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Do females pay attention to secondary sexual coloration in vervet monkeys (*Chlorocebus aethiops*)?

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Abstract Several primate species show sexual dichromatism with males displaying conspicuous coloration of the pelage or skin. Studies of scrotal coloration in male vervet monkeys (*Chlorocebus aethiops*) suggest that it is an important intrasexual signal, with relatively dark, colourful males dominating paler males. To date, no studies have examined the influence of male colour on intersexual social interactions in vervet monkeys. The primary goal of the present study was to evaluate whether female vervet monkeys attend to male coloration. We experimentally introduced females, housed with either "pale" or "dark" males, to stimulus males whose scrota were pale, dark, or pale but painted to look dark. Overall, during introductions, females did not differ in time spent directing affiliative behaviour toward pale, dark, and painted males; however, females, permanently housed with dark males, spent significantly more time directing affiliative behaviour toward pale than painted males. When the stimulus male was pale, affiliative exchanges between males and females were longer than when the stimulus male was painted. Home male colour was not related to female-initiated aggression. Home male colour was also not related to male-initiated aggression, although painted stimulus males were more likely to initiate aggression than pale stimulus males. These findings lead us to conclude that females pay attention to male coloration, but do not bias their interactions toward males solely on the basis of natural male coloration.

Keywords Colour · Signal · Genital · Sexual selection · Vervet monkeys · Primates

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Introduction

Secondary sexual characteristics, including colour, plumage accoutrements, horns, and antlers are widespread across animal taxa (Darwin 1871; Andersson 1994). In some animals, these characteristics serve as armaments in intrasexual competition, but are not involved in mate assessment, e.g., ring-necked pheasant (*Phasianus colchicus*) spur length (Mateos and Carranza 1996). In other animals, members of the opposite sex use these characteristics as a basis for mate selection, such as earwig (*Forficula auricularia*) forcep size (Radesäter and Halldórsdóttir 1993). Still, in other animals, particularly taxa with multiple ornaments, secondary sexual characteristics only appear useful as ornaments to attract mates, but serve no function in intrasexual competition, e.g., red-collared widowbird (*Euplectes ardens*) tail elongation (Pryke et al. 2001).

Despite widespread colour differences between the sexes in primates, until recently, the study of primate ornamen-

tation, and particularly that of chromatic sexual skin, has been neglected. Consequently, little is known of the effects of male primate colour on female behaviour (Dixson 1997; Paul 2002; Gerald 2003; Kappeler and van Schaik 2004). However, recent experimental (Cooper and Hosey 2003; Waitt et al. 2003) and observational findings (Gerald et al. unpublished data; Setchell 2005) suggest that female primates do indeed respond to male colour differences.

Adult male vervet monkeys (*Chlorocebus aethiops*) exhibit conspicuous blue and aquamarine scrotal coloration of varying intensities (Struhsaker 1967; Gerald et al. 2001). Vervet monkeys are native to most of Sub-Saharan Africa, and colour expression varies between populations. For example, although East African vervet monkeys uniformly display a red prepuce (Kingdon 1996), the *sabaeus* sub-species of West African origin, as the one investigated in the present study, does not (Poirier 1972); however, males display yellow-orange hair of variable intensities in the genital region (Figs. 1a–d). As a catarrhine, vervets have uniform trichromatic vision (Jacobs and Deegan 1999); therefore, male coloration is likely to be perceived similarly by males and females.

Although it is not known whether colour variation between males reflects differences in genotypic quality, evidence suggests that scrotal coloration is affected by an animal's social condition and stress. This evidence includes observations of a male's scrotum paling following aggression received within 1 to 2 weeks of joining a new group (Gartlan and Brain 1968). Scrotal paling also has been

observed in wild monkeys in the weeks following entrapment (Gerald, personal observation), under captive conditions of prolonged stress (Bowlig 1978) and food shortages in a wild population (Isbell 1995). Isbell's observation led her to speculate that scrotal colour differences in vervet monkeys could be related to condition and access to resources. Male pair introduction experiments suggest that size-matched dark males dominate paler males (see Fig. 1a), and that similarly coloured males, even if one is artificially coloured, are more likely to interact antagonistically (Gerald 2001).

Vervet monkeys live in multi-male, multi-female matrilineal-based social groups (Struhsaker 1967). They exhibit reproductive seasonality in the wild (Andelman 1987) and even show birth peaks in captivity (Else et al. 1986). There is no evidence showing that females have adaptations for signalling ovulation to male vervet monkeys (Burt 1992). Females lack morphological cues indicating ovarian state (Eley et al. 1989) and there is an absence of proceptive displays associated with ovulation (Andelman 1987). Nevertheless, the timing of conception coincides with a rise in the number of both attempted and successful copulations (Andelman 1987), suggesting that males might attend to ovulatory cues unbeknownst to humans (Burt 1992).

As multiple males live together in a social group, the potential for aggression exists. Given the high probability of repeated social interactions between males, males may benefit from expressing and attending to badges of status or fighting ability. This could reduce the likelihood of costly
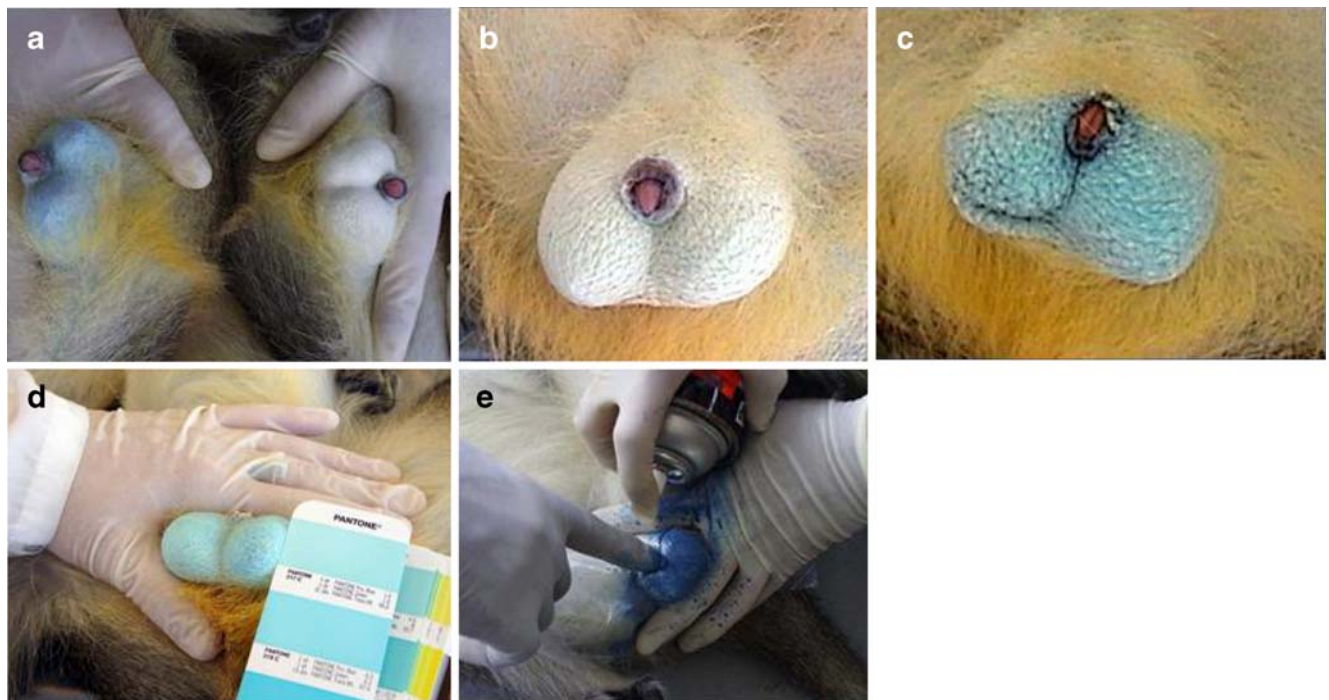

Fig. 1 **a** "Dark" vs. "pale" scrotum. **b** Pale scrotum. **c** Dark scrotum. **d** Colour matching of scrotum. **e** Painted scrotum

aggressive encounters (Johnstone and Norris 1993; also see Hsu et al. 2006), as has been discovered to be the case for distantly related taxa such as Augrabies flat lizards (*Platysaurus broadleyi*; Stapley and Whiting 2006) and collared flycatchers (*Ficedula albicollis*; Pärt and Qvarnström 1997).

Sexual selection theory posits that female mate choice can maintain exaggerated traits or signals in a population, such as colour, as colour could allow selectors to assess the signaller's phenotype (Andersson 1994). As male vervet monkeys are larger than females and can inflict harm, females may minimise potential costs by attending to signals that cue male aggression. Females also should prefer mating with high status males, as dominance may signal high genetic quality, the ability to accrue resources, or the ability to protect offspring. Experimental studies by Keddy (1986) show that female vervet monkeys exercise mate choice and attend to unknown dominance-related proximate characteristics, but which may include morphological or behavioural traits. Furthermore, genetic evidence demonstrates that alpha males sire more offspring than would be expected if reproductive success were evenly distributed (Manson et al. unpublished data).

Another instance when visual badges might come into use is during male transfers. Male vervet monkeys leave their natal groups at puberty and may repeatedly migrate to other groups throughout adulthood. Male transfer patterns appear to be influenced by whether females are aggressive toward males during intergroup encounters (Cheney 1981). Females might use the colour of migrants to decide whether to direct support or aggression toward unknown males.

The present study seeks to test whether vervet scrotal coloration influences male-female interactions. To evaluate this question, we measured affiliative and aggressive reactions of females who were housed with males, whose scrota were pale or dark to males, whose scrota were pale, dark, or pale males whose scrota had been painted dark. This experimental approach allowed us to test whether female interactions with males during paired introductions were influenced by the absolute level of male colour, or the level of male colour relative to that of the male with whom they were permanently housed.

Materials and methods

Subjects

Subjects were 30 adult female and 30 adult male vervet monkeys at the Barbados Primate Research Center (BPRC). Monkeys at the BPRC originate from the feral vervet monkey population on Barbados, and are presumed to be of West African origin (see Gerald 2001 for population

details). Study animals were experimentally naïve, and residents of the BPRC captive population for at least 1 month prior to participating in the experiment.

Vaginal cytology analyses (Keddy 1986) were conducted the day prior to experimental introductions. All samples contained 63% to 100% (mode=100%, mean=92.86%, SD=9.951) cornified epithelial cells, suggesting that all females were cycling (Seier et al. 1991).

Housing and experimental enclosure

Housing conditions were designed to eliminate confounds associated with separating subjects from social groups for dyadic trials. Females were selected from their home enclosures where they were, at the time of study, permanently pair-housed with a male, whereas stimulus males were singly housed. Home enclosures were visually and acoustically remote from the experimental enclosure (experimental enclosure details in Gerald 2001). The experimental enclosure was novel to subjects.

To reduce handling stress, study animals were measured and then held overnight, and, in one case, two nights, in an individual cage in the experimental enclosure. To ensure that subjects would be simultaneously introduced to the novel test setting and that females assessed males exclusively during experimental introductions, individual cages were covered in tarp. Females were taken to the experimental enclosure first.

Experimental design

There were 30 experimental introductions. In each introduction, one female was introduced to one unfamiliar male. Females were randomly assigned to a stimulus male using a random sequence generated by www.random.org. Table 1 summarises the categories of male–female pairings used in experimental trials according to colour of the stimulus male and colour of the male with whom a female was permanently housed (hereafter, "home male" Of the 30 stimulus males, ten were "pale" (Fig. 1b); ten were colourful, "dark"[1] males (Figs. 1c and d); and ten were "painted" males, whose scrota were pale, but painted dark (Fig. 1e).

To examine whether female interactions with stimulus males were influenced by home male colour, we controlled for home male scrotal colour: half of the females in each experimental condition were permanently housed with pale males and half were permanently housed with dark males. To reduce the probability that study animals were familiar with one another, we selected study animals that did not

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[1] The dark males in the present study were comparable in colour measures to the "dark" males in Gerald (2001).

Table 1 Categories of male colour and number of male-female pairs used in experimental trials

	Housemate colour		
	Pale	Dark	Total
Stimulus male colour			
Pale	5	5	10
Dark	5	5	10
Painted	5	5	10
Total	15	15	30

have visual access to one another in their home enclosures. This did not preclude the possibility that animals were familiar with each other through acoustic or olfactory signals.

Procedures

Body measurements

To obtain body and colour measurements, male and female study animals were immobilised with intra-muscular ketamine HCl (12 mgkg^{-1}; Ketaset®; Aveco, Fort Dodge, Iowa, USA) injections. Height was measured to the nearest cm and weight was measured to the nearest 0.01 kg. Testes without skinfold were measured with callipers. Testicular volume was calculated using the formula for a regular ellipsoid (Bercovitch 1996).

Colour manipulations

Previous experiments demonstrated that males whose scrota were painted with clear paint did not differ behaviourally or elicit different reactions from other males (Gerald 2001). In consideration of these findings and given the limited number of available study animals, we did not include a group of males whose scrota were painted with clear paint or males whose scrota were naturally dark but painted to appear pale.

The scrota of males in the painted condition were painted after body measurements were taken. As described elsewhere (Gerald 2001), the scrotum was washed and dried before painting. To restrict painting to areas where colour is naturally displayed in vervet monkeys (Fig. 1d), we placed a plastic sheet with two holes exposing the lower mid-half of the scrotum, and applied non-toxic spray paint (Touch 'n Tone Day® all purpose royal blue and light blue spray paint), to the lower scrotal region.

Colour measurements

Males were defined as "pale" or "dark" based on subjective assessments made simultaneously by at least two raters.

Colour assignment was made when consensus was reached. To assess whether males assigned to the pale and dark conditions statistically differed and to measure coloration of painted males, quantitative colour assessments were made by applying a method originally developed for measuring vervet monkey coloration (Gerald et al. 2001). Colour measurements of males were also taken before introductions. This method involved capturing a digital image of the scrotum from a distance of 29 cm with a Sony Digital Handycam™. We used Adobe PhotoShop™ (version 6.0) to quantify the red, green, and blue measures of two distant 5×5 pixel areas on the midpoint of the lower midsection of the subject's scrotum in the calibrated images (Gerald et al. 2001). Means of these measures were then converted to hue (the colloquial colour term), saturation (the relative purity of the colour values), and lightness (sometimes referred to as brightness).

Experimental procedure

Trials began 1 h after feeding. The male and female were simultaneously released from their temporary individual holding cages into the experimental enclosure. Trials lasted 90 min, and females and males were returned to their home enclosures immediately afterwards.

One trial was discarded due to experimental error and two trials were discarded because the females never left their individual cages. To retain the balanced design, we conducted three additional introduction trials. One of these trials ended 6 min prematurely when the female went under the cage netting fitted on the top of the enclosure.

Behavioural observations

Vervet monkey sexual behaviour is rarely observed; thus, we did not anticipate that mating would occur during introduction trials. Instead, we recorded affiliative behaviours, which included duration of grooming or sitting in physical contact with males as proxy measures of female preference (Keddy 1986). Aggression was measured by the frequency of contact aggression such as bites, hair-pulls, grabs, and fights. The duration of each affiliative interaction and the sex of the animal initiating each interaction were recorded using continuous recording methods. A single observer was responsible for recording observations during all experimental trials.

Data analyses

Significance tests were one-tailed. Statistical analyses were conducted using SPSS™ 14.0. Independent *t*-tests were used to evaluate relationships between colour and body measures.

General linear model (GLM) analyses were used to conduct two-way analyses of variance. We tested for the fixed effects of stimulus male colour (pale, dark, or painted) on the duration of female- and male-initiated affiliative behaviour. It is also possible that the colour of the male with whom a female was housed could impact the way a female interacted with a stimulus male. The home male's colour might have a main effect, i.e., influence overall levels of affiliative or aggressive behaviour toward stimulus males. Alternatively, there may be an interaction effect in which females might prefer stimulus males that differ in colour from the male they were housed with or show a greater preference for stimulus males that are the same colour as home males. To test these possibilities, we included the fixed effects of home male colour (pale or dark) and the home male × stimulus male interaction.

As aggression either occurred frequently or not at all in a trial, the distribution was skewed. We, therefore, used logistic regression analyses to examine the likelihood of female- and male-initiated aggression (0=aggression absent, 1=aggression present) as a function of home and stimulus male colour.

Results

Colour and body measures

The t-test analyses revealed unequal variances when comparing hue levels. Pale and dark males were significantly different in hue (pale $M=100.77$, $SD=30.53$, dark $M=123.35$, $SD=7.45$; $t=3.126$, $df=23.104$, $p=0.005$), saturation (pale $M=63.4$, $SD=49.15$, dark $M=117.0$, $SD=33.58$, $t=-3.096$, $df=28$, $p=0.004$), but not lightness (pale $M=193.4$, $SD=21.68$, dark $M=185.7$, $SD=23.79$; $t=0.897$, $df=28$, $p=0.377$). Although we attempted to paint pale males to resemble naturally dark males, scrotal painting resulted in a colour with components exceeding the range of natural colour variants (hue $M=202.60$, $SD=14.70$; saturation $M=57.30$, $SD=24.66$; and lightness $M=62.10$, $SD=13.19$). Pale and dark males did not significantly differ in height (pale $M=35.58$ cm, $SD=2.296$, dark $M=35.73$ cm, $SD=2.337$, $t=-0.170$, $df=28$, $p=0.866$), weight (pale $M=5.03$ kg, $SD=0.5293$, dark $M=4.96$ kg, $SD=0.6293$, $t=0.312$, $df=28$, $p=0.758$), or testicular volume (pale $M=63.52$ cc, $SD=30.74$, dark $M=65.95$ cc, $SD=28.83$, $t=-0.207$, $df=28$, $p=0.837$) ruling out the possibility that male colour is merely a proxy for size.

Did colour influence affiliative interactions?

Mean durations of affiliative behaviour for each of the six groups are presented in Table 2. The GLM analysis

Table 2 Means (M) and standard deviations (SD) of durations of female- and male-initiated affiliative behaviour and summed affiliative behaviour exchanged between males and females

Stimulus male	Female-initiated						Male-initiated						Summed affiliative					
	Housemate				Total		Housemate				Total		Housemate				Total	
	Pale		Dark				Pale		Dark				Pale		Dark			
	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Pale	4.25	3.35	15.03	9.64	10.24	9.11	14.73	9.07	9.56	6.38	11.86	7.66	18.98	6.39	24.59	13.84	22.10	10.95
Dark	10.60	6.87	7.34	6.45	8.79	6.44	4.62	2.63	12.27	8.19	8.87	7.24	15.22	6.89	19.61	12.16	17.66	9.85
Painted	4.44	2.59	2.42	3.44	3.43	3.06	7.72	8.35	3.21	3.12	5.47	6.40	12.16	10.37	5.64	4.60	8.90	8.31
Total	6.28	5.08	8.26	8.40	7.34	7.01	8.92	7.97	8.35	7.00	8.61	7.33	15.20	8.15	16.61	13.12	15.96	10.92

revealed that females housed with pale males did not significantly differ from females housed with dark males in the duration of female-initiated affiliative behaviour ($\eta_p^2 = 0.029$, $F_{1,22}=0.651$, $p=0.428$). Comparing the extent to which females initiated affiliative behaviour toward males of the three different scrotal stimulus types, this same analysis indicated that there was a non-significant bias for female-initiated affiliative behaviour with males based on the colour of the stimulus male ($\eta_p^2 = 0.221$, $F_{2,22}=3.113$, $p=0.064$). Finally, the GLM analysis revealed a significant home×stimulus male colour interaction for female-initiated affiliative behaviour ($\eta_p^2 = 0.257$, $F_{2,22}=3.808$, $p=0.038$).

To better understand the significant interaction, we conducted follow-up simple main effects tests (Kirk 1982, p. 365–369) to compare estimated marginal means of the effects of the experimental male condition within each level of the home male condition. These tests revealed that, of the females housed with pale males, there were no significant differences among females introduced to pale, dark, and painted males ($\eta_p^2 = 0.121$, $F_{2,22}=1.509$, $p=0.243$). However, these tests indicated that, of females housed with dark males, there were significant differences among females introduced to pale, dark, and painted males ($\eta_p^2 = 0.339$, $F_{2,22}=5.645$, $p=0.010$). In particular, pairwise comparisons revealed that these females spent significantly more time (mean difference=12.6 min; $p=0.003$) directing affiliative behaviour toward pale than painted males. This difference was significant even after adjusting the alpha value for multiple tests via a Bonferroni correction (adjusted alpha=0.008). On the other hand, pairwise comparisons indicated that females housed with dark males spent 7.7 more minutes affiliating with pale than dark males, but this difference was not significant ($p=0.054$). These same females also spent on average 4.9 more minutes directing affiliative behaviour toward dark than painted males, but this difference was also not significant ($p=0.207$).

The main effects of home male colour ($\eta_p^2 = 0.003$, $F_{1,22}=0.068$, $p=0.797$) and stimulus male colour ($\eta_p^2 = 0.171$, $F_{2,22}=2.272$, $p=0.127$) as well as the home×stimulus male colour interaction ($\eta_p^2 = 0.188$, $F_{2,22}=2.550$, $p=0.101$) were not significant predictors of the duration of male-initiated affiliative behaviour. In all three cases, the η_p^2 values indicate that the effect sizes were small to modest.

We also examined whether the combined duration of male- and female-initiated affiliation was related to male colour as a means to examine whether male coloration contributed to joint affiliative exchanges between males and females, as an indicator of mutual interest. The main effect of home male colour was not significant ($\eta_p^2 = 0.004$, $F_{1,22}=0.096$, $p=0.760$). We found a statistically significant main effect of stimulus male colour ($\eta_p^2 = 0.277$, $F_{2,22}=4.208$, $p=0.028$). A post hoc Scheffe test revealed males

and females spent more time in affiliative interactions when the male was pale as opposed to painted (Cohen's $d=1.36$, $p=0.028$). Finally, the home×stimulus male colour interaction did not predict the duration of affiliative behaviour ($\eta_p^2 = 0.091$, $F_{1,22}=1.103$, $p=0.349$).

Did colour influence the likelihood of aggression?

The frequency of female- and male-initiated contact aggression for each of the six groups is presented in Table 3. Binary logistic regression analysis revealed that home male colour was not related to the likelihood of female-initiated aggression (odds ratio=0.292, Wald= 1.123, $p=0.289$). Although the overall effect of stimulus male colour was not significantly related to the likelihood of female-initiated aggression (Wald=3.320, $p=0.190$), females paired with painted males were more than ten times as likely to initiate aggression than those paired with pale males (odds ratio=10.428, $p=0.068$).

Home male colour was not significantly related to male-initiated aggression (odds ratio=1.000, Wald<0.001, $p=1.000$). However, although the overall effect of stimulus male colour was not significant (Wald=4.812, $p=0.090$), females were 13.5 times more likely to receive aggression from painted males than they were from pale males (odds ratio=13.500, $p=0.035$).

Discussion

The present experiment evaluated whether scrotal coloration in vervet monkeys influences ways in which females and males interact. Females did not bias their affiliative behaviour toward males with naturally dark coloured scrota. However, those females who were housed with dark males and who were introduced to pale males initiated and sustained significantly longer affiliative interactions than those who were introduced to painted males. When

Table 3 Number of trials where female- and male-initiated aggression occurred

	Female-initiated			Male-initiated		
	Housemate			Housemate		
	Pale	Dark	Total	Pale	Dark	Total
Stimulus male						
Pale	1	0	1	0	1	1
Dark	0	0	0	1	2	3
Painted	3	2	5	4	2	6
Total	4	2	6	5	5	10

considering affiliative exchanges between males and females, as an indicator of mutual interest between males and females in these interactions, we found that male-female pairs where the male was pale exchanged more affiliative behaviour than those pairs where the male was painted. Home male colour and stimulus male colour were not significant predictors of female- or male-initiated aggression. Females exhibited, though not significantly, aggression toward painted males more so than toward pale males, and perhaps in turn, painted males were significantly more likely to direct aggression toward females, relative to pale males.

Even though painted males interacted more aggressively toward females than pale males did, it is not clear why it was only females housed with dark males that spent more time directing affiliative behaviour toward pale males over painted males. As the paint colour of painted males did not fall within the normal range of colour variation, one possibility is that the colour of painted males' scrota surpassed a colour threshold criterion that females possess (Gerald 2003). This could have resulted in females reacting differently when paired with naturally coloured males as a result of neophobia or negativity bias generated through mechanisms of peak shift (Spencer et al. 2005; ten Cate and Rowe 2007). However, only females housed with dark males interacted favourably with pale over painted males; thus, this or other supernormal stimulus explanations seem unlikely.

It is also possible that painted males behaved in an inconsistent way with how males with their coloration normally behaved. Faced with this mixed signal, this resulted in female indifference. Still, this does not explain why only females housed with dark males directed more affiliative behaviour toward pale males, whereas those housed with pale males did not.

An alternative explanation is avoidance learning. Females may have associated dark scrota with aggression and this learning generalised to painted males. Females with a more recent learning history, i.e., those housed with dark males, would then be expected to show less affiliation with painted males, perhaps as a function of positive behavioural contrast. Positive behavioural contrast occurs when there is an increased response to a stimulus when it is presented after a less preferred stimulus (Domjan 2003). As we did not conduct observations on heterosexual pairs in their home enclosures, and as naturally dark males did not behave any more aggressively toward females than pale males during experiments, no evidence at present supports this explanation.

The present study does not allow us to rule out these possibilities. To distinguish between these possibilities, empirically, future studies should include dark males painted to resemble pale males in addition to a control condition where males' scrota are painted with clear paint. If female behaviour reflects avoidance learning, females housed with dark males should prefer naturally or painted pale males. If female behaviour results from some sort of incongruence between scrotal colour and behaviour, they should avoid pale males whose scrota were painted dark and dark males whose scrota were painted pale.

It is possible that female interactions with males are related to a female' stage of the ovarian cycle. Female vervet monkeys exhibit a long estrous period extending over 31.4 days in the wild (reviewed in Girolami 1985) and captivity (Else et al. 1986). Females would be expected to attempt to bias and confuse paternity, by mating with preferred males when they are fertile and mate with multiple males when they are less fertile (e.g., van Schaik et al. 2000). Clearly, our experimental approach does not allow us to evaluate whether females pursued this reproductive strategy with males based on colour. Nevertheless, there is little reason to expect that a female patterning of behaviour related to the ovarian cycle contributed to the results in the present study. First, females were randomly paired with males. Second, there is an absence of proceptive displays associated with ovulation (Andelman 1987). Furthermore, in captive settings, proceptive behaviours in vervet monkeys are independent of female hormonal state (Girolami 1985). Although males could attend to some unknown ovulatory cues in female vervet monkeys (Burt 1992), such as olfactory ones, again, as females were paired at random with males, this explanation cannot account for the present results.

Given the relatively small sample size, these results should be interpreted with caution. Furthermore, as we did not observe any instances of mating behaviour, we cannot rule out the possibility that females use scrotal colour, or even red prepucial or yellow-orange genital coloration to choose mates. It is also possible that females would demonstrate colour-based preferences if simultaneously presented with several males of variable colour. Alternatively, females may favour other morphological features such as large male body or canine size, or aspects of behaviour more heavily than colour. Findings obtained in male-male pair experiments (Gerald 2001) showed that vervet monkey coloration may play an important role in communication between males. Although females did not appear to distinguish between males based on natural colour variants in the present study, their affiliative response toward pale males over those artificially colored suggests that coloration can influence both male and female social interactions in vervet monkeys. In conclusion, these results suggest that females notice male coloration, but do not support the notion that females bias their interactions with males based solely upon scrotal colour.

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