lanka. There is no discontinuity between the regional populations corresponding to the subspecies classification in the study, and it was clear that nuclear genes have lower differentiation among the groups in Sri Lanka (an estimate of relative genetic differentiation G_{ST} was 0.136 in *M. sinica*), compared with similar studies of other species. The authors inferred that this low intergroup genetic differentiation was due to frequent gene exchanges by male migrations throughout the island. In other words, genetic studies with mtDNA and nuclear genes have shown that no differentiation comparable with morphologically distinguished subspecies is found in *M. sinica* populations in Sri Lanka. It should be noted however that there is a difference in the status of genetic differentiation within Sri Lanka between mtDNA and nuclear genes.

Studies on *M. fuscata* have recently revealed intraspecific regional morphological differences among populations (e.g., Buck et al., 2018; Kawamoto, 2010). Kawamoto (2010) categorized the regional differences of *M. fuscata* traits into three types and considered their evolutionary relationship. Similar to the three *M. sinica* subspecies, the two morphologically classified subspecies of *M. fuscata* (*M. fuscata fuscata* and *M. fuscata yakui*) do not correspond to the recognized regional population clusters distinguished by mtDNA and nuclear genes. In *M. fuscata*, eco-climatic gradients, especially regional differences in annual minimum temperature, are reflected in morphological variation, such as coat color and hair density, revealing a distinctive mode of regional differentiation (Kawamoto, 2010), in support of Allen's rule.

As an analogy, it may be plausible to place local populations of *M. sinica* living in regions under different environmental conditions as different subspecies. Sri Lanka is made up of a series of three plains,

called peneplains (Beenaerts et al., 2010; Crusz, 1986), land surfaces of considerable area and slight relief shaped by protracted erosion, undisturbed by crustal movement. These plains represent three distinct elevational gradients (Figure 1), with distinct topography. These plains have been linked to the unique zoogeographical distribution and regional subspecies classification of many endemic animal species on the island (Beenaerts et al., 2010; Crusz, 1986). This unique structure is also responsible for the island's present ecological and climatic characteristics.

If these observations are correct, then epigenetic factors may also be involved in the generation of characteristic regional variation in *M. sinica* physical characteristics such as hair length and color, as well as body size and appendage proportions. The environmental effects on other morphological characteristics should be further studied and verified in the future under natural conditions and in captivity.

In support of this view, it has been shown that environmental temperature irreversibly regulates appendage length and body mass at a critical time of neonatal development (Serrat, 2013; Serrat, King, & Lovejoy, 2008; Weaver & Ingram, 1969). That is, Allan's and Bergman's rules are strongly influenced by epigenetic factors, within the bounds of a species' overall phylogenetic traits.

4.2 | Pros and cons of sampling methodology

One of Fooden's (1979) earliest studies on intraspecific morphological variation in the genus reviewed the status of *M. sinica*. Based on all the then available material, 33 museum skeleton specimens collected from 17 locations across Sri Lanka, he found no significant variation in RTL. At the time of Fooden's (1979) analysis, however, only two subspecies were recognized, with *M. s. sinica* located in the north, *M. s. aurifrons* in the southwest and an intermediate area of subspecies mixture, which he called the contact zone. All of these samples originated from low elevation, dry zone, and wet zone locations between 5 and 240 m.a.s.l., with the exception of a single specimen collected at 1,400 m.a.s.l., a specimen of the third subspecies of the toque macaque, *M. s. opisthomelas*, recently recognized to inhabit elevations from approximately 1,060 m. a. s. l. and above, in the highland wet zone (Mittermeier et al., 2013; Roos et al., 2014).

The results of Fooden (1979), at no fault of his own, were biased due to the paucity of higher elevation samples of this then unrecognized *M. s. opisthomelas*. Using a noninvasive method developed for this study to sample even unhabituated individuals, we were able to obtain an overall more robust sample size, increasing elevational, habitat and subspecies representation (259 samples; 36 locations). In doing so, a more accurate picture of the relationship between elevation and RTL was obtained for *M. sinica*.

The pixelated morphometric method described here and used for approximating RTL was validated using the previously published data by Fooden (1979), allowing us to expand upon his earlier work through the noninvasive sampling of several troops of the higher elevation living subspecies, *M. s. opisthomelas*, as well as sampling

from a wider representation of the other two subspecies across the island in a variety of different representative ecogeographical habitats. These results demonstrate that our noninvasive method for estimating and calculating the TTI is a useful alternative to capturing and physically measuring toque macaques and other primates in the wild, with limitations as to the types of measurements possible. This study joins a growing number of noninvasive methods recently developed for the assessment of such parameters as weight, body size, nutritional status, relative trunk length, hybrid status, and coat color of free-ranging primates (Breuer et al., 2007; Jadejaroen et al., 2015; Kurita et al., 2012; Rothman et al., 2008).

The greatest advantage of our method is that we are able to readily collect usable photos from unhabituated troop members as they passed by or remained still, as long as we did not approach them too closely. While we were not always able to position ourselves in a perpendicular position to monkeys, we were not dependent on them walking across a fixed structure (Kurita et al., 2012). Because of this flexibility, we could collect enough photos of various individuals in a troop to select enough suitable photos for the reliable relative measures of tail length and trunk length, starting from easily identifiable points of reference along the back. This method was also able to take into account back and tail curvature that occurs when animals move or remain stationary on a variety of natural and artificial substrates. Distance from the individual was not a critical factor in collecting the data, because we calculated a ratio of trunk and tail length.

The major difficulty we had was that some unhabituated groups tended to spend more of their time high up in the canopy or moved on the ground in dense vegetation, making it difficult to obtain a proper perpendicular view of target animals. However, this is inherent for any photo-based measurement currently described in the literature. In such situations, placing camera traps up in the canopy or on the ground along habitual travel routes could be a solution to this problem (e.g., Gregory, Carrasco Rueda, Deichmann, Kolowski, & Alonso, 2014; Whitworth, Braunholtz, Huarcaya, MacLeod, & Beirne, 2016). In principle, we believe this method is transferable to any study species, but we caution the reader that proper validation with precise hand-measured values is desirable.

In the future, more work is needed to see whether this method can be used for other purposes. One possible next step is to use this method to approximate relative body mass, by calculating total body area (pixel area) from profile photographs. If validated from true measurements of captive individuals, it may be used to investigate Bergmann's rule of variation in body mass for body temperature regulation (Bergmann, 1847). This would further open up a variety of possibilities for the noninvasive measurement of individual morphological characteristics, as well as intra- and inter-site variation.

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