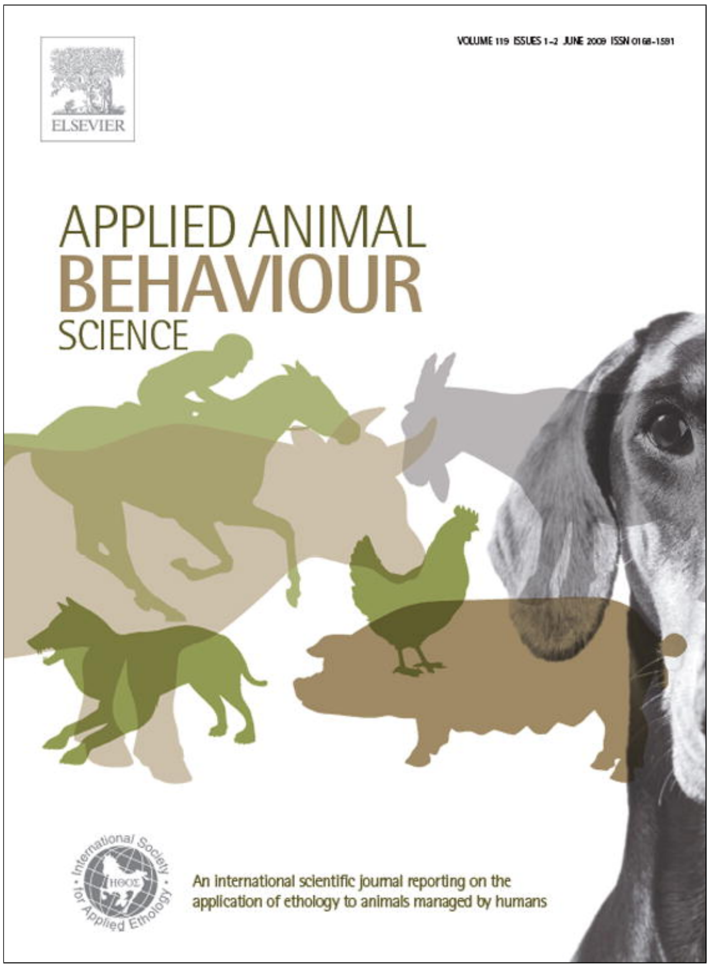
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Factors influencing hair loss among female captive rhesus macaques (*Macaca mulatta*)

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ABSTRACT

Although rare among wild animals, hair loss is common among captive animals, which suggests that some aspect of the captive environment contributes to abnormal hair loss. Female rhesus macaques (*Macaca mulatta*) at the California National Primate Research Center (CNPRC) housed in outdoor enclosures exhibited hair loss that varied significantly by pregnancy, season, ground substrate, rank, and age as well as by several pair-wise interactions. Pregnant females were 2.4 times more likely to have worse coat condition than non-pregnant females ($P < 0.001$). Among pregnant females, pronounced hair loss was apparent 1–2 months into gestation, as well as during the month following parturition. Females in general exhibited the lowest degree of hair loss in Fall (Fall vs. Winter: $P < 0.001$; Fall vs. Spring: $P < 0.001$; Fall vs. Summer: $P < 0.001$). Independent of reproductive condition and seasonality, macaques housed in enclosures with gravel substrate were 3.7 times more likely to have greater hair loss than those in enclosures with grass substrate ($P < 0.001$), and low-ranking females exhibited significantly greater hair loss than high-ranking females ($P < 0.001$). Older females had significantly greater hair loss than younger females ($P < 0.001$). Finally, females in larger groups tended to have greater hair loss than those in smaller groups. These results indicate that multiple factors influence the degree of hair loss among female captive rhesus macaques, some of which include housing conditions that can be modified to improve coat condition, such as planting grass in outdoor enclosures and adopting management procedures that reduce levels of social stress experienced by lower-ranking animals and animals living at higher densities.

1. Introduction

Hair and feather loss is common among animals kept in captivity and may be extensive enough that the skin is partially or fully exposed for a period of time (Garner et al., 2004; Gerold et al., 1997; Huber-Eicher and Wechsler, 1997; Steinmetz et al., 2006). Molt occurs in wild animals, but it is rare that free-ranging, wild mammals exhibit hair loss as extensive or frequent as that seen in captive mammals (Isbell, 1995; Vessey and Morrison, 1970), which suggests that some aspect of the captive environment contributes to abnormal hair loss.

Understanding the etiology of alopecia among mammals in captivity is important because hair loss may be an indicator of overall welfare. Multiple factors have been shown to influence abnormal hair loss, including reproductive condition (Davis and Suomi, 2006), deficient diets (Gerold et al., 1997; Isbell, 1995), parasites and skin diseases (Steinmetz et al., 2005), hair pulling or over-grooming (Reinhardt, 2005), and social stress (Roloff et al., 1998; Steinmetz et al., 2006). Thus there may be multiple

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causes of hair loss, and the challenge is to determine the relative contributions of the different potential causes as a first step in ameliorating hair loss in captivity.

1.1. Over-grooming and social conditions

The captive environment can be stressful for animals, partly because spatial restrictions make it difficult to avoid conflicts with others (Judge and DeWaal, 1997). Such conditions can increase aggression and social tension by increasing contact between animals. Grooming is a tension releaser in primates, lowering heart rate among those being groomed and lowering cortisol levels among both groomers and those being groomed (Boccia et al., 1989; Gust et al., 1993; Shutt et al., 2007). Captive primates may cope with aggression by increasing grooming (DeWaal, 1984; Terry, 1970). Thus, alopecia may occur either because animals over-groom as a way to reduce their stress or because stress itself causes hair to fall out. If social conditions affect hair loss, then lower-ranking individuals, who are more frequently the targets of aggression and are presumably under greater stress as a result (Abbott et al., 2003), should exhibit greater hair loss than higher-ranking individuals, and animals living at higher densities should exhibit greater hair loss than those living at lower densities. Age may also be a factor if the effects of stress accumulate over time.

1.2. Over-grooming and foraging

There may be other causes of over-grooming in addition to social stress, such as redirected foraging behavior. Captive animals are often unable to forage as much as their wild counterparts because their food is provided for them in easy to find quantities and locations. Foraging is a complex behavior that consists of appetitive and consummatory phases (Lindburg, 1998), and studies suggest that foraging is a highly motivated behavior (Neuringer, 1969; Rushen et al., 1993). For example, callitrichid primates choose unshelled over shelled peanuts 80% of the time (Chamove, 1989). Animals that cannot satisfy their motivation to forage may redirect motor patterns involved in foraging to some other behavior, such as grooming or plucking hair. There is some evidence in birds and mammals, including primates, that frustrated motivation to forage is indeed correlated with redirection toward hair-plucking and feather pecking cagemates (Beynen et al., 1992; Boccia and Hijazi, 1998; Meehan et al., 2003).

1.3. Hair loss among socially housed rhesus macaques

Our goal here is to elucidate the most important factors associated with hair loss in captive outdoor groups of rhesus macaques. If hair loss is related to social or physical conditions of the captive environment that can be ameliorated by management decisions, then hair loss may serve as a reliable signal that captive conditions need to be modified to improve well-being.

Like many captive rhesus groups, rhesus macaques housed in outdoor enclosures at the California National Primate Research Center (CNPRC) experience hair loss (Beisner and Isbell, 2008). Hair loss affects both males and females, and appears to be most pronounced during winter and spring months, an unusual and potentially dangerous phenomenon given that fur is an important barrier between the animal and its environment. Seasonal changes in hair loss may be due to either photoperiod or reproductive condition as the breeding season coincides with decreasing daylight hours (September–December). It may be possible to tease apart hormonal from seasonal changes in females because not all females become pregnant. We hypothesize that if hormonal changes during pregnancy cause hair loss in these captive macaques, then non-pregnant females should have less hair loss than pregnant females. Alternatively, if seasonal changes in photoperiod cause hair loss among females, then all females should be equally affected by hair loss regardless of reproductive condition.

Although little might be done to reduce seasonal and reproductively driven hair loss, there is some evidence that other, more modifiable factors, e.g., physical or social conditions contribute to hair loss in macaques. At the CNPRC, for instance, macaques live in outdoor enclosures with either gravel or grass substrate. Animals in gravel enclosures spend less time foraging and more time grooming relative to those living in enclosures with grass substrate, and preliminary analysis suggests that they also have greater hair loss (Beisner and Isbell, 2008). Thus, we predict animals with limited foraging options (i.e., gravel substrate) will have more hair loss than animals with more foraging opportunities. Similarly, animals at the CNPRC live in age-variable groups ranging from 70 to 180 individuals within the same-sized enclosures. We predict that animals that are low-ranking or live in larger groups, both of which have been shown to increase stress (Abbott et al., 2003; Manogue, 1975; Pearson et al., 2007), will exhibit greater hair loss than animals that are high-ranking or live in smaller groups. Similarly, we predict that stress should be more apparent in older animals due to the cumulative effects of stress and they will have greater hair loss than younger animals.

2. Methods

2.1. Study subjects

The study was conducted at the CNPRC in Davis, CA, USA from September 2006 to October 2007 and was approved by the University of California Davis IACUC (#12063). The subjects of this study were seven groups (Groups 1, 2, 5, 8, 14, 16, and 18) of rhesus macaques housed in 0.2 ha enclosures (Table 1). Only the observations on female rhesus macaques are treated here. All enclosures had 10 A-frame houses, multiple suspended barrels and swings, and several perches. Monkey chow was given to each group at approximately 07:00 h every morning, and again between 14:30 and 15:30 h in the afternoon. Monkey chow was typically available throughout the day because groups usually do not eat all of the chow that is given.

Rhesus macaques in this outdoor colony were managed with a minimal level of disturbance, thus individuals of

Table 1
Characteristics of study groups.

Group	Ground substrate	Group size[a]	Animal density (ind./ha) [a]	Adult sex ratio M:F
1	Grass	141 (129–156)	707 (660–780)	1:3.2
2	Both[b]	155 (141–180)	775 (705–900)	1:3.1
5	Grass	170 (160–187)	849 (800–935)	1:5.2
8	Gravel	164 (156–180)	820 (800–900)	1:3.8
14	Grass	88 (78–102)	437 (390–510)	1:7.8
16	Grass	134 (122–146)	669 (610–730)	1:7.8
18	Gravel	140 (123–158)	704 (615–790)	1:4.5

[a] Means and (ranges).
[b] Group 2 was moved to an enclosure with grass ground substrate after 7 months.

each enclosure/group were free to interact with one another as they chose. Disturbances were limited to daily morning health checks, round-ups four times per year to conduct health examinations on all animals, and periodic removal of injured or sick animals for medical treatment.

Four groups had naturally growing grass in their enclosure (at least 30% grass within the 0.2 ha area) and two groups had gravel/dirt substrate with no grass. Another group (Group 2) began the study in a gravel enclosure and was moved to a grass enclosure (approximately 30% grass coverage) after 7 months (Table 1). This group provides an opportunity to compare degree of hair loss in the same animals facing both conditions.

Information on females' pregnancy status, age, and rank within their group's dominance hierarchy was obtained from the behavioral management staff of the CNPRC. Relative dominance ranks were obtained from records kept by the behavioral management staff, who conduct weekly systematic behavioral observations of displacements and aggressive interactions. Females were divided into three rank categories: high, middle and low. Females in the top third of the dominance hierarchy were assigned a rank of high, those in the middle third a rank of middle, and those in the bottom third of the hierarchy were assigned a rank of low. Those females in the exact middle of two categories were placed in the lower rank category. Relative ranks changed for some individuals over the 14-month study period. The rank held by each individual at each of the seven time-points of hair loss assessment could be different from those of other time points if an animal changed rank. Therefore, the rank associated with each hair loss score is the rank held by the animal at the time of each assessment. One or two individuals per group changed rank categories over the study period.

2.2. Sampling methods

One observer (BAB) recorded the degree of hair loss of 434 adult and immature females (3 years and older) on a five-point categorical scale modified from Honess et al. (2005). The hair loss scale consisted of nine score levels: 1–5, including half-scores, where 1 represented perfect coat condition and 5 represented bald condition (Table 2).

Hair loss was visually assessed approximately once every 45 days for each group. For all groups, hair loss was recorded at seven time points during the study, in September, November, January, March, April, June and August. For Group 2, hair loss was recorded for an additional time-point in October 2007 to compare hair loss scores for the same animals during the same season (Fall 2006 vs. Fall 2007) on the two different substrates. The 45-day scoring interval was determined by earlier noting that two bald females had grown nearly full coats after 2 months. This is in agreement with reported hair growth rates among rhesus macaques (Dolnick, 1967). Therefore, a 45-day scoring interval allowed the greatest amount of variation in individual scores while also allowing that a previous score may predict the subsequent score.

All individuals were identified when assessing hair loss so that each individual was scored once each month. Individuals who were not in the enclosure or could not be found on the day of scoring were not scored for that month.

2.3. Inter-observer reliability

To verify that the scores BAB assigned accurately represented the level of hair loss, another observer with no prior experience in hair loss scoring was asked to use the five-point categorical hair loss scale to assign a score to 23 animals in a group that had already been scored. A high correlation was observed between the scores of both observers (Spearman $r = 0.96$, $n = 23$). Scores recorded by this second observer were not included in analyses.

2.4. Statistical Analyses

A total of 2688 observations on 403 females were included in the analyses out of the possible 3038 observations on 434 females at seven time points. Thirty-one females were excluded from analyses because

Table 2
Definitions of hair loss categories.

Hair loss score	Definition
1	Perfect coat condition
1.5	1–2 small patches of fur missing
2	3–4 small patches of fur missing, totaling 2–5 cm^2
2.5	Multiple patches/one large patch of fur missing, $<$25% of body
3	Multiple patches/one large patch of fur missing, 25–50% of body
3.5	Generalized alopecia, $\leq$50% of body
4	Generalized alopecia, $>$50% of body
4.5	Alopecia involving 75% of body
5	Bald or nearly bald

they were missing scores for more than three of the seven time points. To simplify the analysis, the hair loss scores were condensed into four whole-score categories 1, 2, 3, and 4. All half-scores were rounded up to the nearest whole-score, and category 5 was aggregated into category 4 due to small sample size.

For 311 females, approximately three of the seven hair loss scores were recorded while they were pregnant. The timing of pregnancy coincides with the winter and spring months as the number of pregnant females peaked at 284 of 434 females in January and 289 of 434 females in March. Therefore, season and pregnancy status were both included in the analysis to separate their effects.

To determine the effect of pregnancy, females were coded as being pregnant or not pregnant on the day hair loss was assessed for each month. However, the influence of hormonal change during pregnancy is likely to be delayed, rather than immediate. Therefore, degree of hair loss during the first month of pregnancy may reflect hormone levels prior to becoming pregnant. Similarly, degree of hair loss during the month immediately following parturition may reflect the hormone levels of the recent pregnancy. Therefore, the analysis was conducted twice, with pregnancy assigned to hair loss scores in two different ways. First, females were designated as being pregnant only during the months in which they were actually pregnant, and second, the first month of pregnancy was designated as not pregnant, and the month following parturition was designated as one of the months being pregnant.

The seven time points were aggregated into four seasons: Fall (September and November), Winter (January and March), Spring (April), and Summer (June and August). Seasons, rather than months, were used in the analysis because pregnant females were represented by only three individuals in the months of September and August, and therefore the effect of non-pregnancy could not be separated from the individual effects of these months.

In addition to the main effects of substrate, pregnancy, season, rank, age and animal density, there are several potentially important pair-wise interactions among the predictors. First, female mammals typically have different nutritional requirements during pregnancy than when not pregnant. If grass substrate provides additional nutrition to pregnant females, then grass substrate might be expected to modify the effect of pregnancy on hair loss. Second, captive groups of rhesus macaques having gravel substrate spend more time grooming (Beisner and Isbell, 2008), which may contribute to greater hair loss if grooming is excessive. If grooming is directed up the hierarchy, as in other groups of macaques (Schino et al., 2000), then high-ranking animals living in enclosures with gravel substrate may receive more grooming and exhibit worse hair loss than high-ranking animals with grass substrate. Third, stress may affect hormonal pathways and reproduction (Ha et al., 2000; Moberg, 2000). Therefore, social indicators of stress such as dominance rank and animal density may exacerbate the affect of pregnancy on hair loss. Fourth, if stress can have a cumulative effect over a lifetime, then a female's age may influence the effects of both pregnancy and rank on hair loss.

2.4.1. Model Fitting

The data were analyzed in MIXOR (Hedeker and Gibbons, 1996) using the extended version 2 which allows for non-proportional odds (Hedeker and Mermelstein, 1998). A two-level partial proportional-odds ordered logistic regression model was fit to the data on hair loss for female rhesus macaques with random effects for female and fixed effects for substrate, pregnancy, season, rank, age, and animal density and interaction terms for substrate × pregnancy, substrate × rank, pregnancy × rank, pregnancy × age, pregnancy × animal density, and age × rank. Traditional multiple regression analysis was not possible with an ordered categorical response variable. However, the analysis used here is essentially the same as multiple regression analysis but is designed for categorical response variables. Means and standard errors for all variables are presented in Table 3.

To determine that this was the best model to use, we initially fit a three-level proportional-odds ordered logistic regression model to the hair loss data with random effects for female and group and fixed effects for substrate, pregnancy, season, rank, age, and animal density. The effect size of the random effect for group was quite small. Therefore, we decided to fit the simpler two-level proportional odds ordered logistic regression model. With proportional odds, the effect size is assumed to be the same regardless of the level of the ordered variable (i.e., the hair loss categories 1–4). Thus the odds ratio calculation (which generates the model coefficient) is forced to be the same for all possible divisions of the ordered category; these divisions are called thresholds (threshold 1 = 1 | 2 3 4; threshold 2 = 1 2 | 3 4; threshold 3 = 1 2 3 | 4). Thus a single coefficient is used to relate each predictive variable to all levels of hair loss (Agresti, 2002).

The proportional odds assumption can be tested using the Brant test (Brant, 1990). The Brant test is designed for fixed-effects models, and to our knowledge has not been adapted for multilevel models such as the model used in

Table 3
Mean and median hair loss scores for all variables.

Parameter	Categories	Mean ± SE hair loss score	*N*
Substrate	Grass (4 groups)	1.5 ± 0.05	230
	Gravel (2 groups)[a]	2.2 ± 0.10	135
Pregnancy	Pregnant	1.9 ± 0.06	311
	Not pregnant	1.6 ± 0.09	123
Season	Fall (September and November)	1.5 ± 0.03	434
	Winter (January and March)	2.0 ± 0.04	434
	Spring (April)	2.2 ± 0.06	434
	Summer (June and August)	1.7 ± 0.03	434
Rank	High	1.5 ± 0.08	144
	Middle	1.8 ± 0.09	146
	Low	1.8 ± 0.09	144
Age	3–4 years	1.5 ± 0.10	120
	5–9 years	1.8 ± 0.08	185
	10–14 years	1.9 ± 0.12	80
	15+ years	2.1 ± 0.16	49

[a] Group 2 was not included in mean calculations because it moved from gravel substrate to grass substrate in April 2007, half-way through the study.

this analysis. However, the Brant test, when applied to a fixed effects model, may provide conservative inferences about whether the proportional odds assumption is valid for the analogous multilevel model. Results of the Brant test indicated that two variables (middle-rank, substrate) may not meet the proportional odds assumption, and therefore a model allowing some variables to have non-proportional odds was necessary.

We used a log likelihood ratio test to select an appropriate sub-model in which some variables had proportional odds and others did not. A partial proportional odds model, specifying non-proportional odds for middle-rank, and proportional odds for all remaining explanatory variables, was the simplest model that met the goal of not differing significantly from the full non-proportional odds model (Chi-square distribution, df = 16, $X = 18.78$, $P = 0.28$). Specifying non-proportional odds for the variable middle-rank resulted in three different coefficients to be estimated, one coefficient for each threshold division of the ordered categories of hair loss (threshold 1 = 1 | 2 3 4; threshold 2 = 1 2 | 3 4; threshold 3 = 1 2 3 | 4).

3. Results

3.1. Hair loss and reproductive condition

Females exhibited hair loss more at some times of the year than others, and part of this was due to reproductive condition. Among females that were pregnant during the same months (e.g., January–April), hair loss was most pronounced in the final months of pregnancy as well as in the month following parturition, which indicates that the effect of pregnancy on hair loss is better represented by the model where pregnancy designation is shifted to exclude the first month of gestation and to include the month following parturition. Therefore, effect sizes for all predictors reported here are from the model that defines pregnancy as being shifted by one month relative to the actual gestation dates.

Pregnant females had significantly poorer coats than non-pregnant females. The model indicates that non-pregnant females are 2.4 times more likely to have better coat condition than pregnant females ($P < 0.001$), assuming null or reference values for the remaining variables (i.e., females are high-ranking, of average age, and living in a group of average animal density). Due to the inclusion of interaction terms, the interpretation of all coefficients involved in interactions assumes all other variables are at null or reference values (Gelman and Hill, 2007). The reference values for this analysis are: gravel substrate, not pregnant, high rank, average age of the sample (8.2 years), and average animal density of the sample (731 animals/ha).

3.2. Hair loss and seasonality

Females had significantly better coats during Fall than during Spring, Winter, and Summer (Fig. 1). The model indicates that females were 2.8 times more likely to have better coat condition (at any point on the hair loss scale) during Fall than during Spring, the season with most pronounced hair loss ($P < 0.001$), and females were 2.0 times more likely to have better coat condition during Fall than during Summer ($P < 0.001$). Finally, the model indicates that females were 2.5 times more likely to have better coat condition during Fall than during Winter ($P < 0.001$).

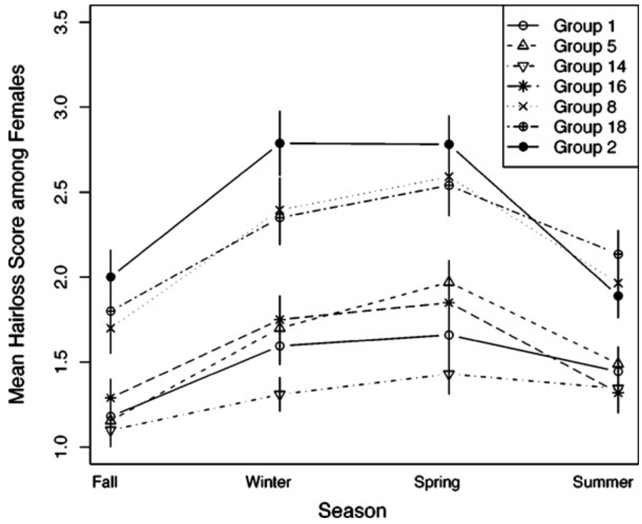

Fig. 1. Hair loss by season. Mean hair loss score for females in four grass groups (1, 5, 14, 16), two gravel groups (8, 18), and for the group that moved from gravel to grass substrate in April 2007 (Group 2). Compared to Fall, females had significantly poorer coat condition in Spring, Winter and Summer ($P < 0.001$). Hair loss was measured on a five-point categorical scale where 1 represented a full coat and 5 represented baldness. See Table 2 for complete definitions of hair loss scores.

3.3. Hair loss and substrate

Females living in enclosures with gravel substrate had significantly poorer coats than females with grass substrate (Fig. 2). The model indicates that females in enclosures with grass substrate are 3.7 times more likely to have better coat condition than females in enclosures with gravel substrate ($P < 0.001$), assuming females are high-ranking, of average age, and living in a group of average animal density.

Group 2 was moved from a gravel enclosure to a grass enclosure halfway through the study. A fixed-effects proportional-odds ordered logistic regression model was fit to the data on hair loss for females in Group 2 for the two fall seasons only, as fall was the only season in which the animals were sampled more than once. As with the other groups, females showed better coat condition when living in grass compared to gravel. Females in Group 2 were 1.6 times more likely to have better coat condition in the enclosure with grass substrate during Fall 2007 than in the enclosure with gravel substrate during Fall 2006 ($t = -2.03$, $P = 0.04$).

3.4. Hair loss and rank

High-ranking females had better coats than middle- and low-ranking females (Fig. 3). The model indicates that high-ranking females were 2.6 times more likely to have

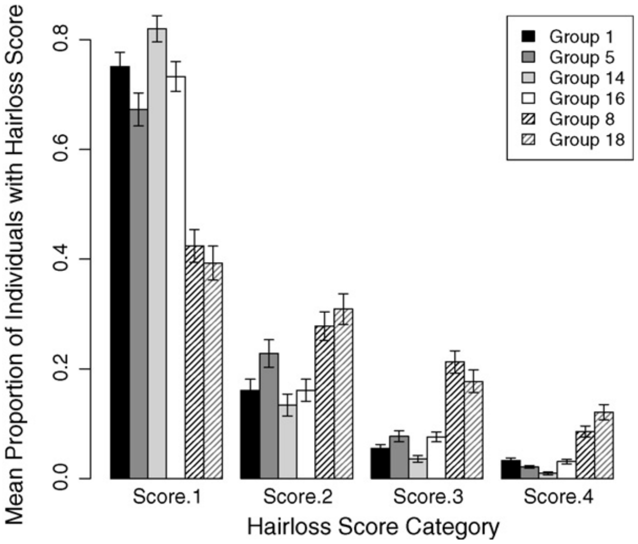

Fig. 2. Hair loss by substrate. The mean proportion of individuals having each hair loss score over the 12-month study period for four groups with grass substrate (solid bars: 1, 5, 14, 16) and two groups with gravel substrate (hatched bars: 8, 18). Females in enclosures with grass substrate had significantly better coat condition than those in enclosures with gravel substrate ($P < 0.001$). Hair loss was measured on a five-point categorical scale where 1 represented a full coat and 5 represented baldness. See Table 2 for complete definitions of hair loss scores.

better coat condition than low-ranking females ($P < 0.001$). The results are more complicated for high-ranking relative to middle-ranking females. The coefficient of middle-rank was allowed to vary by degree of hair loss in this model because middle-rank did not conform to the proportional odds assumption. Allowing middle-rank to have non-proportional odds resulted in three different estimated coefficients which correspond to three effect sizes (2.6, 2.7 and 4.1). These three effect sizes are all of the same sign and approximate magnitude and indicate that high-ranking females have better coat condition than middle-ranking females (threshold 1: $P = 0.002$; threshold 2: $P = 0.002$; threshold 3: $P < 0.001$).

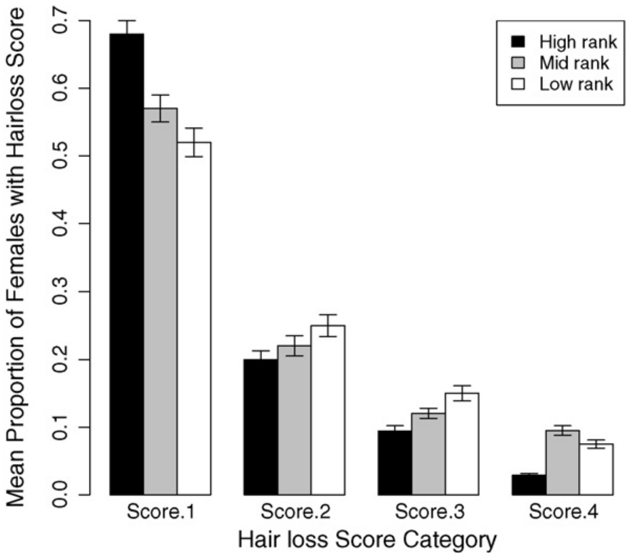

Fig. 3. Hair loss by rank. The mean proportion of females having each hair loss score over the 12-month study period for three rank categories: high-ranking, mid-ranking, and low-ranking. High-ranking females had significantly better coat condition than both middle- and low-ranking females ($P < 0.001$). Hair loss was measured on a five-point categorical scale where 1 represented a full coat and 5 represented baldness. See Table 2 for complete definitions of hair loss scores.

3.5. *Hair loss and age*

Younger females had better hair condition compared to older females. The model indicates that a female of average age is 1.1 times more likely to have better coat condition than a female that is 1 year older ($P < 0.001$). This effect becomes more apparent when considering a larger time increment such as 5 years. A female of average age is 1.8 times more likely to have better coat condition than a female that is 5 years older.

3.6. *Hair loss and animal density*

There was no significant effect of animal density on hair loss ($P = 0.2$). However, the interaction between animal density and pregnancy was significant (see below).

3.7. *Interaction terms*

3.7.1. *Substrate × reproductive condition*

The model indicates that a change in substrate from gravel to grass does not affect the influence of pregnancy on hair loss ($P = 0.9$).

3.7.2. *Substrate × rank*

The model indicates that a change in substrate from gravel to grass reduces the effect of middle-rank on hair loss among female rhesus macaques. Allowing middle-rank to have non-proportional odds resulted in three different estimated coefficients for the interaction between substrate and middle-rank which correspond to three effect sizes (6.6, 8.9, and 13.2). Therefore, middle-ranking females in enclosures with grass substrate are 6.6, 8.9, or 13.2 times more likely to have better coat condition than middle-ranking females in enclosures with gravel substrate, although the effect size for this interaction is only significant for thresholds 2 and 3 (threshold 1: $P = 0.11$; threshold 2: $P = 0.01$; threshold 3: $P = 0.002$). There was no significant effect from the interaction between substrate and low-rank ($P = 0.10$).

3.7.3. *Reproductive condition × rank*

The model indicates that a change in reproductive condition from not pregnant to pregnant exacerbates the influence of middle-rank on hair loss. Allowing middle-rank to have non-proportional odds resulted in three different estimated coefficients for the interaction between reproductive condition and middle-rank which correspond to three effect sizes (4.5, 4.8, and 6.0). Therefore, non-pregnant, middle-ranking females are 4.5, 4.8, or 6.0 times more likely to have better coat condition than pregnant, middle-ranking females (threshold 1: $P = 0.02$; threshold 2: $P = 0.02$; threshold 3: $P = 0.003$).

The model indicates that a change in reproductive condition from not pregnant to pregnant exacerbates the influence of low-rank on hair loss. Therefore, non pregnant, low-ranking females are 5.7 times more likely to have better coat condition than pregnant, low-ranking females ($P < 0.001$).

3.7.4. *Reproductive condition × age*

The model indicates that an increase in age of 1 year reduces the influence of pregnancy on hair loss. A pregnant female of average age is 1.07 times more likely to have better coat condition than a pregnant female that is 1 year older. This effect becomes more apparent when considering a larger time increment such as 5 years. Therefore, a pregnant female of average age is 1.4 times more likely to have better coat condition than a pregnant female that is 5 years older.

3.7.5. *Reproductive condition × animal density*

The model indicates that an increase in animal density of 1 animal/ha exacerbates the influence of pregnancy on hair loss. Pregnant females living in enclosures of average animal density are 1.004 times more likely to have better coat condition than pregnant females living in enclosures with one more animal/ha ($P < 0.001$). The effect becomes more apparent when considering a larger increase in animal density, such as 100 more animals/ha, a difference in animal density observed among the study groups. Thus, pregnant females living in enclosures of average animal density are 1.5 times more likely to have better coat condition than pregnant females living in high density enclosures (additional 100 animals/ha).

3.7.6. *Rank × age*

There was no significant effect from the interaction between low-rank and age ($P = 0.8$) or between middle-rank and age (threshold 1: $P = 0.5$; threshold 2: $P = 0.2$; threshold 3: $P = 0.2$). Table 4 summarizes the relative effect on coat condition of the factors examined here as estimated by effect size.

Table 4
Output for the two-level partial proportional-odds ordered logistic regression model of hair loss in female rhesus macaques.

Variable	Effect size[a]	Coefficient	SE	P
Substrate—gravel	3.7	1.312	0.24	< 0.001
Pregnancy[b]	2.4	0.874	0.22	< 0.001
Rank[c]— middle				
Threshold 1	2.6	0.962	0.31	0.002
Threshold 2	2.7	1.01	0.33	0.002
Threshold 3	4.1	1.411	0.34	< 0.001
Rank—low	2.6	0.973	0.3	< 0.001
Winter	2.5	0.9	0.14	< 0.001
Spring	2.8	1.016	0.17	< 0.001
Summer	2	0.69	0.14	< 0.001
Age	1.1	0.122	0.03	< 0.001
Animal density	1.001	0.001	0.0008	0.18
Substrate × pregnancy	–	0.034	0.19	0.85
Substrate × middle-rank				
Threshold 1	–	−0.574	0.36	0.11
Threshold 2	–	−0.887	0.36	0.01
Threshold 3	–	−1.27	0.4	0.002
Substrate × low-rank	–	−0.516	0.32	0.1
Pregnancy × middle-rank				
Threshold 1	–	0.631	0.27	0.02
Threshold 2	–	0.705	0.3	0.02
Threshold 3	–	0.941	0.32	0.003
Pregnancy × low-rank	–	0.866	0.23	< 0.001
Pregnancy × age	–	−0.058	0.02	0.004
Pregnancy × density	–	0.003	0.0008	< 0.001
Age × middle-rank				
Threshold 1	–	−0.034	0.05	0.5
Threshold 2	–	−0.067	0.05	0.19
Threshold 3	–	−0.064	0.05	0.23
Age × low-rank	–	−0.01	0.04	0.82
Random effect for female (std. dev.)	–	1.468	0.08	0.000

[a] Effect size is calculated as e^coefficient.
[b] Pregnancy designation for hair loss scores is shifted 1 month forward relative to actual pregnancy dates.
[c] Thresholds 1, 2, and 3 refer to the three possible divisions of the ordered category response variable which are called thresholds (threshold 1 = 1 vs. 2 3 4; threshold 2 = 1 2 vs. 3 4; threshold 3 = 1 2 3 vs. 4).

4. Discussion

These results show that hair loss among rhesus macaques is complex and affected by multiple factors. Hair loss among female rhesus macaques in outdoor enclosures at the CNPRC varied significantly by substrate, reproductive condition, rank, season, and age as well as by some pair-wise interactions among the factors. While some of these factors are amenable to modification to improve coat condition, others are not, and we may have to accept some degree of hair loss among captive rhesus macaques.

4.1. *Factors that are not easily manipulated to reduce hair loss*

Rhesus macaques exhibited the most pronounced hair loss during Spring (birthing season), which is similar to seasonal fluctuations in coat condition reported for captive rhesus macaques in Germany (Steinmetz et al., 2006), India (Venatesan et al., 2004) and Cayo Santiago, Puerto Rico (Vessey and Morrison, 1970). Measurements of hair follicle activity in rhesus macaques is slowest in April (Dolnick, 1967), which is consistent with the observed seasonal pattern of hair loss.

Reproductive condition also influenced hair loss. The effect of hormonal changes during pregnancy on hair loss appears to be delayed, such that hair loss is not apparent until at least the second month of gestation, and hair loss continues after giving birth, most likely because it takes time to re-grow a full coat (Dolnick, 1967). These results agree with previously reported findings that captive rhesus macaques experience hair loss during pregnancy, and begin hair growth following parturition (Davis and Suomi, 2006).

Hair loss during pregnancy was exacerbated by the social conditions rank, age, and animal density. The common theme among these factors may be social stress. Therefore, although pregnancy itself may not be amenable to modification to improve coat condition, modifications to the social environment which reduce social stress can reduce the influence of pregnancy on hair loss among female rhesus macaques.

4.2. Factors that can be manipulated to reduce hair loss

4.2.1. Physical conditions

Ground substrate had the strongest main effect (effect size = 3.7) on hair loss. Females living in enclosures with gravel substrate had significantly poorer coats than those with grass. It is unlikely that this is the result of a dietary deficiency, whereby grass provides supplemental foods such as grass and arthropods. First, the monkey chow is formulated to supply their dietary needs and the macaques also get supplemental foods, e.g., fruits, vegetables, and seeds, regularly. Second, the lack of significance of the interaction between substrate and reproductive condition indicates that hair loss among pregnant females, which typically have greater nutritional demands than non-pregnant females, is independent of substrate, and this suggests that the absence of grass in their diet does not reduce the quality of their diet enough to cause hair loss by itself.

Insufficient dietary fiber was initially hypothesized to be the cause of hair loss in guinea pigs (*Cavia porcellus*) and rabbits (*Oryctolagus cuniculus*). However, provisioned hay actually reduced hair loss by providing more nibbling material, which reduced fur chewing, whereas extra fiber added to the normal pelleted diet did not change hair loss (Beynen et al., 1992; Gerold et al., 1997). It is more likely that, like guinea pigs and rabbits, macaques that forage more reduce grooming and hair plucking, thereby reducing hair loss.

Our multi-factorial statistical analysis is consistent with a one-factor study in which we found that hair loss was associated with differences in activity budgets of rhesus macaques living in grass and gravel enclosures (Beisner and Isbell, 2008). In that study, animals living in enclosures with grass foraged more (20–24% vs. 8–10%) and groomed less (8–10% vs. 14–16%) than those living in enclosures with gravel, and it was suggested that greater foraging opportunities allow macaques to have more appropriate foraging behavior, which in turn reduces grooming and thus hair loss.

The redirection of motivation to forage toward over-grooming has also been observed in other animals. Hens plucked feathers from conspecifics more frequently when suitable foraging materials were not available (Huber-Eicher and Wechsler, 1997, 1998; but see Newberry et al., 2007). Providing loose hay reduced chewing on pen-mates in pigs (Fraser et al., 1991). Among primates, pigtail macaques (*M. nemestrina*) given sunflower seeds to forage in woodchip bedding stopped hair pulling almost entirely (Boccia and Hijazi, 1998). Rhesus macaques provided with artificial foraging devices also decreased their frequency of hair pulling (Tully et al., 2002; Watson, 1992).

The physical conditions that affect hair loss appear to exacerbate the social conditions that affect hair loss. The interaction between substrate and rank indicates that gravel substrate exacerbates the hair loss of low- and middle-ranking females. Thus, the lack of foraging opportunities in gravel substrate coupled with the social stress associated with lower dominance rank results in even worse hair loss among female rhesus macaques. This result is consistent with foraging enrichment studies which show primates provided with foraging enrichment such as floor litters and small food items also decrease levels of aggression, which may reduce social stress (Chamove et al., 1982). Smaller foods reduce aggression over food either because individuals have greater difficulty usurping them or because they are not worth taking (Mathy and Isbell, 2001). Changing the substrate from gravel to grass may not only enable the monkeys to spend more time foraging but also to reduce aggression. Thus, the addition of grass to outdoor enclosures that currently have gravel or dirt as the ground substrate may be one of the easiest and most effective management tools to implement to improve the well-being of captive macaques.

4.2.2. Social conditions

Rank and age also contributed to hair loss, as did the interaction between animal density and reproductive condition. Rank, age, and animal density are all social factors and may be indicators of social stress. High-ranking females had better coats than low-ranking females. Reinhardt et al. (1986) reported that dominant animals direct hair pulling to subordinate animals. In this study, however, aggressive hair pulling was observed rarely. Since dominance hierarchies are determined on the basis of winners and losers of agonistic interactions such as approach-retreat interactions or more overt aggression, lower-ranking animals are, by definition, subject to more agonism than higher-ranking animals. For example, high-ranking individuals in this captive colony aggressively punish lower-ranking individuals over desirable foods, which enables the high-ranking animals to obtain more food in the future (Chancellor and Isbell, 2008).

Over time, social stress may also take its toll regardless of rank because older females suffered greater hair loss than younger females independent of rank. Although animal density alone did not significantly influence hair loss, higher animal density exacerbated hair loss among pregnant females. Since animals living at high densities, such as those at the CNPRC (this study: 390–935 animals/ha) typically experience social stress to some degree (Li et al., 2007; Pearson et al., 2007), a reduction in group size would likely reduce social stress and hair loss for all, particularly lower-ranking animals, those with greatest hair loss.

5. Conclusions

Our results suggest that hair loss exhibited by rhesus macaques can be greatly reduced by simple changes in housing conditions. In locations where they are kept socially in outdoor enclosures, recommended changes include planting grass in enclosures and reducing densities to levels comparable to those of wild groups of rhesus macaques. Though captive macaques will always have more difficulty avoiding their aggressors than wild macaques, the frequency of agonism should decrease with lower densities, and lower-ranking individuals, in particular, should face less social stress.

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