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Applied Animal Behaviour Science xxx (2004) xxx–xxx
APPLIED ANIMAL BEHAVIOUR SCIENCE
www.elsevier.com/locate/applanim

Welfare implications of captive primate population management: behavioural and psycho-social effects of female-based contraception, oestrus and male removal in hamadryas baboons (*Papio hamadryas*)

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Abstract

In response to over-population, management actions were taken over a 5-year period to reduce group size and slow the population growth rate of hamadryas baboons at Paignton Zoo Environmental Park. Management involved three planned removals of several individuals and implantation of all adult females with Norplant®, a long-acting contraceptive, expected to be effective for 2–3 years. Possible psycho-social effects of these management strategies were monitored in adult males and females using the rate of occurrence of self-directed behaviour (SDB). SDB was more frequent in males than in females, and in both sexes was significantly more frequent in situations where greater social tension was expected. SDB rates were significantly correlated with overall group size, indicating that the managed reduction in group size was beneficial for the welfare of the remaining group members. Female agonistic interactions were significantly more frequent when they or another female in the harem were in oestrus. However, there was no detectable increase in the rate of SDB of males or females as a result of the contraceptive implants. Despite previous work showing that (a) Norplant® does not stop normal physical and behavioural signs of oestrus and (b) that female

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0168-1591/$ – see front matter
doi:10.1016/j.applanim.2004.08.014

hamadryas baboons in oestrus tend to become more aggressive, our results suggest that implantation with Norplant® did not cause a substantial increase in social tension in the group as a whole. However, a small effect could have been masked by the simultaneous and greater effects of changing group size.

Keywords: Aggression; Captivity; Displacement behaviour; Oestrus; Self-directed behaviour

1. Introduction

Most modern zoos include conservation of animals as one of their main objectives, whether through the breeding of animals for planned reintroduction or the maintenance of genetically healthy captive populations as a safety-net against future catastrophe in the wild (IUDZG and CBSG, 1993). For many species excellent modern husbandry conditions can result in captive populations outgrowing the space available for them. In these cases, where reintroduction to the wild is not feasible or supported, population control is required to prevent overcrowding and associated detrimental effects on animal welfare. Culling of surplus animals and surgical sterilisation, although effective methods of population control, can be controversial. Therefore, long-acting, chemical contraceptive implants are often preferred and have been used effectively in a wide range of non-human primates and other mammal species in zoos (e.g. Porton et al., 1990). They have a number of perceived advantages including ease of use, effectiveness, reversibility and no need to separate established social groups or impose other behavioural restrictions. However, numerous behavioural and physical effects of chemical contraception, potentially detrimental to animal welfare, have been reported in a variety of species (e.g. Steklis et al., 1982; Miceli and Fleming, 1983; Linn and Steklis, 1990; Portugal and Asa, 1995; Bettinger et al., 1997). The physical and behavioural effects of contraceptive implants, as well as culling and surgical sterilisation, should therefore be monitored carefully.

In December 1998 the baboon group at Paignton Zoo Environmental Park had grown to 83 animals in an enclosure designed for 40–50. A long-term managed reduction in group size was implemented beginning with the culling of 20 juvenile and sub-adult males and the implantation of all adult females (25) with the contraceptive Norplant® (The Population Council, 1990) in January 1999. In November 2000 a further 25 individuals, comprising a whole one-male unit and additional juvenile males were transferred to Singapore Zoo. In April 2003, a one-male unit of 12 individuals was transferred to South Lakes Wildlife Park.

Norplant® is a long-acting, reversible contraceptive whose active ingredient is levonorgestrel (LNG), a synthetic progestin with progesterone-like activity. It is inserted sub-dermally as silastic capsules from which LNG is released continuously into the bloodstream at a relatively constant rate. A blood level of LNG sufficient to prevent pregnancy is reached within 8–24 h after insertion (Croxatto, 1993). Norplant® prevents pregnancy by a combination of mechanisms including: inhibition of ovulation in about 50% of menstrual cycles (Bettinger et al., 1997), thickening of the cervical mucus making it impermeable to sperm (McIntosh et al., 1995) and thinning of the uterine lining making implantation less likely. Normal physical and behavioural signs of oestrus are not eliminated, but effective contraception will still occur (Greenwood, 1993). Norplant® has been used successfully in other non-human primates (Asa et al., 1996; Bettinger et al., 1997) and in hamadryas baboons it was expected to have an effective life of 2–3 years and be fully reversible.

In the wild state, hamadryas baboon females ordinarily undergo no more than a few successive oestrous cycles before conceiving (Portugal and Asa, 1995). Records of the group at Paignton Zoo show that females typically undergo 1–3 cycles (mean = 2.3) between weaning and conception. It was expected that implantation with Norplant® would result in a population containing an unusually high proportion of females in oestrus at any one time. Females' social interactions are mostly confined to within their one-male unit (or harem), within which the unrelated adult females form a linear dominance hierarchy (Sigg, 1980). Female interactions are particularly influenced by oestrous state (Kummer and Kurt, 1965; Sigg, 1980); oestrous females may temporarily leap-frog in status, becoming the alpha female within the harem for the short period that they are in tumescence (Kummer and Kurt, 1965). At this time they tend to be more aggressive and receive greater attention from the harem leader (Kummer and Kurt, 1965). In addition, the size of a female's perineal swelling increases with successive cycles and therefore may act as a superstimulus to males who, over time, might become increasingly interested in these females (Portugal and Asa, 1995). With females continuing to exhibit monthly signs of oestrus following implantation, the stability of the hierarchy may be disrupted more often than is normal, and aggression and other agonistic interactions between females might therefore be expected to increase. However, previous contraceptive attempts in hamadryas baboons did not result in substantial effects on behaviour, with normal social structure and interactions being maintained (Biquand et al., 1994; Portugal and Asa, 1995). This is not surprising in one case where the contraceptive used was melengestrol acetate (MGA), which eliminates physical and behavioural signs of oestrus (Portugal and Asa, 1995). However, the other case involved male vasectomy after which females continue to cycle regularly (Biquand et al., 1994); but these animals were free-living and may have had opportunities to alleviate increased tension and aggression not available to a captive group.

There is strong behavioural and pharmocological evidence that self-directed behaviour (SDB), such as scratching, autogrooming, yawning and body shaking, is a good indicator of anxiety or stress in non-human primates (Maestripieri et al., 1992), including baboons (Castles et al., 1999). Thus, we monitored the occurrence of SDB before, during and after the implementation of population management measures to assess their possible effects on psycho-social stress in the group. Additionally, detailed observations were made on the social interactions of implanted females for 1 year during which the implants were anticipated to be active. The aims of the study were to:

(1) Evaluate the behavioural welfare effects of population management actions for this group.
(2) Investigate the effects of oestrus on female social behaviour.

2. Methods

2.1. Subjects and housing

Adult study subjects were selected from a captive group of hamadryas baboons held at Paignton Zoo Environmental Park. Due to deaths, transfers and the maturation of young individuals, it was not possible to sample the same study animals throughout the study period, but two males and two females, were present and included in all sampling periods. Group size was variable over the 5-year study period, with a maximum 83 (December 1998) and minimum 46 (November 2000).

The group was held in a large outdoor enclosure (approximately 35 m × 15 m), known as Baboon Rock, consisting of an artificial rocky mountain (13 m high) surrounded by a deep dry moat (3 m deep). The baboons had free access to the rock and adjoining off-show house (approximately 3 m × 3 m × 3 m) throughout the day and night, except for approximately two and a half hours in the morning when they were confined to a further adjoining off-show cage enclosure (approximately 4 m × 8 m) whilst the rock was cleaned. The baboons were given a small feed at 08:00 in the cage, their main feed on returning to the rock at approximately 10:30, and another smaller feed on the rock at approximately 16:00.

2.2. Norplant® implantation

All 25 adult females present in the group were implanted with Norplant® in January 1999. Two 70-mg capsules were implanted subcutaneously between the scapulae. The process was completed harem by harem as quickly as possible so that females were isolated from their harem leader for a maximum of 15 min, and all implants were completed in one morning.

2.3. Self-directed behaviour

All the adult males (between 5 and 10) and a random subset (between 6 and 11 depending on available time) of the adult females (stratified to ensure a representative inclusion of ages and harems) were studied. Each individual was observed using continuous focal sampling for five 30 min sessions in the cage and five 30 min sessions on the rock in each of three sample periods per year (autumn, winter and summer) for 5 years, beginning in autumn 1998. This resulted in a total of 15 h of observation per individual per year. Observations avoided feeding times and took place between 08:30 and 10:30 (cage) and between 11:30 and 16:00 (rock). All occurrences of SDB (Table 1) were recorded within these observation periods.

Mean total rates of SDB for adult males and females within each sample period and location ($n = 30$, 15 periods × 2 locations) were compared using a matched pairs t-test. Due to the differing treatments of males and females, data for subsequent statistical analyses were treated separately. Analyses were performed on the mean total rate of all SDB per hour of each individual in each collection period (i.e. n = 5–10 for males and 6–11 for females). For each sex a three-way ANOVA was performed with year (1–5), season

Table 1
Types of self-directed behaviour and social interactions recorded in captive hamadryas baboons at Paignton Zoo Environmental Park (adapted from Schino et al., 1988; Kummer et al., 1974)

Self-directed behaviour	Description
Scratch	Movement (usually repeated) of the hand or foot during which the digits are drawn across the fur or skin. Scored as individual events
Autogroom	Picking through and/or slowly brushing aside fur with one or both hands. Brief self-touching was included here and includes wiping eyes, inspecting feet and placing hand to mouth. Scored as bouts of undefined duration separated by at least 5 s or a switch to another class of SDB
Yawn	Brief gaping movement of the mouth. Not recorded as SDB if accompanied by other aggressive signals (e.g. eye-flash, canine whetting)
Body shake	A shaking movement of the whole body. Scored as individual events
Nose wipe	Brief circular movement of hand at end of nose
Interactions	Includes
Affiliative	Allogroom, lip smack, comfort grunt, embrace/cuddle
Agonistic (towards others)	Stare with protruding head, eyebrow raise, open mouth pumping cheeks, shoulder or neck bite, aggressive scream, chase
Agonistic (from others)	Fear grin, submissive scream, crouch limbs bent, presentation of rear, flee

(autumn, winter and summer) and location (cage and rock) as fixed main factors (SPSS for windows 11.0). All interaction terms were included and Type III sums of squares used. Scheffé's test was used as the most conservative method for post-hoc comparison. Pearson correlations were performed to investigate the relationships between SDB rate and total group size and number of adult males.

2.4. Female interactions

All adult females in the group (24) were observed once each for 30 min in each season (as above) for 1 year starting in autumn 1999 (nine months after implantation) and all interactions recorded (Table 1). Interactions were classified into affiliative or agonistic (Table 1) and the interaction partner and her oestrous state (if female) were recorded. Since the contraception was not completely effective, some females were pregnant, some were lactating and some were cycling regularly. Chi squared tests were used to examine the relationship between the oestrous state of the focal female, the oestrous states of other females in the same one-male unit and the nature of social interactions.

3. Results

3.1. Self-directed behaviour

Total SDB rates were greater in males than in females ($t_{[29]} = 5.18$, $p < 0.001$) and differed significantly within each sex between the 15 sample periods (Fig. 1). There was a clearly significant effect of location, with higher rates of SDB in the smaller cage enclosure (Table 2). Year, season and the interaction of year × season also had significant

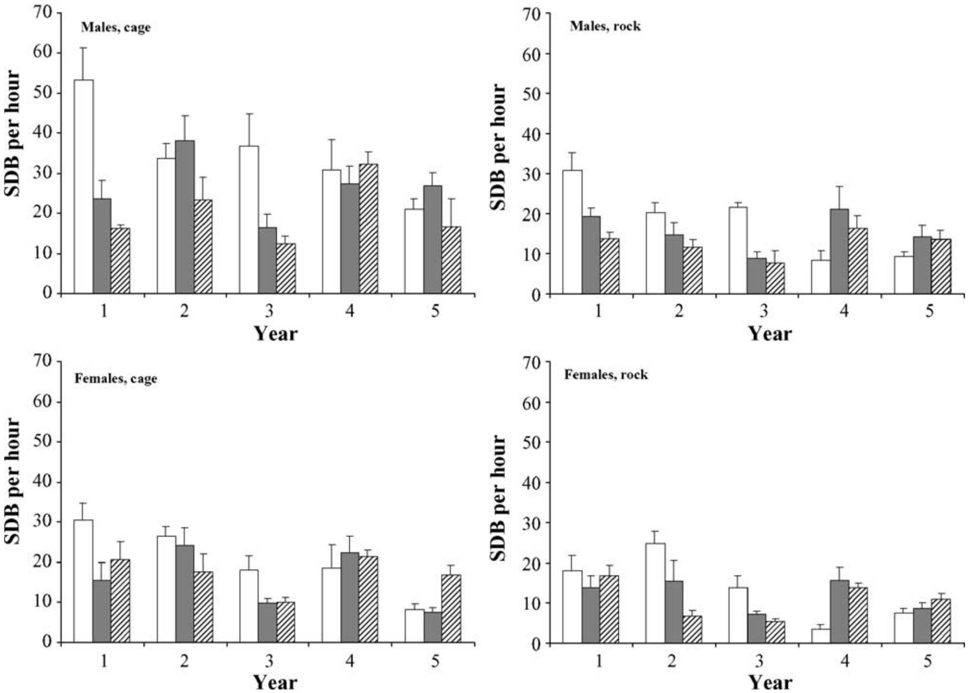

Fig. 1. Mean rate per hour of total self-directed behaviour in captive adult male and female hamadryas baboons when held in a smaller ‘cage’ enclosure and a larger ‘rock’ enclosure during three seasons (autumn [open bars], winter [solid bars] and summer [hashed bars]) in each of 5 years starting in autumn 1998. Error bars are standard error. Immediately prior to winter year 1 all 25 adult females were implanted with a contraceptive expected to be effective for 2–3 years. Initial group size was 82; 20 juvenile males were removed between autumn and winter in year 1; 25 animals including an entire one male-unit plus additional juveniles were removed between autumn and winter in year 3; a one-male unit of 12 animals was removed between winter and summer in year 5.

effects on SDB rate in both sexes (Table 2). Overall SDB rates were higher in years 1, 2 and 4 than in years 3 and 5. In general rates were higher in autumn than in winter or summer but this effect was much more marked in years 1 and 3. The rate of SDB of males and females in the cage and on the rock were all significantly correlated with the total number of individuals in the group, but not with the number of adult males (Table 3).

3.2. Female interactions

Although all females were observed, only the data from those who were regularly coming into oestrus (13) were analysed. The contraceptive was not as effective as hoped, and 10 of the females were either pregnant or lactating during this period (another one was anoestrous). A total of 1162 social interactions of regularly cycling females were observed (Table 4). Of these the majority (679) were interactions with the male harem leader, most of which were affiliative (569), mainly allogrooming. All agonistic interactions involving the

Table 2
Three way ANOVAs and Scheffé post-hoc tests on rates of self-directed behaviour in captive, adult male and female hamadryas baboons

Source	SS	MS	Df	F
Males				
Year	2605	651	4	4.60***
Season	3328	1664	2	11.74***
Location	9625	9625	1	67.91***
Year × season	8148	1018	8	7.20***
Year × location	470	117	4	0.83 ns
Season × location	623	312	2	2.20 ns
Year × season × location	1494	187	8	1.32 ns
Error	31040	141	219	
Females				
Year	4406	1101	4	15.49***
Season	511	256	2	3.60*
Location	2278	2278	1	32.06***
Year × season	3487	436	8	6.13***
Year × location	534	133	4	1.88 ns
Season × location	155	78	2	1.09 ns
Year × season × location	627	78	8	1.10 ns
Error	17988	71	253	
Scheffé post-hoc				
Males	Year 1 > Year 3*		Autumn > winter = summer**	
Females	Year 1 = Year 2 = Year 4 > Year 3 = Year 5*		Autumn > winter = summer*	

The three fixed factors were year (1–5), season (autumn, winter and summer) and location (smaller cage and larger rock enclosures), ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

male consisted of aggression directed from the male to the female, and were significantly more common when both the focal female and another female in the harem were in oestrus ($\chi^2_{[3]} = 101.8$, $p < 0.001$). There were 288 interactions with other adult females in the harem of which 93 were agonistic (Table 4). Agonistic interactions with females were significantly more common when another female but not the focal female was in oestrus ($\chi^2_{[3]} = 43.5$, $p < 0.001$) and these were all instances of aggression by the focal female directed at the oestrous female.

Table 3
Pearson correlations between rates of self-directed behaviour and the number of adult males and the total number of individuals in a captive group of hamadryas baboons over 15 sample periods spanning 5 years

Self-directed behaviour by	Number of adult males	Total group size
Adult males in the smaller cage enclosure	r = 0.36 ns	r = 0.71**
Adult males in the larger rock enclosure	r = 0.33 ns	r = 0.76**
Adult females in the smaller cage enclosure	r = 0.38 ns	r = 0.62**
Adult females in the larger rock enclosure	r = 0.15 ns	r = 0.62**

ns = not significant, ** = $p < 0.01$.

Table 4
Social interactions of regularly cycling females (following implantation with long-acting contraceptive) in a captive group of hamadryas baboons during four conditions: when no females in the harem were in oestrus, when the focal female only was in oestrus, when the focal female was not in oestrus but another female in the harem was and when the focal female and another female in the harem were in oestrus

Interaction	No female in oestrus	Focal female only in oestrus	Other female in oestrus	Focal and other female in oestrus	Total
Affiliative with male	140 (117.3)	189 (163.4)	16 (18.4)	224 (269.8)	569
Agonistic with male	0 (22.7)	6 (31.6)	6 (3.6)	98 (52.2)	110
Total with male	140	195	22	322	679
Affiliative with adult female	105 (86.0)	14 (15.6)	0 (8.8)	76 (84.7)	195
Agonistic with adult female	22 (41.0)	9 (7.4)	13 (4.2)	49 (40.4)	93
Total with adult female	147	23	13	125	288
Total with juvenile	69	34	28	64	195
Grand total	336	252	63	511	1162

Numbers in brackets are expected frequencies for chi-squared tests.

4. Discussion

The Norplant® implants were not as successful as hoped and pregnancy was prevented for more than a few months in only 54% of females (Plowman, 2002). Since the dose administered prevents pregnancy in much larger species for a longer period (e.g. humans, The Population Council, 1990) this suggests that there may have been substantial implant loss due to a tendency to groom at the implant site. Indeed, we believe we observed this in one case although regular checking for the presence of implants was not possible. However, during the period of the study on female interactions (autumn 1999–summer 2000) there were 13 regularly cycling females coming into oestrus approximately every 30 days for the whole year. In common with previous researchers we found a higher rate of agonistic interactions when at least one female in a harem was in oestrus (Kummer and Kurt, 1963; Sigg, 1980). This was mainly due to increased instances of aggression towards females in oestrus by females not in oestrus, and by increased aggression from the male harem leader towards oestrous females, particularly when more than one female in the harem was in oestrus at the same time. Oestrous females will attempt copulation with sub-adult and juvenile males but rarely with other harem leaders. Although these extra-pair copulations rarely result in conception they are ‘punished’ by the harem leader with neck-biting and increased aggressive herding behaviour (Kummer and Kurt, 1965). This may be more likely if more than one female in the harem is in oestrus, since there would be greater opportunity for females to escape their male’s attention for long enough to attempt extra-pair copulation.

The 13 regularly cycling females observed between autumn 1999 and summer 2000 had undergone at least 16 consecutive cycles by the end of this period. Subsequently, between 2001 and 2004, 11 of these females have become pregnant and given birth at least once. Thus, it is assumed that the implants were still present and effective in at least these 11 females during the study period. Therefore, Norplant® implantation did result in more females being in oestrus at any one time, although not as greatly as anticipated if it had been successful in all females.

In addition to being smaller than the rock, the cage enclosure provided no opportunity for visual avoidance, which may be an important tension-reduction strategy (Kummer, 1995). In contrast, the rock enclosure had many visual barriers including the rock itself and numerous tunnels, caves and other features. Therefore, it was anticipated that restriction of the baboons to the cage during cleaning times would be likely to result in increased social tension. As expected SDB rates, in both male and females, were greater at this time. Thus, for this group of hamadryas baboons, as for many other primates (e.g. Schino et al., 1988; Maestripieri et al., 1992) SDB appears to be a good indicator of psycho-social stress.

SDB rates decreased with decreasing overall numbers in the group as a result of population management actions. Although the decrease was not smooth, the overall trend in group size was downwards from 83 in the autumn of year 1, to 50 in the summer of year 5, with a corresponding decrease in the number of adult males from 10 to 5. SDB rates correlated strongly with group size but, perhaps surprisingly, not with the number of adult males. This suggests that competition between adult males is not the major source of social tension in this species, despite the fact that SDB rates of males are clearly higher than those of females. A main source of social tension and anxiety for males is maintaining their harem, whereas for females it appears to be the herding behaviour of the males. Juvenile and sub-adult (rather than adult) males are most threatening to an established harem (Kummer and Kurt, 1965; Kummer et al., 1974). Since most of the major changes in this group over this period involved a significant reduction in the number of juvenile males this could explain the greater correlation of SDB rates with overall group size rather then number of adult males. Overall, these SDB results appear to confirm that the managed reduction of group size has reduced tension and thus promoted enhanced welfare in the group.

There were significant differences in the rates of SDB in both males and females between the 15 sample periods. Although it is difficult to separate the effects of more than one management strategy deployed simultaneously, if the contraception had affected SDB rates we would have expected the period from winter in year 1 to autumn in year 3 (and possibly through to autumn in year 4) to have differed from other periods. However, this was not the case suggesting that Norplant® contraception did not substantially affect social tension in the whole group, despite more females repeatedly coming into oestrus. Rather, rates of SDB were significantly correlated with total group size, and the significant effects of year, season and the year $\times$ season interaction could be explained by group changes at certain times. There was an overall significant effect of season, which indeed may be partly real, due to a large amount of time ‘sunbathing’ in summer resulting in less social interaction altogether and, therefore, less tension. However, the seasonal effect was particularly strong in years 1 and 3 when there was clearly a higher rate of SDB in autumn than in winter or summer. Therefore, it seems likely that a large part of the apparent seasonal effect was in fact due to two major group changes in these years: the removal of 20 juvenile males between autumn and winter in year 1 and a further removal of 25 individuals comprising a complete one-male unit plus additional juvenile males between autumn and winter in year 3. As a result, far fewer individuals were present in the winter and summer samples than in the autumn samples of these years.

5. Conclusions

1. SDB rates decreased with group size, particularly following the removal of large numbers of juvenile and sub-adult males, indicating that this management strategy was beneficial for the welfare of the remaining group members.
2. When in oestrus, female hamadryas baboons were involved in a greater number of agonistic interactions with other females and with their male harem leader than during their non-oestrous periods.
3. Successfully contracepted females underwent more consecutive oestrous cycles than normal, resulting in more females being in oestrus at any one time as a result of the contraceptive.
4. Despite 2. and 3. above, there was no detectable effect on the level of social stress in the group as a whole during the expected duration of effectiveness of the contraceptive, suggesting that Norplant® does not have substantial negative effects on welfare in this species. However, the implants may have been lost or were otherwise ineffective in almost half the females and small effects may have been masked by the greater influence of simultaneous changes in group size. This conclusion should therefore be regarded as preliminary.
5. Self-directed behaviour (SDB) was more frequent in situations of supposed increased social tension (small enclosure with no visual barriers) further supporting that it is a reliable indicator of psycho-social stress in hamadryas baboons.

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