



The limitations of external measurements for aging small mammals: the cautionary example of the Lesser Treeshrew (Scandentia: Tupaiidae: *Tupaia minor* Günther, 1876)

NEAL WOODMAN,^{*,*} ANANTH MILLER-MURTHY, LINK E. OLSON,[°] AND ERIC J. SARGIS[°]

U.S. Geological Survey, Eastern Ecological Science Center, Laurel, MD 20708, USA (NW)

Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC-108, Washington, DC 20013, USA (NW, LEO, EJS)

Division of Vertebrate Zoology, Yale Peabody Museum of Natural History, New Haven, CT 06520, USA (AM-M, EJS)

University of Alaska Museum, University of Alaska Fairbanks, Fairbanks, AK 99775, USA (LEO)

Department of Anthropology, Yale University, P.O. Box 208277, New Haven, CT 06520, USA (EJS)

* Correspondent: woodmann@si.edu

Age is a basic demographic characteristic vital to studies of mammalian social organization, population dynamics, and behavior. To eliminate potentially confounding ontogenetic variation, morphological comparisons among populations of mammals typically are limited to mature individuals (i.e., those assumed to have ceased most somatic growth). In our morphometric studies of treeshrews (Scandentia), adult individuals are defined by the presence of fully erupted permanent dentition, a common criterion in specimen-based mammalogy. In a number of cases, however, we have had poorly sampled populations of interest in which there were potentially useful specimens that could not be included in samples because they lacked associated skulls. Such specimens typically are associated with external body and weight measurements recorded by the original collectors, and we sought to determine whether these data could be used successfully as a proxy for age or at least to establish maturity. We analyzed four traditional external dimensions (head-and-body length, tail length, hind foot length, and ear length) and weight associated with 103 specimens from two allopatric populations of the Lesser Treeshrew (*Tupaia minor* Günther, 1876) from Peninsular Malaysia and from Borneo, which we treated as separate samples (populations). Individuals were assigned to one of eight age categories based on dental eruption stage, and measurements were compared among groups. In general, mean sizes of infants and subadults were smaller than those of adults, but the majority of subadults fell within the range of variation of adults. The large overlap among infants, subadults, and adults in external measurements and weight indicates that such measures are poor proxies for age in this species, probably for treeshrews in general, and possibly for other small mammals. This has significant implications for any investigation wherein relative age of individuals in a given population is an important consideration.

Key words: body size, measurement error, ontogeny, Southeast Asia, *Tupaia malaccana*

Age is a fundamental life-history trait that is necessary for studying demographic characteristics of populations. In morphological studies, age is important for limiting variation in a population sample and for understanding ontogenetic change. Because of the difficulty in determining true ages for individual animals, particularly members of wild populations, a number of means for estimating age have been established. These include some that use external measurements or weight, either alone or in combination with other factors (e.g., Sanderson 1961; Grau et al. 1970; Rowe et al. 1985;

Salvioni and Lidicker 1995; Karels et al. 2004; Olifiers et al. 2010; Eghbali and Sharifi 2018). Such estimates meet with variable success depending on the species of interest, the precision of the age estimate, and the amount of error that is acceptable within a given study (Lidicker and MacLean 1969; Dapson and Irland 1972; Thomas and Bellis 1980).

In our recent morphometric studies of treeshrews (Scandentia), we employed suites of variables obtained by measuring the skull and the manus, which represent functionally distinct parts of the skeleton (Sargis et al. 2013a, 2013b,

2014a, 2014b, 2016, 2018). Our methodology requires that we use measurements only from individuals that are determined to be adults based on fully erupted permanent dentition. To increase sample sizes for rarer species and from poorly represented localities in our studies of the manus, we recently investigated the effects of adding infants and subadults to our samples (Woodman et al. 2020). Although the inclusion of older subadults may be informative for populations with extremely small sample sizes, we found that infants and subadults could bias results by lowering sample means for individual variables. This, in turn, can artificially obscure or inflate differences among populations, thereby hindering attempts at taxonomic circumscription and the quantification of phenotypic differentiation.

In our studies of the manus of treeshrews, we primarily rely on dried study skins because such specimens typically include the distal limb bones, which can be imaged noninvasively. The associated skulls are used only to assign a specimen to a dental age category. Another possible strategy for increasing small sample sizes for manus variables would be to include study skins lacking associated skulls. Study skins of terrestrial mammals typically are accompanied by external measurements recorded by collectors or preparators and include four common external body measurements (total length; tail length; hind foot length; ear length) and, less commonly, weight. These data are inherently imprecise because of the malleable nature of mammalian bodies and the crude (and rarely specified) means of obtaining measurements. They are all the more problematic because of variation caused by postmortem changes in the proportions of the body and because samples generally include specimens measured by a variety of collectors of different levels and types of experience and training (Sumner 1927; Blackwell et al. 2006; Stephens et al. 2015). These issues generally render external measurements unsuitable for studies on a finer scale than approximating relative mean body sizes for a particular set of species. Despite such problems, external measurements are convenient because recording them has been standard protocol for the last ca. 130 years (Merriam 1889; Miller 1899), and they are readily available for many specimens, generally on skin tags and in field notes.

If one or more external measurements could be used as a proxy for dental age in tupaids, it would help alleviate issues with small sample sizes. For this reason, we investigated whether any of the four commonly recorded external measurements or weight could be reliably correlated with age in two large samples of the Lesser Treeshrew, *Tupaia minor* Günther, 1876.

MATERIALS AND METHODS

We aged and recorded external measurements from 103 specimens of Lesser Treeshrews from Peninsular Malaysia ($n = 57$) and Borneo ($n = 46$). Original measurements for the samples are provided in [Supplementary Data SD1](#). These two populations have been recognized as distinct subspecies: *Tupaia minor malaccana* Anderson, 1879, on Peninsular Malaysia,

and *T. m. minor* on Borneo (Hawkins 2018). To avoid potentially confounding geographic variation, we treat these populations as two geographically isolated samples. All specimens used for this project are housed in the Division of Mammals, National Museum of Natural History (USNM), Washington, DC ([Appendix 1](#)). This is a subset of the same sample used by Woodman et al. (2020) for a study of age-related changes in the proportions of the manus; additional information can be found therein.

Relative age of each individual was determined from dental eruption patterns following Woodman et al. (2020). In addition to the three general age categories of infant, subadult, and adult, we further classified infants into stages from 1 (youngest infant) to 4 (oldest infant) and subadults into stages 5 (youngest) to 7 (oldest) to represent relative stages of tooth eruption. These numbers reflect only those stages that we observed within our two samples rather than a complete sequence of tooth eruption. This yielded a Peninsular Malaysian sample with 43 adults, 12 subadults, and two infants and a Bornean sample composed of 37 adults, five subadults, and four infants.

We obtained total length (TOT), tail length (TL), hind foot length (HF), ear length (EL), and weight (WT) from all specimens as recorded by the collectors. In our tests, we used head-and-body length ($HB = TOT - TL$) instead of total length because it is independent of tail length, which can grow at a different rate than the rest of the body (Martin 1968; Collins and Tsang 1987). We also calculated tail length as a proportion of head-and-body length ($\%TL = TL \div HB \times 100$) because this proportion increases substantially during early growth in *Tupaia belangeri* (Wagner, 1841) (Martin 1968; Collins and Tsang 1987) and might therefore be useful in determining relative age. Collectors of the specimens we used were from the United States, so hind foot length generally should include the length of the claw of the longest ray; traditionally, claw length is not included in hind foot length as recorded by European-trained collectors (Merriam 1889; Miller 1899; Hall 1962).

To test whether external measurements could be used to distinguish adults from younger animals, we classified infants and subadults from each population into the seven stages and compared the measurements from each stage individually with those from adults from the same population. To graphically illustrate the comparisons, we used plotted measurements from infants and subadults against bar and whisker plots of summary statistics (mean, standard deviation [SD], range) for adults for each population. In some cases, equality of means was tested using t -tests for unequal sample sizes in the statistical program PAST v. 4.03 (Hammer et al. 2001).

RESULTS

Peninsular Malaysia.—The Peninsular Malaysian sample included two infants and 12 subadults in five categories, from stage 3 through stage 7, although not all individuals had complete external measurements ([Table 1](#)). These were compared with a sample of 43 adults. For head-and-body length (HB), all measurements for infants and subadults fell within the total

Table 1.—External measurements (mm) for age samples of *Tupaia minor* from Peninsular Malaysia and Borneo. Statistics are mean \pm *SD* and range. Sample sizes are in parentheses. Relative tail length is proportional to head-and-body length. There were no samples of stage 1 or 2 infants from Peninsular Malaysia or stage 4 infants from Borneo.

Sample	Head-and-body length	Tail length	Relative tail length (%)	Hind foot length	Ear length	Weight (g)
Peninsular Malaysia						
Adult (<i>n</i> = 43)	129 \pm 5 114–139	154 \pm 6 132–169	120 \pm 7 105–144	31 \pm 1 29–34	13 \pm 1 11–15 (<i>n</i> = 41)	48 \pm 9 35–80 (<i>n</i> = 39)
Subadult 7 (<i>n</i> = 2)	126, 130	155, 155	119, 123	32, 32	13, 13	50, 54
Subadult 6 (<i>n</i> = 1)	122	157	129	32	13	34
Subadult 5 (<i>n</i> = 9)	123 \pm 3 118–130	152 \pm 6 144–165	123 \pm 5 115–134	32 \pm 1 30–33	12 \pm 1 10–14	44 \pm 3 40–49 (<i>n</i> = 5)
Infant 4 (<i>n</i> = 1)	125	157	126	31	12	50
Infant 3 (<i>n</i> = 1)	123	140	114	30	12	46
Borneo						
Adult (<i>n</i> = 37)	126 \pm 4 119–136	156 \pm 10 135–172	123 \pm 9 106–141	32 \pm 2 27–35	12 \pm 1 10–14 (<i>n</i> = 22)	56 \pm 7 45–78 (<i>n</i> = 18)
Subadult 7 (<i>n</i> = 1)	126	165	131	33	—	—
Subadult 6 (<i>n</i> = 2)	135, 135	140, 156	104, 116	30, 35	10, 12	52
Subadult 5 (<i>n</i> = 2)	129, 130	149, 155	115, 120	28, 30	12, 12	35, 48
Infant 3 (<i>n</i> = 2)	118, 134	141, 142	105, 120	32, 34	11, 12	—
Infant 2 (<i>n</i> = 1)	109	160	147	31	12	30
Infant 1 (<i>n</i> = 1)	125	133	106	25	11	30

range of variation for adults (Fig. 1). Two individuals of stage 5 and stage 7 had HB greater than the mean value for adults. All 12 others measured below the adult mean, and of those, five stage 5 and one stage 6 subadults measured below 1 *SD* less than the adult mean. The mean value (124 mm) for all 14 infants and subadults was significantly less than that for adults (129 mm; $t = 3.174$, $P = 0.002$). This was one of the few measurements that appeared to show a general increase in size with age, although such an increase was not supported by a similar pattern for HB in the Bornean sample (see below).

All infant and subadult measurements of tail length (TL) were within the range of variation for adults, and all but three (one stage 3, two stage 5) were within 2 *SDs* of the adult mean (Fig. 1). The mean value for all 14 infants and subadults (152 mm) was only slightly less than that for adults (154 mm), although fully half of the TLs from infants and subadults (one stage 4, three stage 5, one stage 6, two stage 7) were greater than the adult mean (Table 1).

Relative tail lengths (%TL) of all infants and subadults were within the adult range, and all infants and all but two subadults (one stage 5, one stage 6) fell within 2 *SDs* of the adult mean. The mean for infants and subadults (123%) was slightly greater than that for adults (120%), suggesting that the tail decreases in relative length during ontogeny, the opposite of what has been reported for *T. belangeri* (Martin 1968; Collins and Tsang 1987).

All infant and subadult measurements of hind foot length (HF) were within the range of variation for adults (Fig. 1), and all but two stage 5 subadults were within 2 *SDs* of the mean for adults; these two stage 5 subadults both had hind feet greater than 1 *SD* longer than the adult mean. The mean value for all 14 infants and subadults for HF (32 mm) was slightly higher than the adult mean (31 mm).

Two stage 5 subadults had ear length (EL) below the range of variation of adults, and one other stage 5 subadult had EL less than 1 *SD* below the adult mean (Fig. 1). All other infants and subadults were within 2 *SDs* of the adult mean. The mean value of EL for all 14 infants and subadults (12 mm) was 1 mm lower than the adult mean (13 mm). When plotted (Fig. 1), EL is one of the few measurements that appears to show possible lengthening with increased age. The magnitude of the increase, however, is only about 1 mm, which is within the range of error for external measurements (Sumner 1927; Blackwell et al. 2006; Stephens et al. 2015).

Weights of all infants and subadults, with the exception of one stage 6 subadult, were within 2 *SDs* of the adult mean. The mean value for 10 infants and subadults (45 g) was only slightly less than that for adults (48 g), although the range for adults reached a high value of 80 g for one lactating female.

Borneo.—The Bornean sample included four infants representing stages 1–3 and five subadults of stages 5–7 (Table 1). These were compared with a sample of 37 adults. Not all

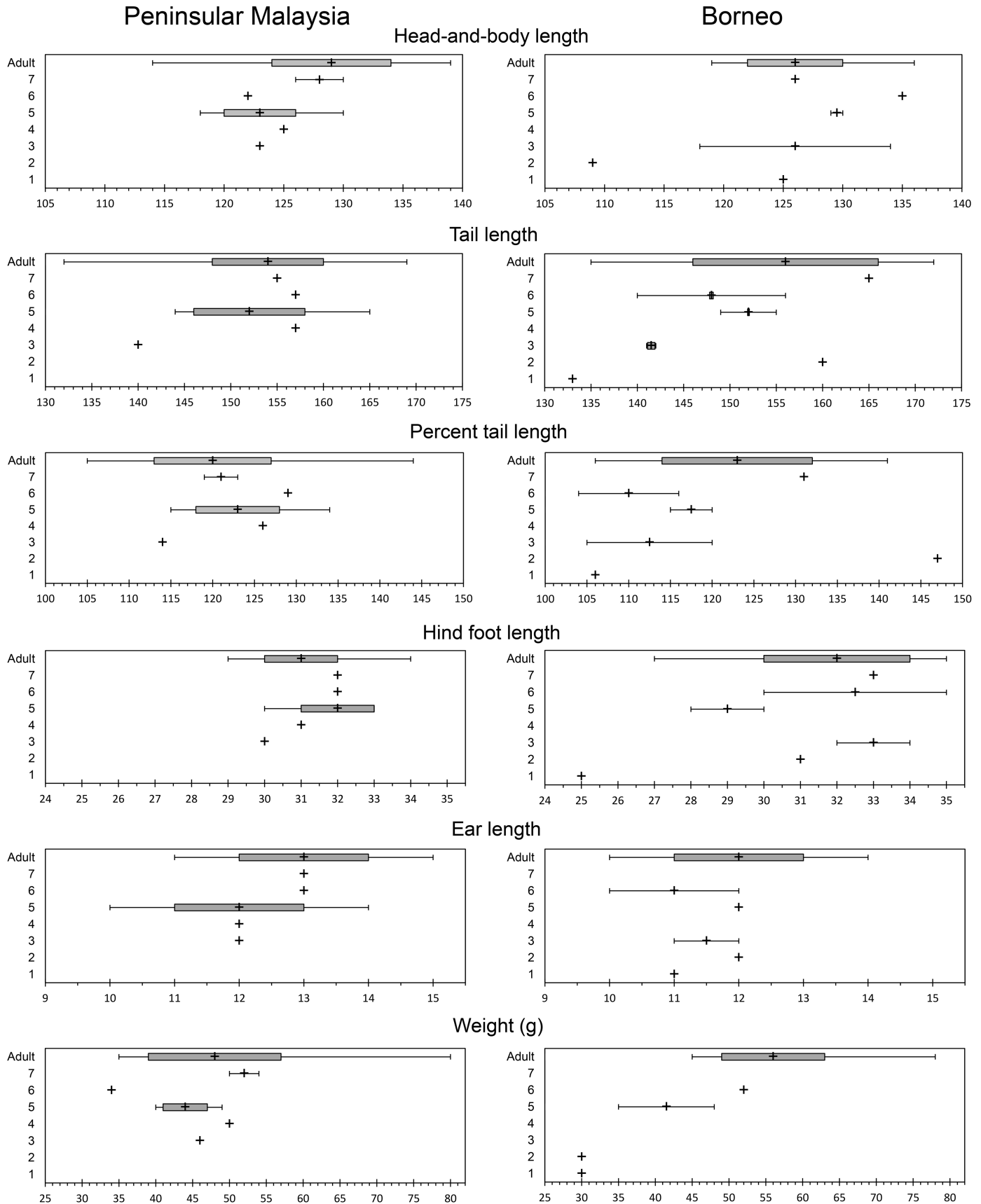


Fig. 1.—Univariate graphs of measurements (mm) from infant (stages 1–4), subadult (stages 3–7), and adult *Tupaia minor* from Peninsular Malaysia and Borneo. Crosses represent mean values or individual values, boxes represent SD, and “whiskers” represent ranges.

individuals had all external measurements. Most HBs for infants and subadults were within the range of variation for adults, with the exception of one stage 2 and one stage 3 infant, which both were below the adult range (Fig. 1). In contrast, HB for one stage 1 infant (125 mm), the youngest animal in our sample, was only 1 mm less than the adult mean (126 mm), and five individuals (one stage 3 infant, two stage 5 subadults, two stage 6 subadults) had HB greater than the adult mean. Unlike the Peninsular Malaysian sample, mean HB for all infants and subadults was slightly greater (127 mm) than that for adults (126 mm).

With the exception of one stage 1 infant, all infant and subadult measurements of TL were within the adult range of variation (Fig. 1). All but three (one stage 2 infant, one stage 6 subadult, one stage 7 subadult), however, were shorter than the adult mean length. Mean TL for all infants and subadults (149 mm) was shorter than the adult mean (156 mm), but not significantly so ($t = 1.7615$, $P = 0.085104$).

Six of the nine infants and subadults were within the adult range of variation for %TL (Fig. 1; Table 1). One stage 3 infant and one stage 6 subadult were below the adult range, whereas one stage 2 infant was above the adult range. Mean %TL for all infants and subadults was lower (118%) than that for adults (123%).

All but one stage 1 infant and all subadults had HF values within the adult range of variation, and all but three infants and subadults (one stage 1 infant, one stage 5 subadult, one stage 6 subadult) had values within 2 SDs of the adult mean (Fig. 1). The mean value for all nine infants and subadults for HF (31 mm) was slightly lower than that for adults (32 mm). Despite this, three individuals (one stage 3 infant, one stage 6 subadult, one stage 7 subadult) had HF greater than the adult mean (Table 1).

All infants and subadults had EL within the range of variation of adults, and all but one stage 6 subadult were within 2 SDs of the adult mean (Fig. 1). Despite this, EL from each infant and subadult was equal to or below the mean length for adults (12 mm). Mean EL for all infants and subadults (11 mm) was only slightly lower than that for adults.

Only five infants and subadults (one stage 1, one stage 2, two stage 5, one stage 6) had recorded weights. One stage 5 and one stage 6 subadult were within the adult range. The remaining three were below the adult range of variation. In the plot for this Bornean sample (Fig. 1), WT appears to show an increase with age. Mean WT for the five infants and subadults (39 g) is considerably lower than the adult mean (56 g).

Across all six measurements and both populations, 76% of infants and 95% of subadults had measurements that were within the range of variation for adults from the same population, and 59% of infants and 73% of subadults had measurements within 2 SDs of the adult mean. Moreover, 6% of infant measurements and 9% of subadult measurements were more than 1 SD greater than the adult mean and, therefore, easily mistaken for adult measurements. The measurement with the highest number of infants and subadults (43%) below 1 SD of the adult mean was HB. The measurement with the greatest proportion of infants and subadults (27%) below the adult range was weight.

DISCUSSION

Variation in standard external body measurements of mammals resulting from intra-observational differences, inter-observational inconsistency, and postmortem changes in the body is well documented (Sumner 1927; Blackwell et al. 2006; Stephens et al. 2015). These sources of error probably contributed to the variances in the measurements we studied, and they may have artificially masked some natural differences among our samples of infant, subadult, and adult Lesser Treeshrews. The extensive overlap we observed among age samples, however, more likely reflects certain aspects of reproduction and life history common to many tupaiids, particularly early growth patterns and behavior of nestlings and the extent and type of parental investment in the young.

Species of *Tupaia* engage in an absentee system of parental care (Martin 1966, 1968; D'Souza 1974) that has been most extensively studied for tupaiids in the Northern Treeshrew, *T. belangeri* (Martin 1968; Collins and Tsang 1987), but also has been documented for *T. minor* and the Large Treeshrew, *T. tana* Raffles, 1821 (D'Souza and Martin 1974; Emmons 2000). Probably evolved as a predator avoidance mechanism (Emmons 2000) or possibly as an economical means of reducing maternal energy expenditure (Martin 1982), absentee parenting involves a minimum of physical contact between the mother and her young during the period from birth to weaning. Other instances of the absentee system in mammals have been reported for the Short-beaked Echidna, *Tachyglossus aculeatus* (Shaw, 1792), the Round-eared Sengi, *Macroscelides proboscideus* (Shaw, 1800), the Central American Agouti, *Dasyprocta punctata* Gray, 1842, the European Rabbit, *Oryctolagus cuniculus* (Linnaeus, 1758), and the Desert Cottontail, *Sylvilagus audubonii* (Baird, 1858) (Martin 1968; Eisenberg 1975).

The young of *T. belangeri* are born in, and occupy, a nest separate from those occupied by the mother, who visits the natal nest only once every 48 h for short (maximum of 10 min) suckling bouts (Martin 1966, 1968). Except to burrow through the nesting material to and from the mother when she arrives to nurse, nestlings remain relatively immobile. They exhibit no exploratory behavior and do not leave the nest during this time (Martin 1966, 1968). This nestling phase lasts about 30 days (Martin 1968; D'Souza and Martin 1974), after which the young emerge from the natal nest. During the following 3 days, Northern Treeshrews transition to an adult diet, move to a new nest site, and begin puberty, a developmental period that lasts another 60 days (Martin 1968; Collins and Tsang 1987).

The nestling phase spent in the natal nest is a period of rapid growth. Body weight of the Northern Treeshrew increases quickly from a mean weight of 10 g at birth to 50–60 g by day 30 (D'Souza and Martin 1974; Collins and Tsang 1987), when they emerge from the nest. They reach final adult weight (145 g—D'Souza and Martin 1974; 160–175 g—Collins and Tsang 1987) at about 75–90 days (Martin 1968). Proportional tail length (%TL) increases even more rapidly, reaching adult size by the time the young first emerge (Martin 1968; Collins and Tsang 1987). Coincident with the opening of the eyes and the auditory meatus, deciduous teeth first erupt at approximately day 19 and

continue erupting through day 28, while the young still are in the natal nest. The permanent dentition erupts from about day 75 to day 90, so that permanent teeth are in place about the time an individual reaches reproductive age (Martin 1968).

Although Lesser Treeshrews have much smaller adult body size (35–80 g—Table 1; 33–59 g—D'Souza 1974; 30–77 g—Sargis 2002), the nestling phases in this species and in the larger Large Treeshrew (200 g—D'Souza and Martin 1974; 205 g—Sargis 2002) are of similar duration as that observed in the Northern Treeshrew (D'Souza and Martin 1974; Emmons 2000). Patterns of ontogenetic development, dental eruption sequence, time to maturity, and behavior are probably also similar. All of the infants and subadults in our two samples either had deciduous or permanent upper and lower third and fourth premolars in place. Based on the dental development and replacement schedule, they all should be individuals who had emerged already from the natal nest (Martin 1968). The lack of younger individuals in our museum-derived sample makes sense. Nearly immobile nestlings would be unlikely to be obtained by field collectors unless a natal nest was discovered, and the nests of Lesser Treeshrews, one of the most arboreal tupaids, typically are well aboveground (13–21 m; D'Souza 1974) and difficult to locate (D'Souza 1974; Emmons 2000; Hawkins 2018).

The broad overlap of most measurements from infants and subadults with those of adults in our two samples (Fig. 1) is consistent with there being individuals that already had emerged from the natal nest. More relevant to our original question, the similarity in these variables among infants, subadults, and adults indicates that external measurements are a poor method of gauging age once individuals have emerged. The one measurement for which there was the least overlap with the adult range was weight, in which half of the infants and 18% of subadults were below the adult range for their population. Unlike most linear external measurements, for which adult size is reached about the time of emergence from the natal nest, adult body weight may not be reached until near the end of puberty, although increase in weight typically slows considerably after emergence and again near maturity, so that there is an uneven pattern to ontogenetic increase (Martin 1968; Collins and Tsang 1987). Moreover, there is considerable variation among weights of individuals within a given age cohort (Martin 1968; Collins and Tsang 1987), including among adults. Weights of individual wild, adult, female Common Treeshrews have been documented to increase and decrease by > 40 g between captures (D'Souza 1974). The nursing schedule of females with nestlings, which requires mothers to store up to 48 h worth of milk, undoubtedly contributes to this variation. The changes in ontogenetic rates of increase in weight and the great variation in weight among individuals of the same age (Martin 1968; Collins and Tsang 1987) render weight, like the other measures, an unreliable proxy for determining age or even maturity with any confidence.

Given the broad overlap among infants, subadults, and adults in external measurements, one might then question whether nonadults might be combined with adults as representative of a

particular population. We found that mean values for infants and subadults, although not typically significantly different from mean values for adults, were sufficiently different that, as in the case of manus measurements (Woodman et al. 2020), they could potentially bias a sample mean, generally by moving it toward a smaller value. This could artificially change the degree of difference or similarity between two populations or other groups of interest. Most studies of variation among populations—particularly those focused on phenotype—require comparisons among demographically comparable samples. Limiting studies to adults minimizes potentially confounding ontogenetic variation within a population (e.g., Woodman et al. 2020). Despite the general similarity in external measurements, it remains best practice to exclude infants and subadults from adult samples in such studies.

ACKNOWLEDGMENTS

We thank Darrin Lunde and Michael McGowen of the USNM Division of Mammals for access to the specimens under their care. AM-M's work was supported by the Yale Peabody Museum/Smithsonian Institution Joint Summer Internship, and we thank David Heiser and Michael McGowen for their assistance with this program. R. Terry Chesser, Lawrence R. Heaney, and Robert M. Timm provided useful comments on previous versions of this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Original measurements from Bornean and Malayan samples of *Tupaia minor* used in this study.

LITERATURE CITED

- BLACKWELL, G. L., S. M. BASSETT, AND C. R. DICKMAN. 2006. Measurement error associated with external measurements commonly used in small-mammal studies. *Journal of Mammalogy* 87:216–223.
- COLLINS, P. M., AND W. N. TSANG. 1987. Growth and reproductive development in the male tree shrew (*Tupaia belangeri*) from birth to sexual maturity. *Biology of Reproduction* 37:261–267.
- DAPSON, R. W., AND J. M. IRLAND. 1972. An accurate method of determining age in small mammals. *Journal of Mammalogy* 53:100–106.
- D'SOUZA, F. 1974. A preliminary field report on the lesser tree shrew, *Tupaia minor*. Pp. 167–182 in *Prosimian biology* (R. D. Martin, G. A. Doyle, and A. C. Walker, eds.). University of Pittsburgh Press, Pittsburgh, Pennsylvania; Duckworth, London, United Kingdom.
- D'SOUZA, F., AND R. D. MARTIN. 1974. Maternal behaviour and the effects of stress in tree shrews. *Nature* 251:309–311.
- EGHBALI, H., AND M. SHARIFI. 2018. Postnatal growth, age estimation, and wing development in Geoffroy's bat *Myotis emarginatus* (Chiroptera: Vespertilionidae). *Mammal Study* 43:153–165.

- EISENBERG, J. F. 1975. Phylogeny, behavior, and ecology in the Mammalia. Pp. 47–68 in *Phylogeny of the primates* (W. P. Luckett and F. S. Szalay, eds.). Plenum Publishing. New York.
- EMMONS, L. H. 2000. *Tupaia: a field study of Bornean treeshrews*. University of California Press. Berkeley.
- GRAU, G. A., G. C. SANDERSON, AND J. P. ROGERS. 1970. Age determination of raccoons. *Journal of Wildlife Management* 34:364–372.
- HALL, E. R. 1962. Collecting and preparing study specimens of vertebrates. *Miscellaneous Publications of the University of Kansas Museum of Natural History* 30:1–46.
- HAMMER, Ø., D. A. T. HARPER, AND P. D. RYAN. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologica Electronica* 4:1–9.
- HAWKINS, M. T. R. 2018. Family Tupaiidae (treeshrews). Pp. 242–269 in *Handbook of the mammals of the world. 8. Insectivores, sloths and colugos* (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions. Barcelona, Spain.
- KARELS, T. J., A. A. BRYANT, AND D. S. HIK. 2004. Comparison of discriminant function and classification tree analyses for age classification of marmots. *Oikos* 105:575–587.
- LIDICKER, W. Z., JR., AND S. F. MACLEAN, JR. 1969. A method for estimating age in the California vole, *Microtus californicus*. *The American Midland Naturalist* 82:450–470.
- MARTIN, R. D. 1966. Tree shrews: unique reproductive mechanism of systematic importance. *Science* 152:1402–1404.
- MARTIN, R. D. 1968. Reproduction and ontogeny in treeshrews (*Tupaia belangeri*), with reference to their general behaviour and taxonomic relationships. *Zeitschrift für Tierpsychologie* 25:409–532.
- MARTIN, R. D. 1982. Et tu, tree shrew? *Natural History* 91:26–33.
- MERRIAM, C. H. 1889. Brief directions for the measurement of small mammals and the preparation of museum skins. U.S. Department of Agriculture, Division of Economic Ornithology and Mammalogy, Circular 11:1–4.
- MILLER, G. S. 1899. Directions for preparing study specimens of small mammals. *Bulletin of the United States National Museum* 39:1–10.
- OLIFIERS, N., R. DE CASSIA BIANCHI, P. S. D'ANDREA, G. MOURÃO, AND M. E. GOMPPER. 2010. Estimating age of carnivores from the Pantanal region of Brazil. *Wildlife Biology* 16:389–399.
- ROWE, F. P., A. BRADFIELD, R. J. QUY, AND T. SWINNEY. 1985. Relationship between eye lens weight and age in the wild house mouse (*Mus musculus*). *Journal of Applied Ecology* 22:55–61.
- SALVIONI, M., AND W. Z. LIDICKER, JR. 1995. Social organization and space use in California voles: seasonal, sexual, and age-specific strategies. *Oecologia* 101:426–438.
- SANDERSON, G. C. 1961. Techniques for determining age of raccoons. *Illinois Natural History Survey Biological Notes* 45:1–16.
- SARGIS, E. J. 2002. A multivariate analysis of the postcranium of tree shrews (Scandentia, Tupaiidae) and its taxonomic implications. *Mammalia* 66:579–598.
- SARGIS, E. J., K. K. CAMPBELL, AND L. E. OLSON. 2014a. Taxonomic boundaries and craniometric variation in the treeshrews (Scandentia, Tupaiidae) from the Palawan Faunal Region. *Journal of Mammalian Evolution* 21:111–123.
- SARGIS, E. J., V. MILLIEN, N. WOODMAN, AND L. E. OLSON. 2018. Rule reversal: ecogeographical patterns of body size variation in the common treeshrew (Mammalia, Scandentia). *Ecology and Evolution* 8:1634–1645.
- SARGIS, E. J., N. WOODMAN, N. C. MORNINGSTAR, T. N. BELL, AND L. E. OLSON. 2016 [2017]. Skeletal variation and taxonomic boundaries among mainland and island populations of the common treeshrew, *Tupaia glis* (Mammalia: Scandentia: Tupaiidae). *Biological Journal of the Linnean Society* 120:286–312 (published online 26 September 2016; in print 1 February 2017).
- SARGIS, E. J., N. WOODMAN, N. C. MORNINGSTAR, A. T. REESE, AND L. E. OLSON. 2013a. Morphological distinctiveness of Javan *Tupaia hypochrysa* (Scandentia, Tupaiidae). *Journal of Mammalogy* 94:938–947.
- SARGIS, E. J., N. WOODMAN, N. C. MORNINGSTAR, A. T. REESE, AND L. E. OLSON. 2014b. Island history affects faunal composition: the treeshrews (Mammalia: Scandentia: Tupaiidae) from the Mentawai and Batu Islands. *Biological Journal of the Linnean Society* 111:290–304.
- SARGIS, E. J., N. WOODMAN, A. T. REESE, AND L. E. OLSON. 2013b. Using hand proportions to test taxonomic boundaries within the *Tupaia glis* species complex (Scandentia, Tupaiidae). *Journal of Mammalogy* 94:183–201.
- STEPHENS, R. B., K. H. KARAU, C. J. YAHNKE, S. R. WENDT, AND R. J. ROWE. 2015. Dead mice can grow—variation of standard external mammal measurements from live and three postmortem body states. *Journal of Mammalogy* 96:185–193.
- SUMNER, F. B. 1927. Linear and colorimetric measurements of small mammals. *Journal of Mammalogy* 8:177–206.
- THOMAS, R. E., AND E. D. BELLIS. 1980. An eye-lens weight curve for determining age in *Microtus pennsylvanicus*. *Journal of Mammalogy* 61:561–563.
- WOODMAN, N., A. MILLER-MURTHY, L. E. OLSON, AND E. J. SARGIS. 2020. Coming of age: morphometric variation in the hand skeletons of juvenile and adult Lesser Treeshrews (Scandentia: Tupaiidae: *Tupaia minor* Günther, 1876). *Journal of Mammalogy* 101:1151–1164.

Submitted 25 November 2020. Accepted 19 April 2021.

Associate Editor was Deyan Ge.

APPENDIX I: SPECIMENS EXAMINED

Malayan sample (*Tupaia minor malaccana*, $n = 57$).—Malaysia: Johor: Sungei Malayu (USNM 143271); Sembrong River (USNM 112618). Pahang: Rompin, Bukit Payong, Kampong Bukit (USNM 487970, 487971). Selangor: near Kuala Lumpur (USNM 291269); Kuala Lumpur, Batu Caves (USNM 152186); Bekok, Labis Forest Reserve (USNM 487960, 487961, 487962, 487963, 487964, 487965, 487966, 487967, 487968, 487969); Subang Forest Reserve (USNM 487988, 487989, 487992, 487993, 487998, 487999, 488000, 488002, 488003, 488004, 488005, 488006, 488007, 488008); Tanjong Duablas, Kuala Langat Forest Reserve (USNM 487990, 487994, 488011, 488012, 488013, 488015, 488017, 488021, 488022, 488023); Bukit Kemandul, Sungai Rasu, Batu (USNM 487997); no locality (USNM 291270); no locality (USNM 355346). Wilayah Persekutuan: near Kuala Lumpur, Kepong (USNM 290150, 291267, 291268); Batu (Kepong), Bukit Legong Forest Reserve (USNM 487987, 487991, 487995, 488009, 488014, 488016, 488018); Sungei Buloh, Sungei Buloh Forest Reserve, Bukit Lanjan (USNM 487996, 488019, 488020); Batang Berjuntai, Batang Berjuntai Forest (USNM 488010).

Bornean sample (*T. m. minor*, $n = 46$).—Indonesia: Borneo: mouth of Simpang River (USNM 145575); Mankol, Kendawangan River (USNM 153857); Batoe Panggal, Mahakam River, N. Bank (USNM 176419, 176420); Birang River (USNM 176421, 176422,

176423, 176424, 176425, 176426, 176427, 176428); Segah River, S Bank (USNM 176429); Sungai Menganne (USNM 197197, 198038); Mahakkam River (USNM 198680, 198681). Malaysia: Borneo: Sabah: Mount Kinabalu, Bundu Tuhan (USNM 292468, 292470); Mount Kinabalu National Park, Ranau District, Poring (USNM 487972, 487974, 487975, 487976, 487977, 487978, 487979, 487982, 487983, 487985); Petergas (USNM 317178, 317179); Ranau (USNM 300901, 300902, 300905, 300906, 317180, 317181, 317182, 317183); ½ mile N of Ranau (USNM 300903, 300904); Kampong Nalapak, Ranau District, Hutan Malacau (USNM 487981); Kampong Morok, Ranau District, Morok Forest (USNM 487980, 487984, 487986). Sarawak: Kadit, Nanga Pelagus (USNM 311453).