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Research article

A note on the social compatibility of an all-male group of hamadryas baboons (*Papio hamadryas*)

Susanne Koot[1], Chantal M. Kapteijn[1], Ronald H. Huiskes[1] and Godelieve Kranendonk[1,2*]

[1]*AAP, Rescue Centre for Exotic Animals, P.O. Box 50.313, 1305 AH, Almere, The Netherlands*
[2]*Animal Ecology, Department of Biology, Utrecht University, The Netherlands*
**Correspondence: Godelieve Kranendonk; godelieve.kranendonk@aap.nl*

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Abstract

In captive primates, the formation of all-male groups is used as a management tool to deal with surplus males. In the wild, hamadryas baboons (*Papio hamadryas*) live in multilevel societies consisting of reproductive one-male/multi-female units, clans, bands and troops. The social compatibility of all-male groups of hamadryas baboons has not been studied thus far. Here we examined the social compatibility of an all-male group of hamadryas baboons as compared to adult males of a mixed-sex group by focusing on social interactions. Additionally we studied the behavioural effects of reproductive status to evaluate whether surgical castration can assist in the social housing of surplus hamadryas baboons. The results indicate that intact males (n=3) in an all-male group show fairly similar behavioural profiles compared with intact males (n=3) in a mixed-sex group, although they are less often observed in social proximity. Furthermore, intact males within an all-male group engaged less in affiliative and submissive behaviours than castrated males (n=3) within the same group. Overall, our results suggest that the formation of an all-male group of hamadryas baboons can be a feasible management tool in housing surplus males, and that submissive behaviours as expressed by castrated males may contribute positively to the social stability of all-male groups.

Introduction

Captive (breeding) groups of primate species naturally living in unimale or harem groups are traditionally established with one adult male and a number of females (Price and Stoinski 2007). Thus, it is necessary to deal with “surplus” males, which can be achieved via castration, solitary housing, the formation of all-male groups or euthanasia. Managerial euthanasia of surplus animals is often ruled out on moral grounds (Graham 1996; Lacy 1991), but solitary housing of naturally social animals prevents them from engaging in social behaviour, and consequently affects welfare (Price and Stoinski 2007). All-male or “bachelor” groups, in contrast, can provide a social environment for surplus male primates in species that form all-male bands in the wild (e.g. gorillas, Pullen 2005; Stoinski et al. 2001, 2004; proboscis monkeys, Sha et al. 2013) or live in multi-male groups (e.g. chimpanzees, Alford et al. 1995; lion-tailed macaques, Stahl et al. 2000; white crowned mangabeys, Fàbregas and Guillén-Salazar 2007), but also for species naturally living in harems (e.g. Javan langurs, Dröscher and Waitt 2012). In captive hamadryas baboons (*Papio hamadryas*), over-population of troops is managed by female-based contraception and by male removal or culling (Plowman et al. 2005). However, no studies have been performed on the formation of all-male groups of hamadryas baboons as an alternative for surplus males.

In the wild, hamadryas baboons live in a multilevel society consisting of one-male/multi-female units, clans (comprising several units), bands (comprising several clans, single units and some single males) and troops (comprising several bands) (Schreier and Swedell 2009). Male kin remain in stable clans for life (Kummer 1984). After detaching from their natal units at about two years of age, males spend the following years loosely associated with several units, mostly of the same clan, before initiating their own one-male unit within that clan (Sigg et al. 1982). The adult and subadult males of one clan tend to stay closer to each other and interact more frequently with each other than with males of other clans (Abegglen 1984). Thus, although frequent interactions between males within the same clan occur, bachelor groups as in gorillas (e.g. Robbins 1996) have not been observed in the wild.

In captivity, castration (i.e. surgical gonadectomy) of surplus males to reduce aggression may allow males to remain in their groups as subordinates. However, it is unclear how and whether social compatibility of both intact and castrated males in one multi-male group can be achieved. Generally, at puberty inter-male aggression increases as testosterone levels increase (Wobber et al. 2013). Testosterone plays an important role in masculinisation, aggression and reproduction (Bermond et al. 1982; Griffin 1996). In domestic animals castration is a common practice to control sexual and aggressive behaviour (Bouissou 1983) and in several primates testosterone and aggressive behaviour are linked, i.e. in the breeding season testosterone levels are positively correlated with male–male aggression (e.g. Cavigelli and Pereira 2000; Muller and Wrangham 2004). Forming all-male groups without castration is possible (e.g. Fàbregas and Guillén-Salazar 2007; Reinhardt 1989), but castration could aid in the formation of multi-male groups. For example, castration of young Javan langur males allows them to remain within their social group while ensuring that the dominant male remains dominant (Waters et al. 2001) and can be used to control aggression levels (Dröscher and Waitt 2012). However, as yet, no studies have been performed on the value of castration as a management tool in all-male groups of hamadryas baboons.

The objectives of the present study were therefore to assess the social compatibility of intact and castrated males in an all-male group of hamadryas baboons and to compare the behaviour of intact males in an all-male group to that of intact males in a mixed-sex group.

Methods

Subjects and housing

Behavioural data were collected on hamadryas baboons at two locations. At AAP, a rescue centre for exotic animals (Almere, the Netherlands), an all-male group (AM group, n=6) with three intact and three castrated (surgically gonadectomised) adult males were studied, and at Amersfoort Zoo (Amersfoort, the Netherlands), three intact adult males from a multi-sex group (MS group) consisting of forty adults (15 males, 30 females) and five juveniles were studied.

The individuals at AAP did not have (visual) contact with female hamadryas baboons. They came from different locations (Table 1). The males at Amersfoort Zoo were all born and raised within either Amersfoort Zoo or Emmen Zoo (Emmen, the Netherlands).

The enclosure at AAP consisted of an indoor section (30 m^2) of three compartments with the floors covered with a wood chip substrate, and an outdoor section of 500 m^2 with a grass substrate. Enclosures included ropes, perches, nets and visual barriers. Individuals were given access to the outdoor enclosure between 0930 and 1630. Animals were fed three times per day, pellets at 1000, carrots and apples at 1200, and other fruits and vegetables at 1630.

The enclosure at Amersfoort Zoo consisted of an indoor section (40 m^2) with a steel floor, and an outdoor section of 815 m^2 with soil. Enclosures included rock formations, wooden climbing structures and visual barriers. Individuals were given access to the outdoor enclosure between 0830 and 1800. Animals were fed three to four times per day. In the morning, they received pellets and seeds, during the day, they received apples and food enrichment (eggs, rice and insects), and in the evening pellets, bread, endive, onions and carrots.

At both locations, food was scattered throughout the enclosure to minimise competition over food.

Data collection

Observations on the AM group at AAP were carried out between 15 August 2011 and 2 July 2013, for a total of 100 days, resulting in more than 63h of total observation time per individual, and between 4 October 2011 and 6 December 2011 for a total of nine days on the MS group at Amersfoort Zoo, resulting in more than 12h of total observation time per individual. Twenty minute focal continuous sampling was used to record agonistic, affiliative and submissive behaviours (see Table 2 for a detailed ethogram). In addition, throughout these sessions we recorded whether the focal animal was solitary or social (i.e. within one arm's length distance from another individual). The sex of any individual that was in close proximity to the focal animal was noted. In the case of the mixed-sex group, interactions with other group members, including individuals other than the focal animals, were recorded. Observations were conducted between 0900 and 1630. The observation of individuals was counterbalanced across the day. Observations were performed during both feeding and non-feeding periods, in the outdoor enclosures.

Statistical analyses

Individual scores for the 20 min periods were corrected for time scored out-of-sight, and converted to proportion of time spent

Table 1. Individual male hamadryas baboons within an all-male group (AM group) at AAP and a mixed-sex group (MS group) at Amersfoort Zoo included in this study.

Group	Individual	Approximate age at start of study (yrs)	Reproductive status	Age at castration	General history	Current group size	Focal data
AM	Jamal	9	Intact	-	Mother reared, previous zoo, now rescue centre	6	64 h 40 min
	Kontar	10	Intact	-	Mother reared, previous zoo, now rescue centre	6	64 h 20 min
	Tarzan	22	Intact	-	Rearing unknown, previous zoo, now rescue centre	6	64 h 40 min
	Akkad	14	Castrated	Prior to age 13	Rearing unknown, previous zoo, now rescue centre	6	63 h 40 min
	Papio	12	Castrated	Prior to age 7	Rearing unknown, animal trader, now rescue centre	6	65 h
	Sumer	14	Castrated	Prior to age 13	Rearing unknown, previous zoo, now rescue centre	6	64 h
MS	1	Adult	Intact	-	Mother reared, zoo	40	12 h
	2	Adult	Intact	-	Mother reared, zoo	40	12 h
	3	Adult	Intact	-	Mother reared, zoo	40	12 h

Table 2. Ethogram of behaviours recorded.

Behaviour		Definition
Affiliative	Lip smack	Rapid, repetitive opening and closing of the lips, directed at a conspecific.
	Touch	Briefly touch a conspecific.
	Sniff	Sniff a conspecific; includes sniffing perio-anal region.
	Embrace	Embrace a conspecific.
	Groom	Moving the fur of a conspecific, searching for foreign objects (insects, dirt, etc.)
	Mutual groom	Two individuals grooming each other at the same time.
	Social play	Play with a conspecific, often accompanied by a play face in the form of an open mouth, while teeth are hidden.
Agonistic	Threat	Staring at a conspecific with raised eyebrows, often accompanied with an open mouth and/or while bobbing its head (short movement of the head and upper body)
	Display	Individual shakes bars, trees or mesh.
	Chase	Individual runs after a conspecific for at least two metres in a non-playing context.
	Lunge	Individual hits the ground with one hand in a vertical movement, followed by a short movement in the direction of a conspecific.
	Contact aggression	Individual hits, bites, pulls or grabs a conspecific; includes fighting or attacking a conspecific.
	Neck bite	Individual bites a conspecific in the neck.
Submissive	Fear grin	Upper and lower lips are drawn back showing all the teeth; often the individual looks around.
	Social present	Individual orients its hindquarters towards a conspecific.
	Lower body position	Crouch or hide, while the torso is lowered towards the ground.
	Avoid	Move away after making eye contact with a more dominant animal when the dominant animal approaches or in response to being threatened.
	Flee	Run away (at least 5 m) from a dominant animal in response to a lunge, attack, chase or other form of aggression.

(duration) or rate per hour (frequency); scores were summed and the mean was used for analyses. SPSS 22.0 was used for all statistical analyses. Mean values (rates or percentage) of performance of target behaviours were compared using Mann–Whitney U tests to test for differences between the intact and castrated individuals in the AM group at AAP, and for differences between the intact individuals in the AM group at AAP and intact males in the MS group at Amersfoort Zoo. All tests were two-tailed and alpha levels of P≤0.05 were considered significant.

Results

Comparison of intact males in an all-male group versus intact males in a mixed-sex group

Intact AM males spent less time in social proximity than intact MS males (10.4% vs. 87.4% of time; Z=-1.964, P=0.05). In more detail, intact AM males spent less time close to other intact males than intact MS males (Z=-1.964, P=0.05; Figure 1A), and less time close to castrated males than intact MS males spent close to females

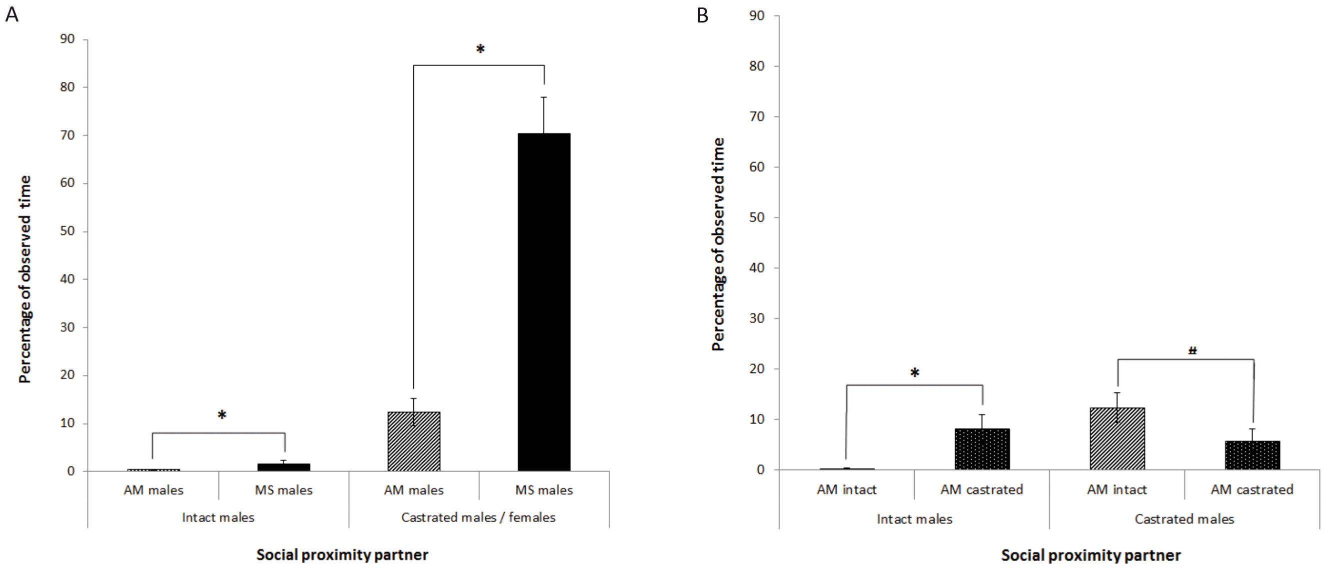

Figure 1. Social proximity partners of intact males in (A) the all-male (AM) group, and in the mixed-sex (MS) group, and in (B) the all-male group, for intact AM males and castrated AM males. Intact AM males and castrated AM males could be close to other intact males or to castrated males, MS males could be close to intact males or females. * P<0.05, # P<0.10.

Table 3. Social behaviour in percentage of time or frequency per hour of intact male hamadryas baboons within an all-male group (AM group) at AAP (n=3) and a mixed-sex group (MS group) at Amersfoort Zoo (n=3). The median and the test statistics of the Mann Whitney *U* test are reported.

		Intact AM	Intact MS	U	Z	p	*r*
Affiliative	Groom (% time)	2.71	9.76	1	-1.528	0.127	-0.624
	Mutual groom (% time)	0.00	0.01	1.5	-1.549	0.121	-0.632
	Social play (% time)	0.00	0.00	3	-1.000	0.317	-0.408
	Lip smack (freq/h)	0.38	1.75	0	-1.964	*0.049*	-0.802
	Embrace (freq/h)	0.00	0.00	3	-1.000	0.317	-0.408
	Touch (freq/h)	0.01	0.00	1.5	-1.549	0.121	-0.632
	Sniff (freq/h)	0.01	0.00	1.5	-1.581	0.114	-0.645
Agonistic	Chase (% time)	0.14	0.09	3	-0.655	0.513	-0.267
	Display (freq/h)	0.05	0.00	1.5	-1.549	0.121	-0.632
	Threat (freq/h)	0.59	0.00	2	-1.107	0.268	-0.452
	Lunge (freq/h)	0.07	0.00	0	-2.087	0.037	-0.852
	Contact aggression (freq/h)	0.03	0.17	3	-0.655	0.513	-0.267
	Neck bite (freq/h)	0.00	0.00	4	-0.258	0.796	-0.105
Submissive	Fear grin (freq/h)	0.00	0.00	3	-1.000	0.317	-0.408
	Social present (freq/h)	0.01	0.25	0	-1.993	*0.046*	-0.813
	Avoid (freq/h)	0.05	0.00	0	-2.087	*0.037*	-0.852
	Lower body posture (freq/h)	0.00	0.00	4.5	0.000	1.000	0.000
	Flee (freq/h)	0.00	0.00	3	-1.000	0.317	-0.408

(Z=-1.964, P = 0.05; Figure 1A). However, intact AM males spent a similar percentage of time near other intact males as near castrated males (Z=-1.604, P= 0.11), and intact MS males did not spend significantly more time near females than near other males (Z=-1.604, P=0.11).

Interestingly, intact AM males showed less lip smacking than intact MS males (Table 3). No differences between the intact AM males and intact MS males were found in other affiliative behaviours (Table 3; all P≥0.114).

Intact AM males showed more lunges than intact MS males (Table 3). No differences were found in other agonistic behaviours (Table 3; all P≥0.121).

The frequency of social presenting was lower in intact AM males than in intact MS males (Table 3). In addition, intact AM males showed higher frequencies of avoidance behaviour than intact MS males (Table 3). The occurrence of other submissive behaviours did not differ between intact AM males and intact MS males (Table 3; all P≥0.317).

Comparison of intact versus castrated males in an all-male group

No differences in time spent in social proximity were observed between intact AM (10.4% of time) and castrated AM males (14.8% of time; Z=-1.528, P=0.127). However, intact AM males spent significantly less time in social contact with intact males than castrated AM males did (Z=-2.121, P=0.034, Figure 1B), and tended to spend less time with castrated males than castrated AM males did (Z=-1.768, P=0.077, Figure 1B).

Intact AM males spent less time on social play than castrated AM males (Table 4). Furthermore, intact AM males touched a group member less frequently than castrated AM males (Table 4). No differences in other affiliative behaviours were found (Table 4; all P≥0.127).

Intact AM males spent more time on chasing a group member than castrated AM males (Table 4). Likewise, the frequency of lunging was higher in intact AM males than in castrated males (Table 4). No differences in other agonistic behaviours were detected (Table 4; all P≥0.121). In addition, intact AM males engaged less in all recorded submissive behaviours than castrated AM males (Table 4; all P≤0.049).

Discussion

In this study we examined the social compatibility of an all-male group (AM group) of hamadryas baboons compared to adult males of a mixed-sex group (MS group), and the behavioural effects of reproductive status, to evaluate whether intact males have a different behavioural profile than castrated males, or than males housed in an intact group. The results indicate that intact males in an all-male group had fairly similar behavioural profiles to intact males in a mixed-sex group, although they spent less time in social proximity. Furthermore, castrated males within an all-male group engaged more in affiliative and submissive behaviours than intact males within the same group.

Comparison of intact males in an all-male group versus intact males in a mixed-sex group

The AM males could interact exclusively with adult male group members, while MS males could interact with females, subadult males and infants. MS males spent more time in social proximity than AM males. It is possible that MS males were closely surrounded mainly by members of their harem (one-male/multi-female unit), resulting in increased social proximity. In the wild, hamadryas baboons live in multilevel societies (Schreier and Swedell 2009), and males within one clan tend to interact more frequently and stay closer to each other than to males of other clans (Abegglen

Table 4. Social behaviour of intact (n=3) and castrated male (n=3) hamadryas baboons within an all-male group (AM group) at AAP. The median and the test statistics of the Mann Whitney *U* test are reported.

Behaviour		Intact AM	Castrated AM	U	z	p	*r*
Affiliative	Groom (% time)	2.71	5.14	1	-1.528	0.127	-0.624
	Mutual groom (% time)	0.00	0.00	4.5	0.000	1.000	0.000
	Social play (% time)	0.00	0.32	0	-1.993	*0.046*	-0.813
	Lip smack (freq/h)	0.38	0.64	3	-0.655	0.513	-0.267
	Embrace (freq/h)	0.00	0.00	4.5	0.000	1.000	0.000
	Touch (freq/h)	0.01	0.04	0	-1.964	*0.049*	-0.802
	Sniff (freq/h)	0.01	0.01	4.5	0.000	1.000	0.000
Agonistic	Chase (% time)	0.14	0.01	0	-1.964	*0.049*	-0.802
	Display (freq/h)	0.05	0.00	1.5	-1.549	0.121	-0.632
	Threat (freq/h)	0.59	0.14	1	-1.528	0.127	-0.624
	Lunge (freq/h)	0.07	0.01	0	-1.964	*0.049*	-0.802
	Contact aggression (freq/h)	0.03	0.01	3	-0.655	0.513	-0.267
	Neck bite (freq/h)	0.00	0.01	4	-0.232	0.817	-0.095
Submissive	Fear grin (freq/h)	0.00	0.24	0	-1.993	*0.046*	-0.813
	Social present (freq/h)	0.01	0.25	0	-1.993	*0.046*	-0.813
	Avoid (freq/h)	0.05	0.18	0	-1.964	*0.049*	-0.802
	Lower body posture (freq/h)	0.00	0.11	0	-2.087	*0.037*	-0.852
	Flee (freq/h)	0.00	0.05	0	-1.993	*0.046*	-0.813

1984), but they do not necessarily spend a lot of time in social proximity (i.e. within one arm's length distance from another individual). Another factor that may have contributed to the close social proximity of the MS males is the fact that these males on average had an enclosure space of 16.3 m^2 per individual, while the AM males had 83.3 m^2 per individual at their disposal.

As far as affiliative behaviours are concerned, MS males engaged more frequently in lip smacking than AM males. Lip smacking is a non-agonistic signal and occurs as part of greeting interactions (Preuschoft and Van Schaik 2000). Greeting interactions take place in, among other contexts, the presence of competition-eliciting attractive resources (e.g. space, food, mates, partners; Preuschoft and Van Schaik 2000). Since the MS group contains females and space is limited, MS males may be more motivated to show lip smacking than AM males. By lip smacking, MS males can reassure, appease, and assess their partner's tendencies, the most common functions of greeting (Estes 1991; Preuschoft and van Schaik 2000). Additionally, greeting of dominant males facilitates social interaction and group cohesion, as it reduces aggressive interactions (Preuschoft and van Schaik 2000), and thus MS males could use this to promote stability within their clan. Indeed, in the present study MS males did not show more agonistic interactions than AM males. Also, MS males engaged more frequently in presenting, which is also part of the greeting ceremony, thus easing conflict avoidance (Preuschoft and Van Schaik 2000).

The AM males had fewer resources (females, space) to compete for than the MS males, which may explain the reduced performance of lip smacking and presenting. Indeed, AM males spent less time in social proximity and avoided their group members more than MS males, which suggests they used a conflict avoidance strategy (Aureli et al. 2002). However, more lunges were observed in the AM group, although other agonistic behaviour did not differ between AM and MS males. It is known that hamadryas baboons rarely engage in contact aggression (Stammbach 1986), a behaviour that was indeed rarely observed in either group.

In a study on an all-male group of proboscis monkeys, males displayed significantly more aggressive interactions during feeding times (Sha et al. 2013). In the current study, the effect of feeding on the baboons' behaviour was not studied, but it was seen that agonistic interactions do occur during feeding times (pers. obs., G. Kranendonk). Therefore, a subsequent study could focus on differences in agonistic and affiliative behaviour specifically during feeding.

Based on the low rates of agonistic behaviour in the current study, intact hamadryas baboon males in an all-male group may be socially compatible. However, rates and duration of affiliative behaviours were also quite low in the AM group. Early familiarity and/or relatedness may be important for long-term compatibility among males in captive all-male groups, as indicated in western lowland gorillas (Stoinski et al. 2004) and lion-tailed macaques (Stahl et al. 2000). All-male groups of unrelated males introduced in late adolescence have been suggested to provide fewer social benefits (Price and Stoinski 2005). This may explain the higher levels of affiliative behaviour in the MS males, since these individuals were presumably related. In the AM group, two of the intact males were siblings and one intact male was introduced as an adult.

Consequently, another factor to take into account when interpreting the results is the background of the individuals. The MS males were all mother reared in a mixed-sex group, and thus had the opportunity to develop species-specific social behaviour. The rearing environment of the AM males was either unknown or they lived in confined enclosures and were socially isolated. It is known that social deprivation results in altered emotional and behavioural regulation (Sanchez et al. 2001), impaired recognition of social signals (Kempes et al. 2008), and increased aggression (Mineka and Suomi 1978; Kempes et al. 2008). Therefore, the differences in rearing environment may partly explain the differences in observed social behaviour between AM and MS males.

Considering the results of the current study and the fact that in the wild, male hamadryas baboons never live completely solitarily but remain in the vicinity of clan members (Abegglen 1984), social housing is preferable to solitary housing. The establishment of all-male groups of hamadryas baboons in captivity can be a feasible strategy in terms of welfare on a temporary basis; however, the long-term stability of all-male groups remains to be explored in future research.

Comparison of intact versus castrated males in an all-male group

In domestic animals castration is commonly used to control sexual and aggressive behaviour (Bouissou 1983) and in several primates testosterone and aggressive behaviour are linked (e.g. Cavigelli and Pereira 2000; Muller and Wrangham 2004). In the present study castrated AM males showed less chasing and lunging than intact AM males. Additionally, castrated AM males displayed more submissive behaviour than intact AM males. This pattern suggests a lower hierarchical position of castrated than intact males. A similar behavioural pattern has been found in Javan langurs (Dröscher and Waitt 2012) and rhesus macaques (Richards et al. 2009). Mazur (1976) suggests that an individual's degree of dominance behaviour (such as threatening and chasing) is correlated with testosterone in its attempt to achieve or maintain status over other animals in the group. Indeed, testosterone levels are positively correlated with the frequency of aggressive behaviour in male mammals (Anestis 2006; Book et al. 2001). However, in marmosets (*Callithrix jacchus*) development of aggressive behaviour may be most affected when males are castrated early in life (Dixson 1993). It is unknown at what age the baboons in the current study were castrated. Although testosterone appears to facilitate aggression, the effect of social factors and experience are often more prominent under stable social conditions than the influence of testosterone levels (Archer 1991; Rubinov and Schmidt 1996). Furthermore, the balance between cortisol and testosterone (Van Honk et al. 2010) as well as serotonin (Higley et al. 1996; Montoya et al. 2012) seem to be important neurobiological modulators of aggression. Thus, reducing testosterone levels by surgical castration does not unequivocally lead to less aggressive behaviour. Moreover, in ferrets (*Mustela putorius furo*) chemical castration with the GnRH agonist deslorelin had more effect on the reduction of aggression that surgical castration (Vinke et al. 2008), possibly triggered by the GnRH agonist decreasing plasma oestradiol level, which is also involved in aggression (Trainor et al. 2006). Likewise, deslorelin reduced aggression in lion-tailed macaques (*Macaca silenus*; Norton et al. 2000). The effect of chemical castration, using a GnRH agonist, as a management tool for reducing aggression in male hamadryas baboons could therefore be explored further.

Our results for affiliative behaviour, showed that castrated AM males touched a group member more frequently and spent more time on social play than intact AM males. Similarly, an increase in play behaviour after surgical castration was observed in ferrets (Vinke et al. 2008). The authors suggested that lower plasma testosterone levels lead to less dominant behaviour and less agonistic interactions, thus less stressful (competitive) conditions, resulting in more play behaviour, as this is often seen under relaxed non-stressful conditions. The same mechanism could apply to the all-male group of hamadryas baboons in the current study; by displaying submission, castrated males may have helped to minimise the chance of agonistic interactions, resulting in a tranquil atmosphere facilitating play behaviour.

Altogether, these results suggest that castration may affect the social dominance of male hamadryas baboons, making them lower ranking than intact males. This could aid in the social compatibility of an all-male group of hamadryas baboons.

Conclusion

Intact male hamadryas baboons in an all-male group showed fairly similar social behavioural profiles to intact males in a mixed-sex group: agonistic behaviours were rare, but affiliative behaviours were also infrequent. Therefore, the formation of an all-male group is a feasible management tool in housing surplus male hamadryas baboon. Castrated individuals are more submissive and thus could contribute positively to the social stability of all-male groups, but this needs further exploration. Although in the current study agonistic interactions were rare, the additional effect of chemical castration with a GnRH agonist on agonistic behaviour as compared to surgical castration should be further explored as management tool.

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