Use of Quantitative Analyses of Pelage Characteristics to Reveal Family Resemblances in Genetically Monomorphic Cheetahs

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African cheetahs (*Acinonyx jubatus*) have extremely low levels of biochemical genetic variation relative to other felids as measured by enzyme electrophoresis, suggesting that interfamilial differences in phenotypic traits may be slight. Quantitative data on the pattern of tail bands collected from both sides of the tails of 64 free-living cheetahs show, however, that individuals differ markedly from each other and that siblings resemble each other significantly more than they do nonsiblings. Furthermore, offspring tail bands show significantly less similarity to the tail bands of their mothers than they do to their siblings. It is argued that environmental factors in utero are responsible for differences in cheetah pelage characteristics in combination with maternal or paternal genetic influences, giving evidence for a degree of phenotypic diversity despite the genetic monomorphism of this species. The analytical techniques developed in this paper are used to show that coalitions of permanently associating male cheetahs are genetically related. These techniques could also be used productively with the many other mammals that have distinctive markings on their bodies and tails.

Cheetahs (*Acinonyx jubatus*) are unusual among mammals in showing an extreme paucity of biochemical genetic variation (O'Brien et al. 1983, 1985, 1987). This finding might lead one to expect little phenotypic variation in this species if morphological features are under tight genetic control. In partial support of this sort of control, the striking "king cheetah" coat pattern (Bottriell 1987; Hill and Smithers 1980) is now known to result from a single recessive gene trait homologous to the *tabby-blocked* in domestic cats (Lindburg 1989; van Aarde and van Dyk 1986), and differences in background coat color that characterize subspecies from different geographical regions (McLaughlin 1970) are, most probably, the result of founder effects. Against the hypothesis of tight genetic control, it is known that individual cheetahs vary in both coat color and in coat pattern even within small populations living in national parks. Indeed, in studies that have focused on the behavior of individual animals, spot patterns have been used as the key feature to distinguish individuals from one another in the field (Bertram 1978; Burney 1980; Frame and Frame 1981). In short, circumstantial observations, at least, suggest that cheetahs exhibit a reasonably high degree of morphological variation within populations despite low levels of genetic diversity; in this sense they show similarities to inbred strains of other species (Dobzhansky and Wallace 1953; Lerner 1954).

In this paper, we first attempt to show quantitatively that cheetahs from the same population do differ morphologically by using data derived from the pattern of black and white banding from the distal portions of cheetah tails. In addition, we find that the tail markings of cheetahs born in the same litter resemble each other more closely than those born in different litters. To determine whether these interfamilial differences are the result of similar genetic or similar environmental influences in ontogeny, we compare tail banding of offspring to that of their mothers. In the last section, we use techniques developed for this analysis to examine evidence for genetic relatedness between members of coalitions of male cheetahs.

Methods

Study Area

Individual cheetahs can be recognized by markings on the face and chest (Bertram 1978; Burney 1980; Caro and Collins 1986; Frame and Frame 1981) (see the different spot patterns on the right-hand sides of the faces of the animals in the cover pho-

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Table 1. Size and sex composition of sibling groups and male coalitions used in the analyses

Group composition[a]	Litters where mother known (no.)[b]	Litters where mother unknown (no.)	Coalitions of males (no.)
M	4		
F	2		
MM	4		7
MF	6	3	
FF	1[c]	1	
MMM			4
MMF	2[c]		
MFF	1		
Total number of individuals[d]	37	8	26

[a] M = male, F = female.

[b] Nineteen mothers were used in the analyses.

[c] One mother had 2 litters represented.

[d] Of 45 animals that were not adults, 17.8% of tails were scored when cubs were 8 mo old, 4.4% when 10 mo, 40% when 12 mo, and 37.7% when cheetahs were 14 mo or older.

tograph). Data on tail markings of individuals identified in this way were collected on free-living cheetahs in the Serengeti National Park, Tanzania, between 1980 and 1983 by T.M.C. Observations on habituated animals were made from a vehicle at 10–25 m distance using 8 × 30 binoculars (Caro and Collins 1987a). Records of tail markings were taken only when the animal was standing or walking parallel to the vehicle.

Cheetah Social Organization

Female cheetahs live alone and, on the Serengeti Plains, are nomadic as they follow the migration of their principal prey species, Thomson's gazelles (Durant et al. 1988). They give birth to litters of up to six cubs, which are dependent on their mothers for solid food until they reach 14–20 mo of age (Caro 1987, 1989; Frame 1984), but in this study only litters of up to three cubs were available. After cubs have separated from their mothers, they remain together as an adolescent "sibgroup" for several months before females leave their brothers and take on a solitary existence (Frame and Frame 1981).

In contrast to females, male cheetahs either live alone or in permanent groups of two or three and show no parental care (Caro and Collins 1987b). Genealogical and other evidence suggests that of a sample of 33 coalitions, 72.7% were composed solely of brothers, while 93.9% contained at least two brothers (Caro in press). Indeed, demographic records indicate that, with one exception, littermates remained together all their lives. Coalitions of males were more likely to be territory holders than were single males (Caro and Collins 1987b), and territorial males were significantly more likely to encounter females that collected in territories during the course of their migration than were nonresident males (Caro in press; Caro and Collins 1987a). The sequential nature of matings among coalition members seen in captivity and once in the wild suggests that mixed paternity of litters is a possibility in this species. Number and identity of individuals recorded in this study are shown in Table 1.

Figure 1. (Top three rows) A coalition of three young adult male cheetahs, all brothers, in ideal poses for scoring tail band widths in the field. Each pair of photographs shows the left- and right-hand sides of the tail of one of the males. (Bottom row) Tails of different younger cheetahs showing how little length, shape, and banding changed with age: (bottom row, left) independent adolescent approximately 14 mo old; (bottom row, right) 6½-mo-old cub in foreground with her mother behind.

Scoring Tail Bands

Toward their distal end, cheetah tails have black and white bands with clear boundaries that can be seen easily and counted when the animal is standing (Figure 1). Further up the tail these bands change into spots, a characteristic of the rest of the body. For both right- and left-hand sides of the tail, starting at the distal end and continuing until spots appeared, bands were scored on a 10-point scale according to width and color. Bands on the right- and left-hand sides of an individual's tail varied in width, and, in this study, their number ranged from 7 to 16 bands per tail. Most of the bands fell between widths 2 and 6 (Figure 2). The smallest band width, scored 1, measured 1.5 cm; for each point on the scale, the width increased approximately 0.75 cm as determined by scoring band widths of a tame cheetah and sub-

sequently measuring each band on her tail by hand while she lay down.

In the field, bands were scored by TMC from a left-hand drive vehicle. Subjects were initially approached on their right to facilitate observation, although obliquely from behind so as not to disturb them (Caro and Laurenson 1989). A cheetah would usually get up and then walk off, away from the direction in which the vehicle had approached, exposing the right-hand side of its tail. It was less likely to walk back toward the car, showing the left-hand side, so it was sometimes necessary to score the left-hand side through the (empty) passenger side window later on as the cheetah moved off. Although the relationship of individuals to each other within a group of cheetahs could quickly be discerned at each sighting from their age and sex, it is unlikely that this could bias the scoring. This is because scoring required quickly looking from the tail to the sheet of paper that was being written on, so it was impossible to look at the scores of other tails just recorded earlier. In addition, scores were long, very often numbering many more than the seven bands reported here, and were therefore difficult to remember from one animal to the next. Time lapses of at least 20 min and up to 1 h were commonplace between taking scores of tails of individuals within a group because of the necessary repositioning of the vehicle. For many of the groups that were followed for consecutive days, scores of different individuals within a group were taken on different days.

From repeated sightings of developing cubs, it was obvious that tail band widths stabilized by the age of 8 mo when the tails of the animals were fully grown (Figure 1). It is unlikely that they would then change in adult animals, and this is supported by evidence from a study in an adjacent area in Kenya (Burney 1980) and by anecdotal evidence from the Serengeti study site (G. Frame, personal communication; T.M.C., personal observation). To avoid the possibility of band-width variation in growing tails of younger cheetah cubs, only individuals 8 mo or older were used in this study; tails were never scored during or after rain because band widths were difficult to discern on wet tails.

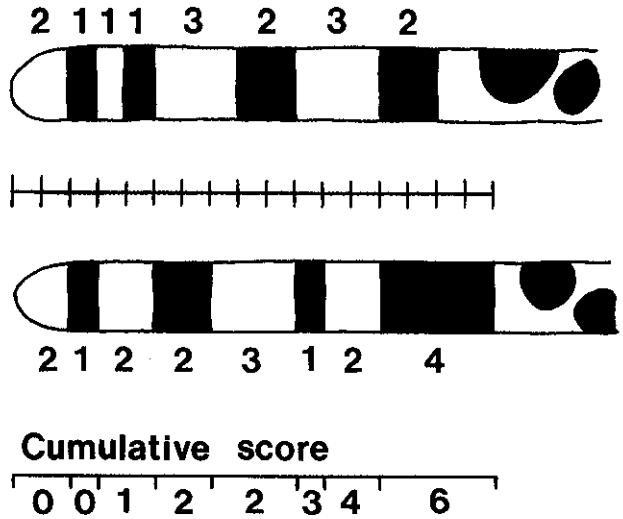

Figure 2. Diagram showing how the right-hand sides of two cheetah tails were coded. Numbers below each tail refer to its band width score. The cumulative score (dissimilarity index) sums the differences in widths of matched tail bands starting at the end of the tail.

Analysis

Widths of bands were written down in order starting at the end of the tail. A cumulative "dissimilarity index" could then be obtained between any two animals by summing the differences between band widths for an increasing number of bands from the end of the tail (Figure 2). Only three animals' tails ended with a black band; in their cases the first band was coded width 0. This ensured that white bands were always compared with white and black bands with black.

Dissimilarity indices were analyzed using simulation techniques (Morgan 1984). A single measurement was taken from the observed family composition; then, family members were randomly allocated to families, including their own, and the measurement was taken again. The latter step was repeated 10,000 times to obtain the frequency distribution of the measurement. If the original measurement fell at the extremes of the distribution, say in the tail end 2.5%, then it would be improbable that this was a consequence of chance alone. For example, in order to test the null hypothesis that siblings' tails are as similar to each others' as to nonsiblings' tails, mean dissimilarity scores were obtained for each sibling group and then averaged to obtain an overall measurement of dissimilarity between siblings. The distribution of this measurement was calculated from repeated random allocations to sibling groups according to the original size and sex composition of the family. If the measurement calculated from the real sibling groups lay to the lowest extreme of the frequency distribution, then the null hypothesis would be rejected, and one could conclude that siblings were more similar to each other than to nonsiblings. The advantage of this method is that no assumptions need be made about interdependence among bands on the same tail or underlying probability distributions, as would be necessary, for example, in an analysis of variance.

Individuals were compared using different numbers of bands up to a maximum of seven, after which the bands changed into spots on some animals. For this analysis, we wished to maximize the possible dissimilarity between animals; however, if a mistake occurred when coding an individual's tail, which resulted in a band going undetected, bands further up the tail would be displaced. Therefore, the dissimilarity index between such an individual and another, whose tail was coded correctly, would not represent the difference between corresponding bands and would no longer be an appropriate measure of dissimilarity. To minimize the occurrence of this type of error, the number of bands analyzed should be small. Because of these two contradictory considerations, we have presented results for analyses done on both four and seven bands. It should be stressed that these are not independent measures and will be correlated; however, the above considerations imply that if we were to use only one of the analyses we would risk losing a significant result, either due to error or to taking too short a length of tail.

Dissimilarity indices were calculated separately for each side of the tail, and then an overall index, the sum of the right and left indices, was calculated for both sides of the tail to minimize any problems of observer error that might have occurred on one side.

Reliability of the Codes

A fraction of the 64 mothers and offspring used in this study were seen more than once, and by comparing repeated measures on the same individual, it was possible to obtain some estimate of the reliability of the scoring system. Table 2 shows mean band scores and their standard errors on tails of individual cheetahs that were scored repeatedly on at least four separate occasions. Tail bands were rarely scored in exactly the same way on repeated sightings; however, they still differed significantly between individuals at each point on the tail (see next section). The standard error of band score does not show any consistent increase with band position as might be expected if bands were missed in observation, but the sample size is small. Nonetheless, this suggests that the slight variability in scores on repeated sightings is due primarily to inaccuracies in estimating band width.

Since the majority of the subjects were scored only once, only one score of the repeatedly sighted individuals was used in analysis. Subjectively, it was felt that the accuracy with which T.M.C. recorded bandwidths improved with experience; therefore, the most recent record of repeatedly sighted animals was chosen for analysis.

Table 2. Mean scores (±SE) for widths of bands on cheetahs' tails (both right and left sides) that were seen four or more times[a]

Abbreviated names of cheetahs	No. observations	Mean scores ± standard error on band no.: 1	2	3	4	5	6	7
Right-hand side of tail								
LS	5	1.60 (0.24)	1.20 (0.20)	1.20 (0.20)	5.20 (0.37)	2.60 (0.60)	4.80 (0.37)	2.40 (0.51)
A	4	1.75 (0.25)	1.75 (0.25)	1.25 (0.25)	5.25 (0.48)	2.00 (0.00)	4.00 (0.00)	3.50 (0.50)
M	4	3.00 (0.41)	1.00 (0.00)	1.00 (0.00)	3.75 (0.25)	2.75 (0.25)	3.50 (0.29)	4.25 (0.25)
NA	4	1.75 (0.25)	1.00 (0.00)	1.00 (0.00)	4.00 (0.00)	3.25 (0.25)	3.50 (0.29)	5.00 (0.00)
KTA	4	3.00 (0.71)	2.50 (0.87)	2.25 (0.48)	4.00 (0.00)	3.25 (0.48)	3.75 (0.25)	3.75 (0.48)
T1	4	2.25 (0.25)	3.00 (0.00)	1.00 (0.00)	2.75 (0.25)	1.00 (0.00)	3.00 (0.41)	2.75 (0.25)
$F_{5,19}$		2.838	5.219	4.189	10.214	4.909	4.253	6.016
P		.0445	.0035	.0098	.0001	.0047	.0092	.0017
Left-hand side of tail								
LS	5	2.00 (0.55)	1.00 (0.00)	1.20 (0.20)	3.80 (0.20)	2.80 (0.37)	4.20 (0.80)	1.80 (0.58)
M	4	4.75 (0.25)	4.75 (0.25)	2.00 (0.25)	2.50 (0.48)	2.50 (0.00)	2.75 (0.00)	3.00 (0.50)
NA	4	2.75 (0.48)	1.00 (0.00)	2.00 (0.41)	4.25 (0.25)	2.50 (0.29)	3.75 (0.25)	1.25 (0.25)
KTA	4	3.00 (0.58)	1.75 (0.75)	1.25 (0.25)	3.75 (0.25)	2.75 (0.48)	3.25 (0.25)	4.00 (0.00)
T1	4	1.75 (0.25)	1.25 (0.25)	1.00 (0.00)	2.75 (0.25)	1.75 (0.25)	2.00 (0.41)	1.00 (0.00)
OC	4	4.00 (0.41)	3.50 (0.50)	2.75 (0.25)	4.25 (0.25)	4.50 (0.29)	4.00 (0.00)	5.50 (0.29)
BO	4	3.50 (0.50)	2.25 (1.25)	1.25 (0.25)	4.75 (0.25)	2.25 (0.25)	3.75 (0.25)	2.00 (0.00)
$F_{6,22}$		4.937	4.178	3.962	10.731	6.847	2.821	22.340
P		.0024	.0059	.0078	.0000	.0003	.0343	.0000

[a] It was not always possible to score both sides of the tail in a single sighting if the cheetah disappeared into high grass or lay down, hence the different identities of some of the cheetahs depicted in the two parts of the table. Results from a one-way analysis of variance across individuals are given at the foot of each part of the table.

Results

Zero standard errors were obtained for 31% of mean scores for repeated measurements made on seven bands for six individuals on the right-hand side of the tail and for seven individuals on the left-hand side of the tail (Table 2). A further 62% of the standard errors for these scores were less than 0.5, and all except two were less than 1. A one-way analysis of variance across these repeated scores on different individuals shows that tails differ between individuals despite errors in measurement. Significant differences ($P < .05$) were found between individuals for each of seven bands on each side of the tail. In all except two cases, the significance level was more than 99% ($P < .01$). These results indicate that cheetahs differ in the pattern of banding seen on their tails and that the method of scoring band patterns on tails is sufficiently accurate to investigate differences between individuals.

Table 3 first shows the overall dissimilarity measurement obtained between siblings, calculated as an average of mean dissimilarity indices for 17 groups of siblings. The measurement was compared with the frequency distribution obtained from a random allocation of individuals to the same number of groups, containing identical numbers of males and females as in the original sibling groups (eliminating possible effects due to sex). Six families with only a single offspring were excluded from this analysis and only one group was included from the single case where two groups of siblings shared the same mother. Results showed that when both sides of the tail were taken together, siblings were significantly more similar to each other than they were to randomly selected individuals (four bands: $P < .01$; seven bands: $P < .05$). Significance was also obtained for the left-hand side of the tail (four bands: $P < .001$; seven bands: $P < .01$) but not for the right-hand side (four and seven bands: $P > .1$).

Table 3 next shows that dissimilarity measured between mothers and their offspring is significantly less than that between mothers and randomly allocated offspring. Here dissimilarity was calculated as an overall average across 19 mean dissimilarity indices obtained for each mother and her offspring. In the randomization, offspring were allocated to each mother according to the number of male and female offspring she had actually had, to prevent the possibility of different family compositions and sizes for each mother biasing the results. Four families where the mother was not known (independent sibgroups) were excluded from this analysis. Offspring were significantly more similar to their mothers than they were when randomly allocated to families when both sides of the tail were taken together (four bands: $P < .01$; seven bands: $P < .05$). Significance was also obtained for the first four bands on the left-hand side ($P < .05$), but not for seven bands ($P > .1$) and not for the right-hand side (four bands: $P < .1$; seven bands: $P > .1$).

Families with more than one offspring, at least one of which was female, were used to test whether siblings were more similar to each other than they were to their moth-

Table 3. Results for analyses of dissimilarities between individuals

Type of dissimilarity	Dissimilarity observed[a]	Dissimiliarty obtained by simulation[b]		Estimated probability of a result < that observed[c]
		Mean	SD	
Between siblings[d]				
Right-hand side				
4 bands	4.157	4.592	0.388	.137
7 bands	8.275	8.490	0.538	.361
Left-hand side				
4 bands	3.333	4.713	0.359	.000
7 bands	6.902	8.488	0.496	.002
Both sides				
4 bands	7.490	9.305	0.557	.001
7 bands	15.176	16.978	0.772	.011
Between mothers and their offspring[e]				
Right-hand side				
4 bands	5.412	6.076	0.395	.048
7 bands	9.237	10.045	0.516	.056
Left-hand side				
4 bands	6.268	7.111	0.374	.009
7 bands	10.619	11.453	0.550	.054
Both sides				
4 bands	11.681	13.187	0.593	.003
7 bands	19.856	21.514	0.808	.013
Between mothers and their offspring minus that observed between offspring[f]				
Right-hand side				
4 bands	−0.050	−0.108	0.674	.456
7 bands	−0.417	0.170	0.969	.711
Left-hand side				
4 bands	3.483	0.881	0.964	.002
7 bands	4.083	1.289	1.127	.004
Both sides				
4 bands	3.433	0.772	1.305	.018
7 bands	3.667	1.419	1.459	.064

[a] The measurement of dissimilarity obtained from the family composition observed.

[b] The mean and standard deviation obtained across 10,000 random allocations of individuals to the family composition.

[c] The one-tailed probability of the observed measurement as estimated from the frequency distribution obtained by simulation. The probability is multiplied by 2 to obtain the values used in the text for two-tailed significance tests.

[d] Dissimilarity between siblings compared with that observed when siblings are randomly allocated to families.

[e] Dissimilarity between mothers and their offspring compared to that obtained when offspring are randomly allocated to mothers.

[f] The difference in dissimilarity between mothers and their offspring and between siblings compared to that difference obtained when mothers are randomly allocated from within families.

ers. A mean dissimilarity index between siblings was calculated for each such family and subtracted from the mean dissimilarity index between offspring and their mother, giving a measure of difference in dissimilarity between mothers and their offspring and between siblings (bottom of Table 3). This quantity was then averaged across the 10 suitable families used for the analysis. Mothers were then allocated randomly from the females within each family (including the actual mother), and the same quantity was calculated, to obtain a frequency distribution. Siblings were significantly more similar to each other than they were to their mothers for the first four bands for both sides of the tail taken together ($P < .05$) and for the left-hand side of the tail (four and seven bands: $P < .01$).

These techniques were then used to investigate dissimilarity scores between the members of 11 male coalitions (Table 4). Mean dissimilarity between coalition members was significantly less than when coalitions were allocated randomly (right-hand side, four bands: $P < .05$; seven bands: $P < .01$; both sides, seven bands: $P < .05$; analysis as for siblings versus nonsiblings). Since our analyses of sibling groups suggest that related individuals are likely to have similar tails (see above), these results support the existing evidence that members of male coalitions are usually brothers.

If some of the adult coalition members in our sample were not siblings, then, on average, they should be less similar to each other than known littermates. Conversely, coalition members could have resembled each other more closely than did the sample of littermates if some of the adult males were identical twins, or if multiple paternity was more common in the sample of littermates than in the sample of coalition members. In order to examine evidence for either hypothesis, a measure of the difference in dissimilarity between coalition members and between male siblings was obtained by subtraction of mean dissimilarity indices (Table 4). Siblings were then randomly allocated to families, and coalition members to coalitions, and an identical quantity was calculated. No significant evidence for either hypothesis was found, suggesting that the great majority of these coalitions were composed of brothers only. In fact, in the sample of coalitions examined here, we knew of only one individual who was, without question, not related to his coalition partners; thus, the tail-banding technique was able to confirm our demographic records in a convincing manner.

Discussion

Results presented here provide the first quantitative evidence that individual cheetahs differ from each other in pelage characteristics and demonstrate that there is still extensive phenotypic variation in this species despite diminished heterozygosity. These results mimic closely differences in health and physiology found in cheetahs from the same population (Caro et al. 1987, 1989). Interestingly, band widths differed between each side of every tail examined (Figure 1), paralleling the dramatic fluctuating asymmetry found in the skull morphology of this species (Wayne et al. 1986). Whether tail banding in cheetahs is more asymmetrical than in other felid species is not yet known.

Despite the accuracy limitations of the method of scoring tail bands, there are few alternatives for obtaining quantitative measures of pelage characteristics. Immobilization and measurement of tails or spot patterns might easily separate family members permanently and is therefore overly intrusive if reasonable sample sizes are to be obtained. Photographing tails and then assigning them scores from the pictures was attempted following a similar technique used to examine the extent of different color patterns on the coats of wild dogs (*Lycaon pictus*) (Frame et al. 1979). However, band widths changed considerably according to slight variations in the angle at which the picture was taken and movements of the tail itself exacerbated the problem considerably. Only by following the cheetah for some time and trying to maintain a perpendicular angle to the

tail was it possible to score tail band widths with reasonable accuracy through checking and rechecking.

Tails of cheetahs from the same litter resembled each other more closely than they did those of nonsiblings. Similarities in spot patterns have also been observed on the chests and faces of related cheetahs (Caro and Collins 1986). This suggested that littermates were influenced by a common variable during the period that melanocytes, which are responsible for an individual's coat color, were activated in the embryo.

Dissimilarity indices observed on the left-hand side and on both sides of the tail differed significantly from that obtained by simulation, but they did not differ significantly when the right-hand side was considered (this situation was reversed in the coalition analysis). It is unlikely that one side of the tail was scored any less accurately than the other because both left- and right-side measures showed similar variances (Table 2). At present, we cannot explain why different sides of the tail yield differing results, so, in general, results should be treated with caution where the two measures differ.

Littermates' tails resembled each other more than they did the tail of their mother. If band width was under tight genetic control, one would expect littermates to show greater phentotypic variance than would mothers and offspring as there is always more variation in allelic similarities between siblings than between parents and their offspring. This is because offspring share 50% of each parent's alleles by descent but share between 0% and 100% (on average 50%) of alleles of full siblings. This suggests that environmental rather than genetic factors were responsible for producing the greater similarity between siblings.

The lower levels of phenotypic variability observed between tails of siblings compared to between offspring and their parents could be explained as a consequence of parents selecting for genetically distant mates, in conjunction with a pattern producing mechanism controlled by alleles with no dominance at a polymorphic locus (Bateson P, personal communication). Currently, the importance of such an explanation is difficult to evaluate because there are no systematic data on cheetah matings in the wild. Circumstantial evidence suggests that males are unlikely to choose mates since territorial males (those that probably sire most offspring) wait for females to enter and collect in their territories, while nonresident males appear interested in most of the females they encounter (Caro et al. 1989). Female ranging behavior is governed principally by the movements of Thomson's gazelles (Durant et al. 1988) and, in conjunction with high litter mortality (Laurenson in press) and consequent frequent estrus, suggests there is little opportunity for free-living females to choose mates. Nevertheless, there are anecdotal accounts of females choosing males in captivity. At present, the extent of preference for males and the criteria of choice are not understood, but it seems more probable that females would select mating partners on the basis of physical condition than on their genetic distance. Calculations by S.M.D. show the same mechanism results in less similarity between siblings compared to between parents and their offspring if there is no selection for genetically distant mates. Therefore, it seems that such a mechanism, reliant as it is on selection of mates for genetic distance, is unlikely to account for our results, although we cannot discount it entirely.

The most likely explanation for the similarity in siblings' tails is that tail banding is influenced by the uterine environment common to littermates. Differences in siblings' dissimilarity indices and those of offspring and mothers support this contention, as mothers would have developed in a different uterine environment from that which they provided for their cubs. However, the mechanism by which coat color develops is still obscure, although a number of models for pattern formation have been proposed (Bard 1981; Murray 1981). In brief, melanocytes are known to produce two types of melanin from a tyrosine precursor—eumelanin, which is black or brown, and phaeomelanin, which is yellow or white in cheetahs—but it is the activity of these cells, not their distribution, that is responsible for an individual's coat color (Silvers 1979). Thus differences in coat color reflect relative densities of these pigments (Findlay 1989). Negative or positive inhibition of melanocytes appears to be genetically controlled or triggered in the fetus well before hair appears (Bard 1977). Variation in the time that the genetic switch initiates pattern formation during embryonic development is thought to result from differences between individuals and may be subject to local, perhaps uterine conditions as suggested here (Murray 1981).

Nongenetic factors, such as temperature, are known to modify genetic determination of coat pattern in other species. For example, in both domestic cats and mice the ability to produce melanin is promoted at low temperatures. Siamese kittens born devoid of pigment subsequently develop it on the cooler extremities (Robinson 1977), and Himalayan mice show a

Table 4. Results for analyses of dissimilarities between coalition members

Type of dissimilarity	Dissimilarity observed	Dissimilarity obtained by simulation		Estimated probability of a result < that observed
		Mean	SD	
Between members of coalitions[a]				
Right-hand side				
4 bands	4.273	5.650	0.486	.006
7 bands	8.333	10.430	0.708	.004
Left-hand side				
4 bands	7.364	7.451	0.714	.453
7 bands	10.727	11.324	0.858	.250
Both sides				
4 bands	11.636	13.100	0.842	.049
7 bands	19.061	21.755	1.111	.011
Between members of coalitions minus that observed between male offspring[b]				
Right-hand side				
4 bands	−0.894	0.193	1.031	.156
7 bands	−1.333	0.854	1.451	.066
Left-hand side				
4 bands	2.030	2.386	1.015	.370
7 bands	2.227	2.792	1.186	.322
Both sides				
4 bands	1.136	2.579	1.473	.172
7 bands	0.894	3.647	1.835	.065

Calculations were made across 11 coalitions and 6 pairs of male siblings.

[a] Dissimilarity between observed coalition members compared to that obtained when coalitions are randomly allocated.

[b] The difference in dissimilarity between coalitions and between male siblings compared to that difference obtained when sibling groups and coalition groups are allocated at random.

pale tan coat but feet, ears, nose, and tail that are dark (Silvers 1979). In the mice, temperature may affect the activity of the C^h allele, which, in turn, controls the activity of tyrosinase perhaps by modifying its production or by making it unable to conjugate properly with other proteins involved in melanin production (Silvers 1979). Similar processes, as yet unknown, may be involved in the mechanism of pattern formation in the tails of cheetahs. The uniformity of the cheetah's genome may increase the relative importance of environmental differences in utero compared to genetic effects. Examination of pelage differences in other felid species is needed to confirm this.

In conclusion, the technique of band scoring and analysis is useful for testing hypotheses about relatedness and does not suffer from problems incurred using other methods. For example, most detailed morphological measurements on free-living animals normally require capture or immobilization, both of which involve limited risk and so are difficult to justify with endangered species. Moreover, immobilizations, or obtaining skin biopsies using projectiles (Karesh et al. 1987), necessitate approaching free-living individuals sufficiently closely to hit the target and thereby restrict the sample to well-habituated animals. In most free-living populations, the number of individuals tolerating such a close approach by humans is extremely limited.

Our results indicate that if individuals are siblings or are related by descent, they will have more similar tails than if they are not related. This allows us to suggest that observed coalitions of male cheetahs are related, and, furthermore, by comparing coalitions to male siblings, we are able to test whether they are more or less related than siblings are to each other. Our finding that littermates' tails are more similar to each others' than they are to their mothers' leads us to suggest that environmental differences in utero exert an effect on tail pattern formation. The methods and analytical techniques developed here could be extended to include the many other species of mammals with banded tails and striped or blotched coat patterns.

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