

Sexual differences in hair morphology of coyote and white-tailed deer: males have thicker hair

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The fur of mammals serves many functions, including thermoregulation, camouflage or visual signaling to conspecifics. Fine-scale features of fur, such as hair morphology are often examined by researchers, especially in animals where pelage is of economic importance. Certain studies from this literature body show that males of many species appear to have thicker guard hair than females. Here, we examined this possibility in coyote (*Canis latrans*) and white tailed deer (*Odocoileus virginianus*) from captive populations in Utah and Georgia, USA. We used image analysis procedures to examine 402 guard hairs from 24 captive coyotes and 568 guard hairs from 29 captive deer, measuring the length and diameter of each hair. In both species, males had significantly thicker hairs than females; in coyotes, male hairs were 17% thicker, in deer, male hairs were 15% thicker. These differences are comparable to other species, where male hair is between 7%–20% thicker than those of females (in all species the average difference is 13%). Considering that there are hundreds of thousands of hairs on any given animal, this difference per unit hair could translate into considerable differences in overall pelt characteristics between sexes. The reason for this difference could relate to the sensitivity of mammalian hair to androgens, such as testosterone, which are more abundant in males of all species. Experimental studies and population surveys demonstrate that high levels of androgens stimulate body hair to grow thicker in diameter. Thus, the greater levels of testosterone in males would act to promote thicker hair. By this same mechanism, within any given collection of males, those with greater levels of androgens should also display greater hair thickness. While further research would be needed to verify this, results from this study nevertheless emphasize the knowledge gaps that yet remain in our understanding of the basic nature of mammalian fur.

Introduction

The properties of mammalian fur have been studied for many decades and on a plethora of species, yet it is surprising that our collective understanding of the full functional significance of mammalian hair is not yet complete. One of the most important functions of mammalian fur is thought to be thermoregulation, since in most species, fur is much thicker and deeper in winter than in summer (Ogle & Farris 1973, Jacobsen 1980, Kulak & Wajdzik 2006). Depth of fur is primarily modified by changes in hair length, especially of the coarse guard hair that overlays the finer underfur hair in most mammals. In fact, guard hair length is thought to be one of the primary characteristics influencing the degree of heat conduction in mammals (McClure & Porter 1983), with hair density being the other (Korhonen & Harri 1989). Guard hair along the dorsal surface of many species can also be raised ('piloerected'), which is a visual sign of aggression and/or apprehension in Canids (Fox 1969). Furthermore, variations in pigmentation of hair, especially of the outer guard hair, can also serve as visual signals to conspecifics or as camouflage (Caro 2005). Each of these functions is commonly raised by mammalogists when referring to fur properties, although there are several bodies of research (on hair morphology) outside the field of mammalogy that may offer additional insights into mammalian hair function, particularly those studies where sexual differences in hair were examined.

There are many species of wool-bearing mammals that are studied because of the economic importance of their fur. These species include blue foxes (*Alopex lagopus*) (Blomstedt 1998), cashmere goats (*Capra* spp.) (Celi *et al.* 2005), domestic sheep (*Ovis aries*) (Adams & Cronje 2003) and even wild muskoxen (*Ovibos moschatus*) (Rowell *et al.* 2001). There is another body of literature on hair properties of primates (Inagaki 1986), including humans (Sağsöz *et al.* 2004), some of which was actually conducted decades ago (Wynkoop 1929, Atkinson *et al.* 1959), but is nevertheless important. And finally, there is a large amount of research to draw upon from the biomedical or dermatol-

ogy literature, much of which is conducted on humans or human models (e.g. Lucky *et al.* 1986). Interestingly, throughout this disparate body of literature, there is at least one recurring pattern: that hair shafts of male animals tend to be thicker (i.e. they have a greater diameter) than females. This has been shown in a wide assortment of animals, such as muskoxen (Rowell *et al.* 2001), goats (Koul *et al.* 1987) and monkeys (Inagaki 1986). The significance of this pattern is unknown, and it has also largely gone unnoticed, perhaps because of the scattered nature of the literature on hair morphology. However, the pattern may indicate some sex-related difference in fur function. In any case, it is an issue that warrants additional study, first by investigating the idea in additional, non-domesticated, mammalian species. In this study, we report the results of such an investigation into sexual differences in guard hair morphology from two very distinct species of mammals from North America, the coyote (*Canis latrans*) and white tailed deer (*Odocoileus virginianus*).

Material and methods

Subjects

The coyotes examined in this study were part of a captive population housed at the National Wildlife Research Center, Predator Research Facility in Millville, UT, USA. The population consists of 98 individuals, which are fed daily rations of 650 g of commercially available mink food (Fur Breeders Agricultural Cooperative, Logan, UT). The enclosure environment consists of a short grass and alfalfa mixture with small patches of bare ground. The deer in this study were members of a captive population maintained at the Whitehall Deer Research Facility, of the Daniel B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA. This facility housed about 80 deer in 5 large outdoor paddocks (0.4–0.8 ha). All deer in this population are fed 21% protein ration (Meadows Edge, 960 Honey Ridge, Millen, Georgia, USA), with fresh perennial peanut hay and water available *ad libitum*.

Hair sampling

Hairs from both coyotes and deer were obtained when animals were immobilized for unrelated studies or procedures during the summer of 2009. For the coyotes, members of the Logan station staff used a surgical clamp to pluck a small tuft of hair from the back of the anesthetized coyote's neck. Tufts varied in size, but most contained over 50 hairs, which were a mix of guard hair and underfur hair. For the purposes of this study, guard hairs from 10 male and 14 female coyotes, which were between 1 and 10 years of age, were used. These individuals were sampled between May and September 2009. The deer hair was obtained in a similar manner from immobilized animals (i.e. a tuft was pulled from the back of the neck). We sampled 7 male and 22 female deer between 23–25 August 2009. The deer varied in age from 2–8 years. All hair samples were stored in plastic bags until measurement.

Measuring hair

The hair samples varied in size, and in the number of guard hairs *versus* underfur hairs. From these samples we attempted to measure 20 intact guard hairs for each individual, although this was not always possible when samples were small, or when the sample included many broken hair shafts. Thus, in a small number of animals, we could only obtain between 8–15 intact guard hairs for measurement. The guard hairs were measured using an image analysis approach that generally followed procedures outlined in Davis (2010). Briefly, the 20 hairs from each individual were laid flat on a transparency sheet and a clear sheet of self-laminating plastic placed over them, creating a sealed, transparent hair 'mount'. Each mount was scanned using a standard flatbed scanner set to 1200 dpi. To create color contrast between the hairs and the background, the hair mounts were scanned in front of a green plastic sheet. The resulting hair images were imported into an image analysis program (FoveaPro, www.reindeergraphics.com) for measurement. Here, each hair was digitally selected and

its total length (regardless of curvature) was measured in mm, based on prior calibration of the software using a scanned ruler image. Then, a 4-mm section of the shaft of each hair was selected at a point midway along the shaft, and the width of the shaft was measured. All measurements were automatically exported to a text file during the image analysis procedures.

Data analysis

Hair widths (μm) were examined separately for coyotes and deer, but with a similar approach for both. For each species we used a mixed-model ANCOVA design where the hair width was the dependent variable, the individual animal was a random factor, sex was a fixed factor and the hair shaft length was a covariate, to account for the possibility that longer hair may be thicker (Inagaki 1986). For each analysis we also initially included the animal age as a fixed factor, but in both deer and coyote, age was not significant in the initial models ($p > 0.5$ for both) and it was therefore removed from final models. Finally, since the coyotes were sampled throughout a 5-month period, we included month of sampling as a fixed factor in the coyote model. Analyses were conducted using the Statistica 6.1 software package (Statistica 2003).

Results

Across all 24 coyotes examined in this study (402 hairs), the average length of guard hair was 80.6 mm and ranged from 45–105 mm (Table 1). This is compared to a maximum length of 90 mm reported by Tumilson (1983) for coyotes in Arkansas, a range of 44–112 mm reported by Hilton and Kutscha (1978) for coyotes in Maine, and 80–115 mm for coyotes in Alberta (Kennedy 1982). Meanwhile, the average guard hair diameter for all coyotes was 70.1 μm , with males having thicker hairs, on average than females (76.8 μm *versus* 65.7 μm , Table 1). Consistent with this difference, the mixed-model ANCOVA showed a significant effect of sex on coyote hair width (Table 2), after taking into account varia-

Table 1. Summary of dorsal guard hair dimensions from male and female coyotes and white-tailed deer. Hairs from 10 male and 14 female coyotes were measured (402 total hairs), and from 7 male and 22 female deer (568 total hairs).

Parameter	Mean	SD	Min	Max
Coyote				
Hair Length (mm)				
Females	81.61	10.24	49.41	98.78
Males	79.02	15.54	45.44	105.44
Both sexes	80.59	12.65	45.44	105.44
Hair Diameter (μm)				
Females	65.74	17.02	41.66	129.23
Males	76.78	23.49	41.66	139.52
Both sexes	70.10	20.53	41.66	139.52
Deer				
Hair Length (mm)				
Females	21.17	4.78	8.20	36.00
Males	21.63	4.17	13.49	31.10
Both sexes	21.28	4.65	8.20	36.00
Hair Diameter (μm)				
Females	80.11	17.09	41.64	130.56
Males	92.03	10.42	58.46	121.30
Both sexes	82.83	16.58	41.64	130.56

tion among individuals and month of sampling (both significant). Interestingly, there was no significant effect of hair length on hair width in coyotes (Table 2).

Guard hairs of white-tailed deer were considerably shorter than those of coyotes, being 21.3 mm in length on average across all 568 hairs (Table 1). This is compared to values of 26–32 mm in white-tailed deer from south-east Georgia (Brisbin & Lenarz 1984) and an average of 17.5 mm in white-tailed deer from the northeastern United States (Jacobsen 1980). Guard hair widths averaged 82.8 μm across all

29 deer, and as with coyotes, the average thickness of male deer hairs was larger than that of females (92.0 μm versus 80.1 μm , Table 1). Moreover, the mixed-model ANCOVA showed that the sexes differed significantly in hair width after effects of individual and hair length were accounted for (Table 2).

For comparison, the average hair thickness of male and female coyotes and deer obtained in this study are shown in Table 3, along with similar values from the published literature on other mammals. This table shows that the magnitude of the sex difference in coyotes (male hairs were on average 17% thicker than those of females) and deer (male hairs were 15% thicker than female hairs) appeared to be on par with that of other species, which ranged from 7%–19.8%. Furthermore, if the average hair diameters of males and females from all species in this table are compared statistically, we find that male hairs are significantly thicker than those of females (paired *t*-test: $t = 3.19$, $df = 5$, $p = 0.024$), with male hairs being on average 13% thicker than female hairs.

Discussion

Results from this study demonstrated that male guard hairs of coyote and deer tend to be thicker in diameter than those of females, which is a pattern that has been found in a number of other mammalian species. In fact, the consistency of the pattern in each study where sexes have been considered separately suggests that this may be a universal pattern in mammals. Furthermore, the

Table 2. Summary of mixed-model ANCOVA models examining factors influencing guard hair widths of coyotes and white-tailed deer. Hair length was a covariate and individual animal was a random factor in both analyses.

Explanatory variable	df effect	MS effect	df error	MS error	<i>F</i>	<i>p</i>
Coyote						
Hair Length	1	0.000	19.727	0.002	0.076	0.786
Individual Animal	18	0.002	377.000	0.000	7.473	< 0.001
Month	4	0.005	18.547	0.002	2.988	0.046
Sex	1	0.011	17.601	0.002	5.098	0.037
Deer						
Hair Length	1	0.005	33.890	0.001	5.732	0.022
Individual Animal	27	0.002	538.000	0.000	9.448	< 0.001
Sex	1	0.014	27.022	0.002	8.336	0.008

magnitude of the difference between sexes found here is also similar to that reported in other species (Table 3), which is on average around 13%. If one considers that there are many hundreds of thousands of guard hairs on any given animal (white-tailed deer have between 750–1000 guard hairs per cm²; Moen & Severinghaus 1984), this seemingly small difference in hair diameter would translate into a considerable difference in overall fur mass and thickness (of coat) between males and females.

The most plausible biological explanation for the pattern we discovered may be the mammalian hair's sensitivity to androgenic hormones (i.e. such as testosterone). These are the hormones that promote the growth of secondary sexual characteristics in males, such as facial and chest hair in humans. In fact, this same mechanism appears to promote greater hair diameter as well; within the biomedical literature, there is work showing that hamsters given exogenous testosterone grow thicker hairs (Lucky *et al.* 1986). The same is true if humans are given androgen supplements (their body hair grows thicker) (Giltay & Gooren 2000). Interestingly, the same study showed that if testosterone levels are experimentally decreased, hairs become thinner. Furthermore, population-level surveys of human females have found a positive relationship between individual hair thickness and natural levels of androgens (Sağsöz *et al.* 2004). Plus, measurements of hairs in different parts of the human body show that hairs tend to be thicker over androgen-dependent sites (Riggott & Wyatt 1983). Combined, these studies all suggest that males tend to have thicker hair than females because males of all species tend to have greater levels of testosterone and other andro-

gens than females (Ferguson 1985).

If androgen-dependence is indeed the reason for the sex-based differences in hair thickness, one may also expect that within a given cohort of males, those individuals with greater levels of testosterone would have thicker guard hairs. Since this pattern has been found in humans (Sağsöz *et al.* 2004), it would not be unreasonable to expect this in other mammalian species. In fact, this may be an area that could be explored in future investigations, since if it bears true, then it may eventually be possible for researchers to use hair thickness as a simple indirect indicator of individual testosterone level in mammalian research projects.

While the mechanistic explanation for the pattern uncovered here appears logical, the functional significance of thicker male guard hairs is less apparent. We consider it unlikely that this has anything to do with thermoregulation, since hair length, not thickness is one of the primary factors regulating fur depth, and therefore heat transfer/loss (e.g. Jacobsen 1980, Moen & Severinghaus 1984). Moreover, it would seem unlikely that males would have different thermoregulation requirements than females at all. In support of this, Moen and Severinghaus (1984) found no sex-related differences in hair depth of white-tailed deer. One possibility may be that thicker hair serves as a signal to conspecifics when hairs on the back of the animal are raised, as in Canids (Fox 1969). Or perhaps the thick guard hairs serve a protective function against wounding during physical combat and aggression between males. Whatever the function may be, results from this study highlight how our understanding of the nature of mammalian fur is not yet complete.

Table 3. Average guard hair diameter of male and female mammals reported in the published literature and this study.

Species	Males (μm)	Females (μm)	Difference (%)	Source
Goat	13.3	12.1	9.9	(Koul <i>et al.</i> 1987)
Muskox	21.5	20.1	7.0	(Rowell <i>et al.</i> 2001)
Japanese monkey	51.8	43.3	19.6	(Inagaki 1986)
Llama	43.0	39.4	9.1	(Martinez <i>et al.</i> 1997)
White-tailed deer	92.0	80.1	14.9	This study
Coyote	76.8	65.7	16.9	This study
Average difference			12.9	

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