

Brief Communication: Hair Density and Body Mass in Mammals and the Evolution of Human Hairlessness

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ABSTRACT Humans are unusual among mammals in appearing hairless. Several hypotheses propose explanations for this phenotype, but few data are available to test these hypotheses. To elucidate the evolutionary history of human “hairlessness,” a comparative approach is needed. One previous study on primate hair density concluded that great apes have systematically less dense hair than smaller primates. While there is a negative correlation between body size and hair density, it remains unclear whether great apes have less dense hair than is expected for their body size. To revisit the scaling relationship between hair density and body size in mammals, I compiled data from the literature on 23 primates and 29 nonprimate mammals and conducted Phylogenetic Generalized Least Squares regressions. Among anthropoids, there is a significant negative corre-

lation between hair density and body mass. Chimpanzees display the largest residuals, exhibiting less dense hair than is expected for their body size. There is a negative correlation between hair density and body mass among the broader mammalian sample, although the functional significance of this scaling relationship remains to be tested. Results indicate that all primates, and chimpanzees in particular, are relatively hairless compared to other mammals. This suggests that there may have been selective pressures acting on the ancestor of humans and chimpanzees that led to an initial reduction in hair density. To further understand the evolution of human hairlessness, a systematic study of hair density and physiology in a wide range of species is necessary. *Am J Phys Anthropol* 152:145–150, 2013. © 2013 Wiley Periodicals, Inc.

Humans are unusual among mammals and unique among primates in appearing hairless. Several hypotheses propose various selective factors that may have influenced hominin pelage including sexual selection (Darwin, 1871), an aquatic period in our evolutionary history (Hardy, 1960; Morgan, 1982), clothing (Glass, 1966; Kushlan, 1985), delayed development (Gould, 1977), bipedality (Wheeler, 1984, 1985), and ectoparasites (Rantala, 1999; Pagel and Bodmer, 2003). One of the most widely accepted hypotheses suggests that the reduction in hair improved evaporative cooling from sweating and provided a thermoregulatory advantage (Wheeler, 1984, 1985; Ruxton and Wilkinson, 2011). This thermoregulatory explanation of human hairlessness is probably taken more seriously than any other in the current literature of evolutionary anthropology (Jablonski, 2008). Nevertheless, there remains a paucity of data to test these hypotheses as we currently lack information on the morphology, physiology, and phylogeny of hair. In addition, a point that is often overlooked is that humans are not completely hairless. The hairless appearance is due to the type of hair over most of the human body. Humans are covered with hair *follicles*, most of which produce small, unpigmented vellus hairs, rather than thick, pigmented, terminal hairs. Including both terminal and vellus hairs, humans have ~350 follicles/cm² on their head, 65 follicles/cm² on their back, and 75 follicles/cm² on their chest (Szabo, 1967). Because vellus hairs are so minuscule, they are often forgotten in discussions of human hair evolution. Nevertheless, the question remains: why do humans have such a low density of terminal hairs? To understand the function and evolutionary history of human “hairlessness,” a broad, comparative approach is needed.

Schultz (1931) conducted the first and only systematic study of hair density in primates. He counted “visible”

hairs that were greater than 2 mm in length, which would include terminal hairs and exclude vellus hairs, and found that great apes have lower densities of visible hair than do monkeys. Using these data, Schwartz and Rosenblum (1981) investigated the role of body size on hair density. They found that as the surface area of the body increased, “relative hair density” (RHD: hairs/cm²/total surface area of the body) decreased. They proposed that the relationship between body size and hair density represents a thermoregulatory adaptation because larger animals have increased difficulty dissipating heat due to the scaling of volume to surface area. While Schwartz and Rosenblum (1981) did not include data on human body surface area or human hair density in their analysis, they related their anthropoid regression to human hairlessness by predicting that australopiths, with relatively large surface areas, would have had relatively low hair densities. Although they acknowledge that hair may not necessarily impede evaporative cooling (Cena and Monteith, 1975), they alluded to the possibility that it was advantageous for our

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

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ancestors to reduce their already sparse coats upon moving to open savanna habitats.

This “allometry hypothesis” suggests that there is a connection between body surface area, volume, and hair density, but questions remain. Specifically, it is not clear why Schwartz and Rosenblum (1981) used the variable of “relative hair density” (hairs/cm²/total surface area of the body). They estimated total surface area by taking body mass raised to the 2/3 power (Schwartz and Rosenblum, 1981). Dividing hair density by estimated body surface area may obscure the physiological significance of hair density. Within anthropoids, body surface area ranges from 47 cm² in marmosets to 2,977 cm² in gorillas (calculated from body mass means from Isler et al., 2008 raised to the 2/3 power). With the denominator differing by several orders of magnitude, relative hair density is heavily skewed by body size making it appear that large animals have sparse pelage and small animals have dense pelage. The “relative hair density” ratio may scale with body mass indicating that body mass itself is not adequately controlled. When plotting “absolute” hair density (hairs/cm²) against body surface area, the negative relationship remains significant (Schwartz and Rosenblum, 1981), but it is not clear that larger primates have less hair than expected for their body size. To determine whether great apes have lower hair density than expected for their body size, it is necessary to conduct an analysis of primate hair density that excludes great apes. While Schwartz and Rosenblum (1981) found a negative relationship between hair density and body size, the functional significance of the scaling relationship remains to be explained.

In this article, I revisit the scaling relationship of hair density and body mass in primates, including additional data on other mammals. Is there a negative correlation between hair density and body mass in nonprimate mammals? If so, do primates, and apes in particular, fit within the general mammalian pattern of hair density and body mass? Adding nonprimate mammals provides data on species that differ considerably in body size, including species with even larger body masses than great apes. If great apes have disproportionately less dense hair than smaller anthropoids, they should exhibit a lower hair density than expected for their body size compared to other primates and mammals. Alternatively, great apes may be in line with other mammals, and the lower hair density of great apes may instead reflect a general mammalian pattern of lower hair density with increasing body size.

METHODS

To reassess Schwartz and Rosenblum’s (1981) allometry hypothesis, I regressed hair density against body mass in 22 anthropoid primates, including humans. Hair density data were extracted from Schultz’s (1931) original sample, and included back, scalp, and chest hair densities (although humans were reported as having 0 back hairs/cm², so were excluded from the back hair analysis). To make the data comparable, I only included adult individuals and excluded specimens in which the author noted any peculiarities. As many primates exhibit sexual size dimorphism, I used body masses from the literature that best reflected the size of the subjects in the hair density study (Supplementary Material; Inagaki and Hamada, 1985; Smith and Jungers, 1997; Muroyama et al., 2006; Isler et al.,

2008). Schultz (1931) reported the sex of the specimens used in his hair study, so I used body masses of the same sex as the specimen in the hair data and averaged male and female body masses when both sexes were used for hair data.

To extend the analyses to a broader array of animals, I compiled additional data on hair density and body mass for 29 terrestrial nonprimate mammal species from the literature representing eight orders, and one primate, the Japanese macaque (Supplementary Material; hair density: Giacometti and Machida, 1965; Dawson and Brown, 1970; Voipio and Hissa, 1970; Jenkinson and Nay, 1975; McClure and Porter, 1983; Maurel et al., 1986; Korhonen, 1988; Webb and McClure, 1988; Flood et al., 1989; Reynolds, 1993; Fish et al., 2002; Sheriff et al., 2009; body mass: McClure and Porter, 1983; Webb and McClure, 1988; Vleck and Kenagy, 1987 in Lovegrove, 1989; Reynolds, 1993; Sidorovich et al., 1999; Pérez-Barbería and Gordon, 2000; Jones et al., 2009; Sheriff et al., 2009). Mammals exhibit variable types of hair, and different terms are used to describe these different types of hair depending on the taxa being studied. For primates, only terminal hairs were counted, as Schultz only included “visible” hairs that were greater than 2 mm in length. To make the mammal data comparable to the primate sample of visible (i.e., terminal) hairs, for this analysis, mammal hair densities represent all types of hair that can be counted discretely (combining primary and secondary hairs, or guard hairs and underfur, where applicable). Hair samples were from the dorsal region of most species (including neck, midback, and/or back), although the specific site varied among species (Supplementary Material). Most studies reported counts of hair/cm², and for studies that did not, I calculated hairs/cm² based on reported hairs/area. Sample sizes ranged from 1 to 33 individuals per species (mode = 1 individual/species, four species had unknown sample sizes; Supplementary Material). Hair data came from both preserved samples and freshly killed animals. As with the primate analysis, body masses were based on the sex of the individuals used for hair density data whenever possible.

I conducted Phylogenetic Generalized Least Squares (PGLS) regressions in R using the “caper” package (Orme et al., 2012; R Development Core Team, 2012). Within anthropoids, I conducted two regressions for back hair density: (1) excluding humans, since humans were not in the sample, and (2) excluding great apes. I conducted three regressions for scalp and chest density: (1) excluding humans, (2) excluding great apes, and (3) including all species. For the anthropoid regressions, I used a consensus tree constructed from the 10kTrees website (version 3) (Arnold et al., 2010). To assess whether primates have similar hair densities in different regions, I conducted pairwise correlations of the residuals for scalp, chest, and back hair density (residuals were based on the regressions excluding humans but including other great apes).

For the mammal regression, I used a phylogenetic tree (best estimate tree) constructed from Bininda-Emonds et al. (2007). The parameter λ scales the internal branches of the phylogeny and estimates the degree of phylogenetic signal of the residuals of the statistical model (Revell, 2010). Lambda values equal to 0 indicate that the unexplained variation is independent of phylogeny, whereas values equal to 1 indicate that the residuals have a distribution predicted by phylogeny under a

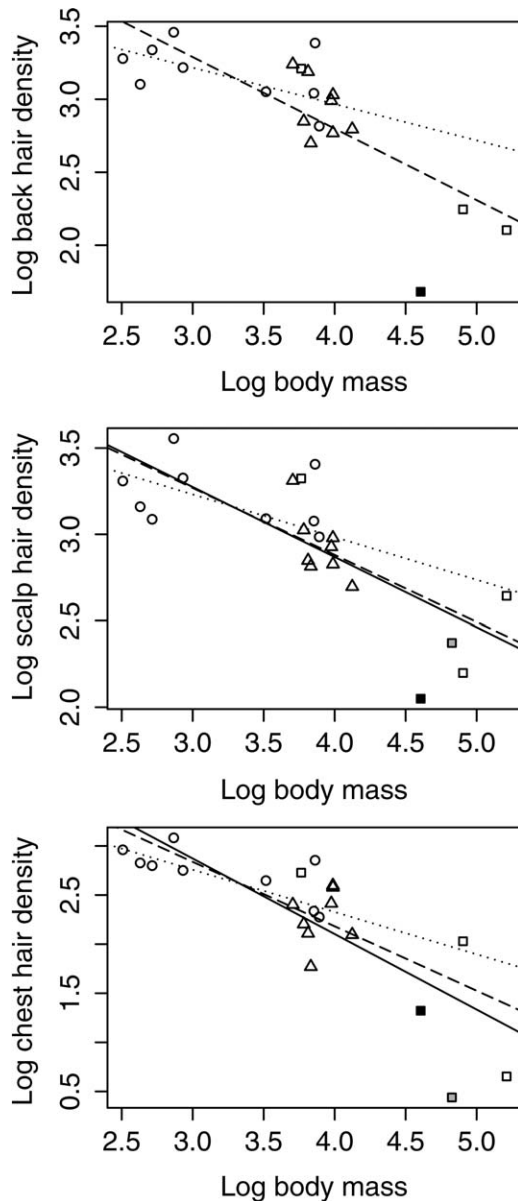


Fig. 1. Log primate back, scalp, and chest hair density (hairs/cm²) against log body mass (g); circles = Ceboidae, triangles = Cercopithecoidea, squares = Hominoidea, black square = chimpanzee, gray square = human; (1) dashed line: regression excluding humans, (2) dotted line: regression excluding great apes, and (3) solid line: regression including all species.

Brownian motion model of evolution. I incorporated the maximum likelihood estimate of λ into the analysis.

RESULTS

Within the 21 anthropoid species (excluding humans), there is a significant negative correlation between body mass and back hair density (log back hair density = $-0.490 \times \log \text{body mass} + 4.759$, SE = 0.092, $R^2 = 0.575$, $P < 0.001$; Fig. 1). Chimpanzees display the largest residuals in magnitude, exhibiting less dense hair than is expected for their body size. Excluding great apes from the analysis, there is still a negative correlation between body mass and hair density (Table 1).

There are significant negative correlations between body mass and chest hair density (log chest hair density = $-0.769 \times \log \text{body mass} + 5.18$, SE = 0.127, $R^2 = 0.628$, $P < 0.001$) and scalp hair density (log scalp hair density = $-0.406 \times \log \text{body mass} + 4.49$, SE = 0.077, $R^2 = 0.560$, $P < 0.001$). There are still negative correlations between body mass and scalp hair density and chest hair density, respectively, when either humans or all great apes are excluded (Table 1). Human densities for scalp and chest hair clump with great apes, and chimpanzees actually have lower scalp hair densities than humans. Species residuals for different body parts from the regressions excluding humans were correlated (Pearson's r , two-tailed test; scalp vs. chest: $r = 0.399$, $P = 0.073$, scalp vs. back: $r = 0.777$, $P < 0.001$, chest vs. back: $r = 0.612$, $P = 0.003$). Thus, even though there are different slopes for different body regions, some primates are generally more or less hairy than expected for their body size. The lambda value for all regressions was 0, indicating that phylogeny did not strongly influence the regression models.

To investigate whether the negative relationship between hair density and body mass holds true across mammals, I regressed body mass against back hair density in 51 nonhuman mammals. There was a significant negative correlation between body mass and back hair density (log hair density = $-0.34 \times \log \text{body mass} + 4.77$, SE = 0.0101, $R^2 = 0.192$, $P = 0.002$; Fig. 2). Among this wider set of mammals, chimpanzees still exhibit the largest residuals in absolute magnitude. In addition, primates consistently display negative residuals (Table 2). The lambda value was 0.71, indicating that there is an influence of phylogeny in this broader comparative analysis.

Excluding primates from the analysis, there is still a negative correlation between body mass and hair density among mammals (log back hair density = $-0.272 \times \log \text{body mass} + 4.507$, SE = 0.064, $R^2 = 0.375$, $P < 0.001$; Fig. 2). To determine whether primates systematically differ from nonprimates in their hair density, I conducted an analysis of covariance (ANCOVA) with hair density as the dependent variable, taxonomic order (primate vs. nonprimate) as the factor, and body mass added as a covariate. There was no interaction between order (primate vs. nonprimate) and body mass (difference, 2.435; SE, 47; df, 1; $P = 0.125$) indicating that the slopes are not significantly different. There was a significant effect of order (primate vs. nonprimate) on hair density (difference, 24.00; SE, 48; df, 1; $P < 0.001$), indicating a difference in elevation between the primate and nonprimate regressions.

DISCUSSION

There is a negative correlation between body mass and hair density in mammals. This is especially apparent among anthropoids, which exhibit a wide range of body sizes (compared to other taxa, such as bovids or rodents), but the negative correlation remains significant among nonprimate mammals. From Schwartz and Rosenblum's analysis, it appears that chimpanzees, gorillas, and orangutans all have similarly low hair densities due to their large body size. Excluding great apes from the primate analysis demonstrates that great apes do have less dense hair than is expected for a primate of their body size. Chimpanzees remain the greatest residual. Given the large difference in body size between great

TABLE 1. Regression coefficients for back, chest, and scalp density (including all species, excluding humans, and excluding great apes)

Hair density	β	SE	Intercept	Adjusted R^2	P
Back (no <i>Homo</i>)	-0.490	0.092	4.759	0.575	<0.001
Back (no great apes)	-0.249	0.085	3.963	0.310	0.0096
Chest (all primates)	-0.769	0.127	5.178	0.628	<0.001
Chest (no <i>Homo</i>)	-0.656	0.112	4.806	0.626	<0.001
Chest (no great apes)	-0.430	0.119	4.049	0.452	0.0023
Scalp (all primates)	-0.406	0.077	4.492	0.560	<0.001
Scalp (no <i>Homo</i>)	-0.388	0.082	4.433	0.514	<0.001
Scalp (no great apes)	-0.247	0.090	3.973	0.280	0.014

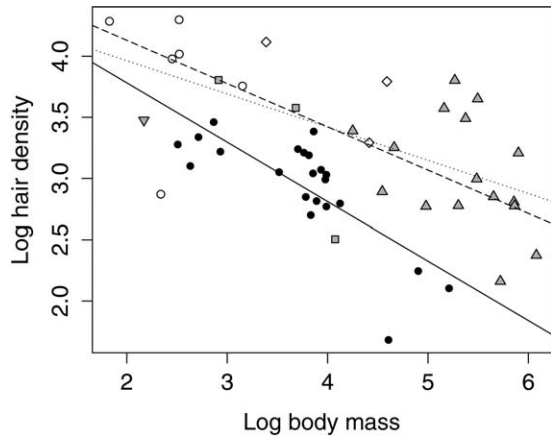


Fig. 2. Log mammal back hair density (hairs/cm²) against log body mass (g); black circles = primates, open circle = Rodentia and Lagomorpha, upward triangle = Artiodactyla, square = Carnivora, downward triangle = Soricomorpha, diamond = Didelphimorphia and Diprotodontia; (1) dashed line: regression including all species, (2) dotted line: nonprimate mammal regression, and (3) solid line: primate regression.

apes and other primates, however, extrapolating great ape hair density from the nongreat ape primate regression should be done with caution. Among all primates, only chimpanzees have especially less dense back hair than expected for their body size. The “relative hair density” score used by Schwartz and Rosenblum reduces the variation among species, obscuring the fact that chimpanzees are an outlier.

What accounts for the overall negative relationship between hair density and body mass? Decreasing hair density may reflect a scaling relationship with increasing total body surface area. Hair follicle formation occurs in embryogenesis, and the absolute number of hair follicles in mammals is set around birth (Szabo, 1967; Mecklenburg et al., 2009). Within an animal’s lifetime, hair density is expected to decrease: as surface area increases, interfollicle distances increases. It is possible that, for species with similar hair densities and body sizes at birth, larger mammals will have less dense hair as a product of greater body surface area. Selective pressures involving climate, seasonality, and activity pattern may act on hair density, leading to interspecific variation in the number of hair follicles at birth and throughout an animal’s life. While body mass may be an important factor in hair density across mammals, a negative correlation is not necessarily expected and deserves explanation.

TABLE 2. Mammal back hair density (hairs/cm²), body mass (g), and residuals from mammal regression (ordered by residuals)

Scientific name	Hairs/cm ²	Body mass (g)	Log residual
<i>Pan troglodytes</i>	48	40,367	-1.525
<i>Sigmodon hispidus</i>	741	218	-1.107
<i>Gorilla beringei</i>	127	162,500	-0.896
<i>Meles meles</i>	320	11,884.03	-0.881
<i>Pongo pygmaeus</i>	176	80,137	-0.859
<i>Saguinus bicolor</i>	1,264	428	-0.775
<i>Macaca mulatta</i>	501	6,793	-0.769
<i>Syncerus caffer</i>	145	526,000	-0.665
<i>Macaca maura</i>	588	9,720	-0.647
<i>Callithrix jacchus</i>	1,896	322	-0.641
<i>Trachypithecus cristatus</i>	706	6,060	-0.637
<i>Ateles geoffroyi</i>	652	7,780	-0.635
<i>Papio anubis</i>	624	13,300	-0.575
<i>Scapanus townsendii</i>	3,000	148	-0.557
<i>Saimiri sciureus</i>	1,653	855	-0.557
<i>Cebus capucinus</i>	1,126	3,286	-0.525
<i>Saguinus geoffroyi</i>	2,179	517	-0.511
<i>Cercocebus torquatus</i>	978	9,470	-0.430
<i>Alouatta palliata</i>	1,099	7,150	-0.420
<i>Nasalis larvatus</i>	1,072	9,730	-0.386
<i>Macaca fuscata</i>	1,177.8	8,604	-0.363
<i>Aotus lemurinus</i>	2,884	734	-0.337
<i>Litocranius walleri</i>	780	35,000	-0.335
<i>Bubalus bubalis</i>	237	1,200,000	-0.330
<i>Tragelaphus imberbis</i>	592	95,600	-0.306
<i>Erythrocebus patas</i>	1,546	6,500	-0.286
<i>Hylobates lar</i>	1,622	5,809	-0.282
<i>Chlorocebus pygerythrus</i>	1,739	5,071	-0.272
<i>Oryx beisa</i>	600	200,576	-0.191
<i>Lagothrix lagotricha</i>	2,422	7,280	-0.075
<i>Bos gaurus</i>	596	727,500	-0.004
<i>Bos javanicus</i>	709	450,000	0.001
<i>Macropus robustus</i>	1,960	25,978.92	0.021
<i>Mustela putorius</i>	6,387.5	820.2	0.024
<i>Bison bonasus</i>	641	718,000	0.026
<i>Rattus norvegicus</i>	9,519	282.9	0.040
<i>Lepus americanus</i>	5,699.5	1,418	0.056
<i>Vulpes vulpes</i>	3,780	4,820.36	0.058
<i>Eudorcas thomsonii</i>	2,452	17,800	0.063
<i>Nanger granti</i>	1,789	46,000	0.066
<i>Bos grunniens</i>	990	306,000	0.089
<i>Sciurus vulgaris</i>	10,425	333	0.104
<i>Dicrostonyx groenlandicus</i>	19,301.5	67.1	0.135
<i>Neotoma floridana</i>	19,900	332	0.384
<i>Bison bison</i>	1,616	795,300	0.443
<i>Didelphis virginiana</i>	13,076	2,442.1	0.497
<i>Kobus ellipsiprymnus</i>	3,095	236,800	0.546
<i>Alcelaphus buselaphus</i>	3,744	144,600	0.556
<i>Macropus rufus</i>	6,210	38,968.39	0.582
<i>Ovibos moschatus</i>	4,480	312,500	0.748
<i>Connochaetes taurinus</i>	6,351	184,900	0.822

Primates, for their body size, are generally less hairy than other mammals. This may represent a thermoregulatory adaptation. Wheeler (1984, 1985) hypothesized that the low hair density in humans was associated with increased sweating capabilities. If the low hair density among primates represents a thermoregulatory adaptation, there should be a negative correlation between eccrine sweat gland density and hair density. There are no comparative data on eccrine sweat gland density in primates, but the distribution of eccrine sweat glands (presence vs. absence in certain body regions) is not consistent with the thermoregulatory predictions (Montagna, 1972; Grant and Hoff, 1975). In sum, the negative relationship between hair density and body mass cannot currently be explained.

Great apes, and chimpanzees in particular, are relatively hairless compared to other mammals. What accounts for the especially low hair density in chimpanzees? The chimpanzee hair pattern may be due to the density of certain types of hair rather than a change in the total number of follicles. While there is a negative correlation between body size and visible hair density in mammals, the human hairless appearance is largely due to the covering of small, unpigmented vellus hairs rather than long, pigmented terminal hairs (Szabo, 1967). In the few studies where it was investigated, vellus hairs account for the hairless appearance of some body regions in other primates, such as the face of gorillas or forehead of stump-tail macaques (Ellis and Montagna, 1962; Montagna et al., 1966). Schultz's hair data on primates only account for visible hairs, and "extremely fine hairs, two millimeters and less in length, were disregarded" (Schultz, 1931:304). Thus, Schultz's sample represents *terminal* hair density, not total hair *follicle* density. This leaves open the possibility that chimpanzees, like humans, have a higher proportion of vellus to terminal hairs than other mammals. In other words, chimpanzees and humans may have the density of hair *follicles* expected for their body size, but a greater number of the follicles produce vellus hairs compared to other primates. To date, I have found no studies reporting vellus hair density in chimpanzees or other apes, which would be key for understanding the evolution of the human hair phenotype.

The similarities in hair among chimpanzees and humans may reflect other similarities in the skin. For example, chimpanzees, gorillas, and humans all share similarities in the distribution of apocrine and eccrine sweat glands (Ellis and Montagna, 1962; Montagna and Yun, 1963). Genetic and physiological studies of hair are needed to investigate the mechanisms underlying the similarities between human and chimpanzee pelage.

The sample of mammal species for which there are data on hair density is still limited. Many species, including chimpanzees, are represented by only one specimen. In addition, individuals in each species are likely to vary in hair density based on age, climate, and other factors. Thus, any conclusions must be made with caution, as hair density values may not accurately represent each species. While I only included hair densities from studies using similar methods, variation in sample collection, preservation of specimens, and other methodological differences may also add error to the analyses. These are problems common to many comparative studies and reflect the current data available on hair density. It will be instructive for future studies to incorporate a larger sample of mammals, including species

that appear less hairy, such as elephants, tapirs, and warthogs.

If chimpanzees are indeed relatively hairless compared to other mammals, there may have been a selective pressure acting on the ancestor of humans and chimpanzees that led to an initial reduction in hair density. Current hypotheses for human hair evolution focus on uniquely human traits, such as bipedality or long-distance running. If a reduction in terminal hair density is shared with chimpanzees, we may need to develop hypotheses for human "hairlessness" based on traits that are shared among chimpanzees, bonobos, and humans. Additional studies on chimpanzee skin are needed with adequate sample sizes, focusing on the density of both vellus and terminal hairs. It will also be important to collect data on bonobos to examine whether the pattern of lower hair density is shared among both species of *Pan*. In addition to hair density in adults, attention to the ontogeny of hair growth is especially important in distinguishing geometric scaling from other adaptations. In studying hair across a wider range of species, we will not only better understand this defining trait of mammals but also shed new light on the peculiar human hair phenotype.

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