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Artificial colour treatment mediates aggression among unfamiliar vervet monkeys (Cercopithecus aethiops): a model for introducing primates with colourful sexual skin

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Abstract

*Aggression and agonism typically accompany the initial interactions exchanged between unfamiliar primates. As a part of a larger study examining the social function of scrotal colour in vervet monkeys (*Cercopithecus aethiops sabaeus*), this paper offers experimental data to show how scrotal colour can influence aggression, and how artificial colour treatment can be used as an effective tool for managing aggression. Study animals were 81 vervet monkey pairs composed of 162 similarly-sized, unfamiliar adult males originating from non-adjacent parishes in Barbados. Non-contact and contact aggression were recorded on a continuous basis during 90 minute introductions. The main effects of the Test male scrotal colour, Stimulus male colour, and the interaction of the Test male and Stimulus male colours were not significant predictors of non-contact aggression. The effects of scrotal colouration of the Test male and Stimulus male were not significant predictors of contact aggression either, but there was a significant interaction effect; pairs of males with similar scrotal colour engaged in contact aggression more often than pairs of males differing in colour. Painting the scrotum dark led to more aggression when these males were paired with dark coloured males and less aggression when these males were paired with pale coloured males. These findings suggest a practical and inexpensive means of reducing the likelihood of aggression when introducing new animals. These results may also be applicable for other taxa that have colourful sexual skin, such as mandrills, drills, talapoins, patas monkeys, and many guenon species.*

Keywords: *aggression, animal welfare, colour, introduction, primates, sex skin*

Introduction

Social enrichment is critical to the welfare of captive primates, but experimental introductions of unfamiliar males and the formation of new groups can be characterised by varying degrees of agonism and aggression which may result in injury or even death (Bernstein & Mason 1963; Gartlan & Brain 1968; Bernstein *et al* 1974; Fairbanks *et al* 1978, Beaver 1989; Line 1987; Line *et al* 1989; Novak & Suomi 1988; Woolverton *et al* 1989; French *et al* 1995; Seelig 1998; Reinhardt *et al* 1995). The inability of captive managers to predict the likelihood of hostile and aggressive interactions creates serious problems when attempting to form novel social groups and the finding of compatible partners can be very time consuming (Reinhardt 1991a). The ability to predict and control aggression would, therefore, be an extremely valuable tool in captive management.

Reinhardt (1989, 1990) proposes that the delineation of rank relationships remains the most important factor in ensuring pair formation success. A fundamental principle of animal behaviour is that animals of similar resource holding power (RHP); the constellation of factors that influence fighting ability, are more likely to aggressively interact than animals of distant RHP (ie Collias 1943; Geist 1966; Parker 1974; Rohwer 1975, 1977; Maynard Smith 1982; Rowell 1988a; Johnstone & Norris 1993).

Primates may use various attributes and cues to predict RHP without interacting aggressively (eg Bernstein & Mason 1963, Reinhardt 1991b). One such characteristic could be colour, as this has been demonstrated in diverse animal taxa (Andersson 1994).

Vervet monkeys, like mandrills, drills, talapoins, patas monkeys, and most guenon species (Gerald 2003), exhibit variable intensities of conspicuous blue and aquamarine colouration concentrated in the genital region (Gerald *et al* 2001). Vervet monkeys inhabit all of sub-Saharan Africa, and they live in multi-male, multi-female matrilineal groups (Struhsaker 1967). The precise range of colours varies across populations, but within each population, colour is age-graded such that infants, juveniles and adults exhibit age-class specific sexual skin colour (Gerald 1999). The precise mechanisms underlying colour variation are not well-known but Bowlig (1978) suggests that captivity or prolonged stress can bring about scrotal colour paling. Indeed in the weeks following trapping colour also pales in free-ranging vervet monkeys in Barbados, (Gerald personal observation 1997). Gerald (2001) also found that scrotal colour was the basis for dominance outcome during paired introductions of male vervet monkeys, with darkly coloured males dominating pale coloured males.

In the present study, we examined whether colour can mediate non-contact and contact aggression, and whether artificial colour treatment can mitigate aggression. Behavioural data were collected during experimental introductions of unfamiliar adult male vervet monkey pairs.

Materials and methods

Study population

The study was conducted at The Barbados Primate Research Center (BPRC), St. Peter, Barbados. Monkeys at the BPRC are ear-tagged for identification and receive routine veterinary surveillance and care when required. A health record is maintained for each individual. The BPRC houses animals in groups, singly, or with a member of the opposite sex in cages of variable size. All cages are metal, with roof covering, to provide shelter from the elements. Animals are fed grains and fresh fruit daily, and water is provided *ad libitum*.

Subjects were 162 adult male vervet monkeys who were paired for a total of 81 experimental introductions. Subjects were tested once to prevent habituation. All subjects were wild caught from the free-ranging population of vervet monkeys on the island of Barbados, and had been residents of the BPRC captive population for time periods ranging from one month to one year prior to the start of the experiment. None of the subjects had participated in any previous experiments. Barbados is an island that is 34 km by 23 km and is composed of 11 parishes. While it is impossible to ascertain whether or not animals had ever encountered each other when free-ranging, the likelihood of existing relationships between subjects was reduced by ensuring that introductions always involved monkeys from non-adjacent parishes. Furthermore, it was possible to determine, through examining cage history, that study animals had not had any previous visual contact with one another, once at the BPRC.

Study animals were in excellent health. Animals resided either alone in single-housed cages or were paired-housed with an adult female. Animals residing with a female were only introduced to other males residing with a female to avoid introducing any potential social housing confounds. An attempt was also made to match individuals within pairs for height, weight and testis volume as body size has been suggested as a predictor of dominance (ie Rowell l988b; Mendoza 1993; Bercovitch 1996) and testis size could relate to testosterone levels, which, in turn could be associated with aggression (Higley *et al* 1996).

Colour pairs

Throughout this paper, we refer to pairs according to the following syntax: Colour_1 - Colour_2. Colour_1 refers to Test male colour and Colour_2 refers to Stimulus male colour. Social interactions were recorded from the perspective of the Test male, meaning those behaviours he directed toward or received from a Stimulus male. The scrotum of Test males was categorised as either Pale or Dark. The Stimulus male's scrotum was one of three types: (i) Pale or Dark (with natural colour), (ii) Control (naturally Pale male whose scrotum was treated with transparent spray paint) or (iii) Painted (naturally Pale male painted to resemble Dark males). In all, seven types of pairs were formed (see Table 1). Given the results of a prior study (Gerald 2001), the Stimulus group was divided into three groups: Pale (natural Pale colour male or painted with transparent paint), Dark (naturally Dark colour male), and Painted (natural Pale male whose scrotum was painted Dark).

Test enclosure

The test-enclosure was an outdoor square-shaped 3 m^3 cage constructed of galvanised wire fencing and PVC pipe frames, equipped with an upper and lower platform. This enclosure was visually isolated from neighbouring social groups. Natural sunlight was available in approximately three-quarters of the test enclosure and for the remaining quarter, an upper platform was covered by a roof shelter to shield monkeys from inclement weather. On the night prior to introductions, animals were housed in individual transport cages covered by a tarpaulin to avoid the potential confound of stress occurring as a result of separation or capture.

Size and colour measures

The day before experiments, study animals were immobilised with intramuscular injections of ketamine HCl (12 mg kg^{-1}, Ketaset®, Aveco, Fort Dodge, Iowa). Height was measured as the distance from the nuchal crest to the base of the tail and recorded to the nearest cm. Weight was measured to the nearest 0.01 kg. Testicular volume was calculated by using the formula for a regular ellipsoid (Bercovitch 1996).

Colour was measured by comparing the colour found on the midpoint of the lower midsection of the subject's scrotum with colours found on the Pantone® Process Color Imaging Guide 1000 (Carlstadt, New Jersey, 2nd printing, 1992) based on the Pantone Matching System®. Colour was assigned when agreement was reached between the first author and a research assistant. Males were defined as Pale or Dark based on a ranking system calculated for the captive population based on the colour measures for value; meaning, the amount of relative darkness or lightness. Males above the median value were assigned to the Dark colour group and males below the median were assigned to the Pale colour group (additional details in Gerald 2001).

Artificial colour treatment

Pale males were randomly assigned to treatment groups. The scrota of these treated Control and Painted animals was washed and dried. A plastic cover with two holes exposing the testes and a small flap covering the penis was placed over the scrotal region to prevent paint application to areas other than the lower scrotum. Colour treatment was achieved by applying non-toxic, commercial, *Touch 'n tone Day*®, all-purpose household spray paint (royal blue and light blue) to the lower scrotal region. Control subjects were sham manipulated with lead-free 100% non-toxic, colourless transparent spray paint (*Zynolyte*® Spray-mate, All-purpose). Paint treatment did not appear to be detrimental to the animals' welfare as Painted male activity and feeding levels were comparable to those of naturally Pale coloured males. A separate set of analyses (Gerald 2001), showed that Control treatment did not produce any discernible effect on social behaviour; thus, control-treated males and Pale males were pooled for appropriate analyses.

Experimental trials

At the time of the experimental trial, an assistant positioned each transport cage in a central location to ensure animals faced each other upon the removal of the covers. The assistant unlocked the cages and lifted the door to each cage before simultaneously removing both cage covers. The experiment officially began as soon as the assistant left the test area. After 90 minutes elapsed or more than three bouts of contact aggression occurred, a trial was terminated. Study animals were not trained to present for injections; therefore, following the experimental trial, animals were either passively trapped by luring them back to the transport cages with fruit, or they were returned to their cages after experienced veterinary-trained technicians had entered the test cage and immobilised them with intramuscular ketamine injections. No permanent injuries occurred during any of the introductions, but if injuries occurred during experiments, appropriate veterinary care was administered. After trapping, animals were returned to their home enclosures and the test area and transport cages were disinfected.

Behavioural observations

Non-contact and contact aggressive behaviours that the Test male initiated, received, and mutually engaged in with the Stimulus male were recorded on a continuous basis (Altmann 1974) throughout the 90 minute experimental trials. Non-contact aggression was defined on the basis of threats (threat vocalisations not included), grimaces, yawns and bite and grab attempts. Contact-aggression was defined as bites, hair-pulls and slaps. These behavioural measures are defined in Table 2.

Statistical analyses

Mann-Whitney U-tests were used to evaluate the effect of size asymmetry on aggression. Individuals of a given pair were considered to be of the same size if there was less than a 5% size difference in any body measure between animals.

Table 1 Categories of colour pairs used in experimental trials.

Test	Stimulus	Colour pairs	*n*
Pale	Dark	Pale-Dark	11
Dark	Control	Dark-Control	13
Pale	Pale	Pale-Pale	10
Pale	Control	Pale-Control	13
Dark	Dark	Dark-Dark	10
Pale	Painted	Pale-Painted	10
Dark	Painted	Dark-Painted	14

In other words, a pair was equal in size if the following equation was true:

$[X_1 - X_2] < \text{Mean } X_1,X_2 \times 0.05.$

To test whether Test male colour, Stimulus male colour, or their combination influenced non-contact or contact aggression between males during paired introductions, we used a general linear model with Type III sums of squares. Colour of the Test (Pale, Dark) and Stimulus (Pale, Painted, Dark) males served as the two main effects, and the Test × Stimulus interaction was used to test the effect of the colour combination. Mann-Whitney U-tests were used to rule out the possibility that scrotal colour painting, irrespective of pairing, influenced non-contact and contact aggression.

Results

Frequency of aggression within pairs

Non-contact and contact aggression was measured as the frequency of occurrence per experimental trial time. Non-contact or contact aggression occurred in 75.3% of the trials (61/81); non-contact aggression occurred in 54.3% (44/81) of the trials; and contact aggression occurred in 45.7% of the trials (37/81).

Does size difference predict aggression?

While we made an attempt to eliminate size asymmetry, inevitably pairs of individuals differed in size (mean differences: weight = 0.57 kg, height = 2.05 cm, and testicular volume = 75.55 cc). Size differences between males within a pair did not contribute to exchanges of non-contact aggression: (testicular volume; $U = 393.0$, $n_1 = 12$, $n_2 = 69$, $P > 0.05$; weight; $U = 687.5$, $n_1 = 29$, $n_2 = 51$, $P > 0.05$; height; $U = 747.0$, $n_1 = 47$, $n_2 = 34$, $P > 0.05$) or contact aggression: (testicular volume; $U = 393.0$, $n_1 = 12$, $n_2 = 69$, $P > 0.05$; weight; U = 577.5, $n_1 = 29$, $n_2 = 51$, $P > 0.05$; height; $U = 780.0$, $n_1 = 47$, $n_2 = 34$, $P > 0.05$). Given these results, size difference was not considered in any further analyses.

Effects of test and stimulus male colour on non-contact aggression

Table 3 shows the mean levels of non-contact aggression for each of the six possible colour pairings. The mean level of non-contact aggression did not differ among the three groups of Test animals ($F_{1,75} = 0\ 887$, $P > 0.05$). Mean levels

Table 2 The behavioural measures.

Measure	Definition
Contact aggression	
Bite	Biting with physical contact
Hair pull	Pulling the hair
Slap	Grabbing, pushing, hitting, and slapping with physical contact
Non-contact aggression	
Threat	Head jerked or bobbing up and down
Grimace	Mouth open approximately ½, lip retracted and teeth exposed
Yawn	Chin raised and complete open mouth display of canines
Bite attempt	Biting at, with no physical contact
Slap attempts	Grabbing and slapping at, with no physical contact

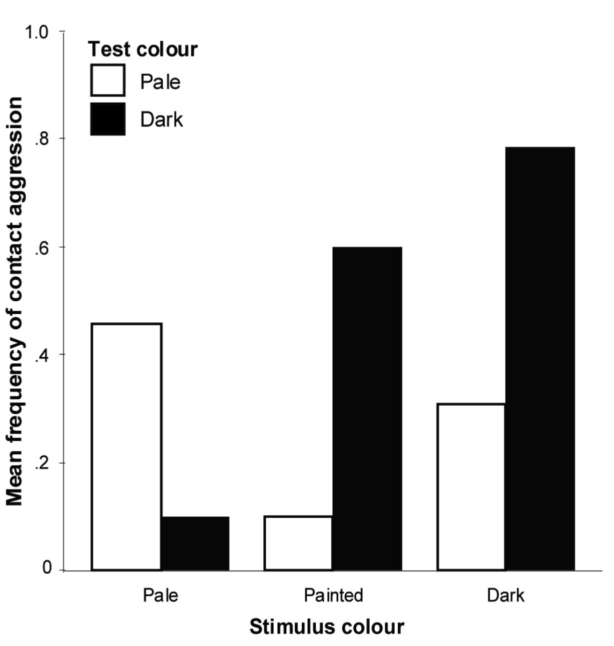
Table 3 Mean frequency and standard deviation of non-contact aggression per experimental trial.

	Stimulus			
Test	**Pale**	**Painted**	**Dark**	**Total**
Pale	3.25 ± 4.20	4.00 ± 8.00	1.24 ± 0.34	0.48 ± 0.70
Dark	0.40 ± 0.97	14.00 ± 32.13	1.86 ± 3.25	5.00 ± 17.92
Total	2.41 ± 3.78	9.00 ± 23.36	1.56 ± 2.47	3.75 ± 12.11

Table 4 Mean frequency and standard deviation of contact aggression per experimental trial.

	Stimulus			
Test	**Pale**	**Painted**	**Dark**	**Total**
Pale	0.46 ± 0.51	0.10 ± 0.32	0.31 ± 0.48	0.35 ± 0.49
Dark	0.10 ± 0.32	0.60 ± 0.52	0.79 ± 0.43	0.53 ± 0.51
Total	0.35 ± 0.49	0.35 ± 0.49	0.56 ± 0.51	0.42 ± 0.50

Figure 1



Mean frequency of contact aggression according to test and stimulus colour.

of non-contact aggression also did not significantly differ among the three stimulus groups, but there was evidence of a trend ($F_{2,75} = 2.824$, $P < 0.07$). Finally, the Test × Stimulus interaction effect was not significant ($F_{2,75} = 1.789$, $P > 0.05$).

Effects of test and stimulus male colour on contact aggression

Table 4 shows the mean levels of contact aggression in each of the six possible colour pairings. The mean level of contact aggression was higher in the Dark colour group but the difference only approached statistical significance ($F_{1,75} = 3.845$, $P < 0.06$).

Levels of aggression were also highest among the groups that were presented with a Dark coloured stimulus male, though this difference was also not statistically significant ($F_{2,75} = 2.551$, $P > 0.05$).

The Test × Stimulus interaction was significant ($F_{2,75} = 7.739$, $P < 0.001$) (see Figure 1). To better understand the nature of this interaction, we conducted two sets of follow-up GLM analyses. In the first set we compared levels of aggression among the three Stimulus male groups for the Pale and Dark Test animals, separately. *Post hoc* Scheffe tests revealed that, among the group of Pale coloured Test males, there were no statistically significant differences in contact aggression elicited by Pale, Painted, or Dark stimulus animals (both P values > 0.05). However, among the group of Dark coloured test animals, although no statistically significant differences were found in the mean levels of contact aggression between the groups presented with Painted or Dark males, Painted and Dark males both elicited significantly higher mean levels of contact aggression than Pale males (both P values < 0.05). Therefore, even though the Stimulus male colour was not related to aggression among subjects in the Pale group, Painted or Dark stimulus animals elicited significantly higher mean levels of aggression from Dark test animals.

In the second set of follow-up GLM analyses we tested whether mean levels of contact aggression were greater in pairs of similarly coloured males. Mean levels of contact aggression between Pale and Dark Test males were compared for each of the three groups of Stimulus animals, separately. When the Stimulus animal was Pale, contact aggression was significantly higher if the test animal was also Pale ($F_{1,32}$ = 4.229, P < 0.05). Furthermore, the frequency of contact aggression was higher when Painted ($F_{1,18}$ = 6.818, P < 0.05) or Dark ($F_{1,25}$ = 7.512, P < 0.05) Stimulus animals were introduced to Dark rather than Pale Test animals.

Does paint treatment affect aggressive behaviour?

To exclude the possibility that the paint treatment had an effect on non-contact and contact aggression, we conducted a series of Mann-Whitney *U*-tests. In the first we compared the Pale-Painted and Pale-Pale groups. Pale-Painted pairs engaged in similar rates of non-contact aggression as Pale-Pale pairs (U = 104.0, n_1 = 10, n_2 = 24, P > 0.05). However, Pale-Painted pairs engaged in contact aggression nearly five and a half times less often than Pale-Pale pairs (U = 69.0, n_1 = 10, n_2 = 24, P < 0.05). In the second we compared levels of aggression of Dark-Painted pairings with those of Dark-Dark pairings. Rates of non-contact aggression within pairs of Painted and Dark males did not differ significantly from that exchanged within pairs of naturally Dark males (U = 49.5, n_1 = 10, n_2 = 14, P > 0.05) nor did rates of contact aggression (U = 55.5, n_1 = 10, n_2 = 14, P > 0.05).

Discussion

Aggression and agonism accompany the formation of groups in a variety of primate species. The key to successful introductions of animals entails minimising injury to all animals in the least amount of time. Given the high likelihood of aggression, as found in the present study where non-contact or contact aggression occurred in precisely three-quarters of the trials, primate caretakers have the arduous task of identifying predictors of aggression during group formation.

The results of the present study demonstrate that, even if pairs are matched for size, the scrotal colour of the individuals within a pair was an important predictor of contact aggression. When adult males were similar in colour there was a far greater likelihood of them interacting aggressively than would otherwise be the case. While ineffective in deterring non-contact aggression, these findings suggest that introductions of males differing in scrotal colour (either naturally or by painting) will be likely to lead to less contact aggression than the introduction of males with similar scrotal colours.

These results also suggest that it may be possible for males to be painted in such a way as to conceal colouration; thereby, minimising injury when paired with naturally Dark animals. We predict that aggression rates will be low in social groups with multiple new males, provided that these groups are composed of males exhibiting continuous variation in scrotal colour. We recommend introducing males of different colour into groups. If this is not feasible then it may be helpful to paint animals to simulate variation prior to introduction.

While the present study focused on paired introductions among vervet monkeys, we believe that our findings might extend to other primates with colourful sexual skin. Nevertheless, various limitations of the present study require further consideration. Here, value measures were used to operationally define colour. It is possible that colour hue or chroma are also important predictors of aggression. Hue may influence behaviour alone or in combination with value and chroma. While rates of aggression were reduced among pairs of Painted-Pale males, even after 90 minute experiments, we encourage the application of long-lasting paint, to ensure successful introduction. It is not possible for us to generalise how predictive our 90 minute observations are of long-term success of a pairing. As is the case for all paired introductions, pairs should be monitored continuously to make certain that relationships formed during introduction last beyond the time paint has worn off the animal.

This study was limited to observations of adult male pairs. It is possible that the relationship between scrotal colour and social interactions is more complex when novel group formation includes animals of different sex and age classes, or when it involves an introduction of more than two adult males. Size asymmetry might be a good predictor of compatibility if the difference is large (Chamove 1978), but it is also important to control for age differences. While we agree that size is an important factor to consider, the data from the present study suggest that colour should be an important consideration when making pairing decisions.

It remains unclear whether the presence of females exacerbates or reduces the relationship between scrotal colour and contact aggression. Females might attend to scrotal colour differences between males to prevent aggression directed at them or their dependent offspring. Individual female vervet monkeys and females in coalitions can harass, attack, and seriously wound newly introduced males (Bloomsmith & Maple 1987; Fairbanks & McGuire 1987; Morland *et al* 1992). Vervet mothers are more protective of infants in response to the recent introduction of unfamiliar males, as a counter strategy to the potential threat of infanticide (Fairbanks & McGuire 1987). By contrast, if colour is related to dominance (Andersson 1994; Gerald 2001) or condition (Isbell 1995), females might attend to individual colour differences between males and preferentially attend to less aggressive individuals.

Specific applications of colour analysis in captive communities

Colour might serve as a cue to mediate aggression to reduce injury to animals during introductions and group formation, to expedite socialisation. Providing visual contact between individuals prior to pairing appears sufficient to delineate status relationships and, indeed, captive managers of primates have achieved tremendous success by offering animals visual contact with one another prior to physical introduction. (Reinhardt 1989, 1991a,b; Fritz 1994; Reinhardt *et al* 1995; Reinhardt & Seelig 1998; Crockett *et al* 1994).

The results of this study demonstrate how primates can use secondary sexual colour during brief introductions, even when colour is artificial. These findings have important implications for colony management of captive primates (reviewed in Gerald 2003) and other mammals that vary in secondary sexual colouration (eg West & Packer 2002).

Species Survival Plan (SSP) and other Advisory management groups can use colour assessment to recommend transfer of primates between Institutions. Through the use of digital photographs and colour customisation software (Gerald *et al* 2001), colour can be inexpensively analysed and shared with other facilities in order to facilitate introduction of animals into a new group. Colouration might be linked to breeding success (Dixson *et al* 1993; Andersson 1994; Gerald 2003); therefore, recommendations can also be made as to which males will be more likely to sire offspring to increase breeding productivity.

While the present investigation highlights the possible importance of colour as a pre-assessment characteristic prior to attempting social housing, not all secondary sexual characteristics in animals may be related to aggression. Furthermore, additional studies on other pre-assessment factors besides colour should also be conducted, as these could be valuable in preventing facilities from wasting time and risking unnecessary injuries by putting together pairs whose low chance of compatibility could have been predicted given prior knowledge of these pre-assessment factors.

Animal welfare implications

(1) Colour might convey an important message to animals as it can predict aggressive outcome during introductions.

(2) Artificial colour can be used to reduce stress and the probability of aggression. Paint treatment of one animal can elicit or reduce contact aggression depending on the colour of the other animal; animals of the same colour are more likely to interact antagonistically than males differing in colour.

(3) Paint treatment did not consistently influence rates of non-contact aggression. This suggests that scrotal colour does not influence all social interactions.

(4) Colour can be a useful tool for animal husbandry in captive primates.

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