GROUP FORMATION AND BEHAVIOURAL CHANGES WITH RELEASE TO FREE-RANGING IN RED RUFFED LEMURS, *VARECIA VARIEGATA RUBRA*

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Abstract

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The social behaviour, ranging, and stereotypic behaviours of four red ruffed lemurs (one female, three males) was observed during group formation and release into a 2.25ha natural habitat enclosure at the Duke University Primate Center (DUPC). The female was immediately dominant to all males and there was no female-male affiliation during the initial stages of group formation. The group became identifiable as a unit after release to free-ranging when affiliation and group vocalizations began. Affiliation and vocalizations continued during subsequent recagings. Male dominance rank reflected relative age, but was subject to reversals. The stresses involved in release and group formation, however, can temporarily produce new aberrant behaviours which are soon replaced by normal behaviours. Once released into the large enclosure, stereotypic behaviours became infrequent but did not disappear. Other novel behaviours such as catatonic huddle and all male huddles were observed during release. Natural habitat enclosures can be important tools in the psychological well-being of captive primates.

Key words: *animal welfare, free-ranging, group formation, psychological well-being, Varecia*

Introduction

The red ruffed lemur (*Varecia variegata rubra*) from the Masoala peninsula of Madagascar remains poorly studied (Petter *et al* 1977, Tattersall 1982, Simons & Lindsay 1987). Little or nothing is known of the social organization of this subspecies although *it is assumed to be similar to the* black-and-white ruffed lemur (*Varecia variegata variegata*) in behaviour and ecology. Black-and-white ruffed lemurs are frugivorous and occupy the highest levels of the forest canopy (Tattersall 1982, White 1989, Morland 1990). Ruffed lemur organization appears to be highly variable, ranging from a male-female pair with immature offspring to loosely cohesive groups that can contain more than one adult male and female (Klopfer & Dugard 1976, Petter *et al* 1977, Kress

et al 1978, Klopfer & Boskoff 1979, Foerg 1982, Pereira *et al* 1987, 1988, Morland 1990, 1991, Tattersall 1982, White 1991, White *et al* 1992).

This paper presents the results of the first release of red ruffed lemurs to free-ranging in a 2.25ha forested enclosure at the Duke University Primate Center. The social group was formed shortly before the release from individuals previously housed in outdoor cages. Two individuals in the new group had shown stereotypic behaviours in their original cages for years. This study, therefore, also allowed the assessment of the impact of free-ranging and novel social situations on stereotypic behaviours as indicators of psychological well-being.

The psychological well-being of captive primates is important to the captive management of primates (Animal Welfare Act Amended 1985, Segal 1989 and references therein). Studies of psychological well-being have focused on the impact of variables such as cage size and cage complexity, group structure, and environmental enrichment. Most studies have, however, focused on anthropoids used in laboratory research so that prosimians have remained relatively unstudied.

At the Duke University Primate Center (DUPC) many of the prosimians are maintained for captive conservation and research in outdoor runs and forested enclosures. Forested enclosures are used as they allow the establishment of social groups of prosimians that are comparable in size and composition to those observed in the wild. The enclosures also promote the expression of many, if not all, of the normal behaviours and survival skills of wild prosimians. Individuals born and raised in such settings are excellent candidates for re-introduction into the wild. The environmental and social complexity possible under these captive conditions, therefore, has important impacts on prosimian behaviour and reproduction (Simons 1986, Macedonia 1987, Pereira *et al* 1989) and as a result welfare.

The present paper examines the changes in indicators of psychological well-being of the red ruffed lemurs during new group formation and release into a natural habitat enclosure.

Methods

The study group consisted of three adult males (NO born 1980 and NO's adult sons AC born 1984 and UR born 1985) and an unrelated female (HI born 1981). The males were originally housed together in a wire cage. HI was originally housed with three of her offspring and an adult male. On 18 October 1989, the ruffed lemurs were placed in adjacent cages (female one side, male and his offspring on the other) inside the enclosure. For the next three days a wire partition separated the males and the female. The partition was then opened. On 25 October 1989, the new group was released into the enclosure. Due to cold weather, the animals were brought back into the outdoor run on several occasions following the initial release (November 16 to 20, November 23 to 26, November 30 to December 4, January 3 to 7 1990, and January 12 to 23).

The behaviours observed in this study group of *Varecia variegata rubra* were compared to the ethogram described for *Varecia variegata variegata* by Pereira *et al* (1988). Agonistic and affiliative behaviours and vocalizations are described in this ethogram.

This study was divided into five phases (with hours of observation):

Phase 1: in original cages before group formation (11 hours for males; 10 hours for female),

Phase 2: in the outdoor run with males and female separated with a wire partition (7 hours),

Phase 3: in the outdoor run with partition open (11 hours),

Phase 4: with access to the enclosure, divided into the first 11 days (31 hours), release from recaging during pre-oestrus (19 hours) and release post-oestrus (12 hours),

Phase 5: during 5 subsequent recaging events (7 hours), including recaging during oestrus (12 hours).

Phase 1. Original caging conditions

The original cage which housed the three males measured 3.7m x 4.0m x 3.4m. Both the sides and roof of the cage were constructed of wire and was bordered on three sides by cages containing groups of *Eulemur rubriventer* (red-bellied lemur), *Eulemur macaco* (black lemur), and *V. v. variegata* (black-and-white ruffed lemur). The males' cage contained a heated shelter box, a wooden shelf, a feeding shelf, a wire shelf formed by the door, several wooden poles and bars, and a rope.

The single female was originally housed in a wire silo measuring 4.9m in diameter, 6.1m from the ground to the top of the cylinder, and an additional 3.1m from the top of the cylinder to the peak of the conical top. The silo contained a feeding shelf, two shelter boxes, two trees and several poles.

Phases 2, 3, and 5. The outdoor run

The outdoor run was 0.9m x 3.4m x 2.1m high, enclosed by chain-link fence and separated into two sides. Each side had a connecting, but partitioned, shelter box, a feeding shelf, and a pole. The group was kept together except briefly for oestrus (approximately 4 hours) and the four subsequent days when NO and HI were recaged separately from the other males to ensure mating between this pair (following US Species Survival Plan recommendations). Observations during the oestrus recaging were only made while the group was together.

Phase 4. The natural habitat enclosure

The natural habitat enclosure was a 2.25ha area containing mixed hardwood and pine forest. The forest had continuous canopy between 15 and 25m and a dense understorey of shrubs and small trees up to 10m. The ground cover was thick and includes vines and

herbaceous plants. Visibility at ground level was limited by the vegetation. Several paths provided access for technicians and observers. The enclosure was surrounded by 1.8m chain-link fence with electric 'hot-wires' extending a further 1m in height. The fence was separated from the forest by a 10m cleared swath of grass. The enclosure contained two cages with shelter boxes, two pans of water, and several food dispensers for monkey chow. Two other primate groups in the enclosure when the group was released consisted of three *Propithecus verreauxi coquereli* (sifakas) and nine *Eulemur fulvus collaris* (collared lemurs). Indigenous animals in the enclosure included raccoons, rabbits, gray fox, squirrels, weasels, hawks, and great horned owls.

Sampling methods and statistical analysis

Observations occurred over a 120 hour period from September 27 1989 to February 7 1990. Sample periods consisted of four fifteen minute focal animal samples (Altmann 1974). All social interactions involving the focal animal were recorded at three minute time points. The focal animal's height from the ground, activity, and nearest neighbour were recorded. Cohesion was estimated as the average distance between all individuals and was recorded at each time point and classed as within 3m, 3 to 6m, or beyond 6m. Data on stereotypic behaviour by the focal animal and vocalizations were recorded as they occurred. A behaviour was classified as stereotypic if the movement pattern occurred in exactly the same manner more than two times in rapid succession. Data were subjected to Goodness of Fit and Tests of Independence G tests with Williams correction and simultaneous test procedure to identify all non-significant subsets (Sokal & Rohlf 1981). Expected rates of behaviour for Goodness of Fit tests were calculated from hours of observation for each phase and assuming equal rates.

Results

Group formation

During group formation there was no affiliation between female HI and any of the males whereas affiliation was observed among the males (Table 1a). Although the female was clearly dominant to the males (winning 9 of 13 interactions) from the first moment of introduction, there were four instances of aggression by UR to HI (Table 2a). If the hierarchy relationships were transitive, then the males dominance rank was in order of age. The first day the partition was open HI was highly aggressive to the males, especially to NO. Aggressive encounters consisted of stares, charges, cuffs, and push down motions. Submissive gestures from the males consisted of chattering, fleeing, and averting the head.

Table 1 Frequency of affiliative interactions during group formation (excluding male huddles).

a) Phase 3 (partition open: 11 hours of observation)

		Initiator				
		HI	NO	AC	UR	Total received
Receiver	HI	-	0	0	0	0
	NO	0	-	2	6	8
	AC	0	9	-	2	11
	UR	0	6	1	-	7
Total initiated		0	15	3	8	

b) Phase 4 including oestrus (in enclosure: 62 hours of observation)

		Initiator				
		HI	NO	AC	UR	Total received
Receiver	HI	-	9	19	7	35
	NO	7	-	20	27	54
	AC	12	8	-	13	33
	UR	10	31	9	-	50
Total initiated		29	48	48	47	

c) Phase 5. Interactions during oestrus shown in parentheses (7 hours of observation during recaging, 12 hours during oestrus)

		Initiator				
		HI	NO	AC	UR	Total received
Receiver	HI	-	1(4)	2(4)	1(2)	14
	NO	1(3)	-	4(0)	6(0)	14
	AC	1(2)	1(1)	-	1(1)	7
	UR	1(2)	1(1)	0(4)	-	9
Total initiated		10	9	14	11	

Table 2   **Frequency of agonistic interactions**
a) Phase 3 (partition open: 11 hours of observation)

Winner						
		HI	NO	AC	UR	Total lost
Loser	HI	-	0	0	4	4
	NO	30	-	0	0	30
	AC	7	1	-	0	8
	UR	9	0	2	-	11
Total won		45	1	2	4	

b) Phase 4 (in enclosure: 62 hours of observation)

Winner						
		HI	NO	AC	UR	Total lost
Loser	HI	-	0	0	0	0
	NO	3	-	11	0	14
	AC	7	9	-	0	16
	UR	7	1	0	-	8
Total won		17	10	11	0	

c) Phase 5. Interactions during oestrus shown in parentheses (7 hours of observation during recaging, 12 hours during oestrus)

Winner						
		HI	NO	AC	UR	Total lost
Loser	HI	-	0(0)	0(0)	0(0)	0(0)
	NO	0(16)	-	0(8)	0(0)	0(24)
	AC	0(0)	1(14)	-	0(12)	1(26)
	UR	0(0)	0(2)	0(0)	-	0(2)
Total won		0(16)	1(16)	0(8)	0(12)	

During the first day after group formation, HI moved over to the shelter box originally occupied by the males. The female aggressively excluded all the males from both this box and the now empty box that she had originally occupied. HI also aggressively prevented the males from entering her original side of the run. If the males moved out of the all male huddle (see below), HI chased them back into a huddle or swatted the male closest to her. By the third day HI's aggressive responses to movement by the males decreased and NO began to make frequent forays to the female's original side of the run. Over this three day period, the number of all male huddles decreased as HI's frequency of aggression decreased (Figure 1).
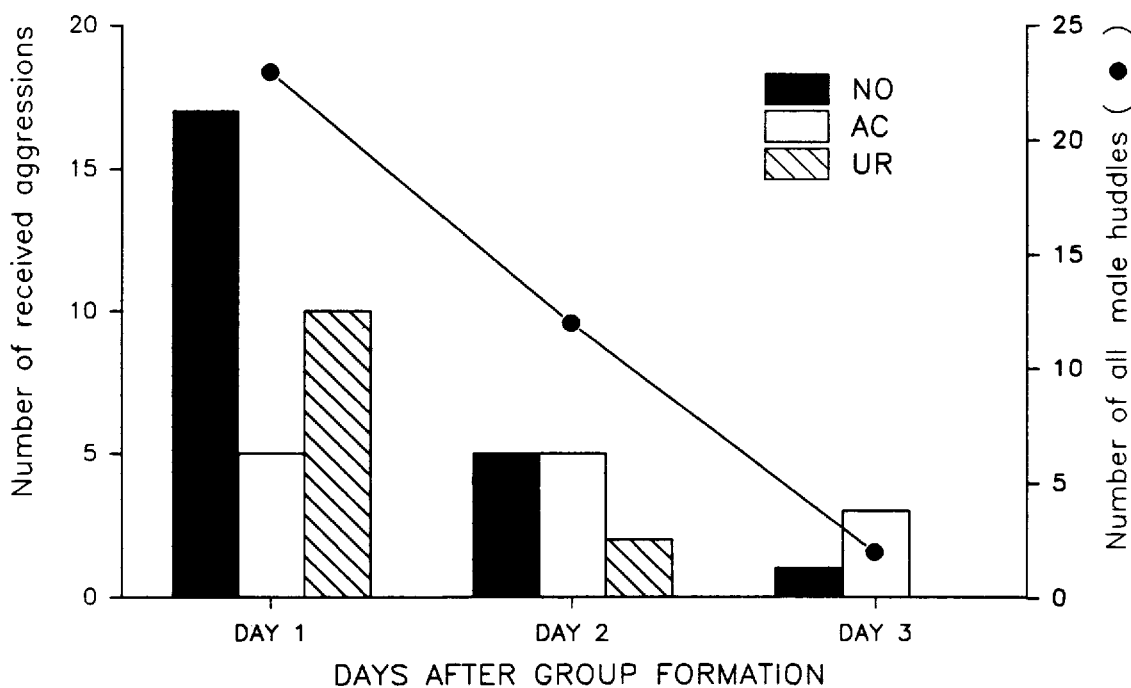
Figure 1   Frequency of aggression received from the female (left axis) and frequency of male huddles (right axis). Product moment correlation coefficient = 0.977, P<0.05

Ranging and interactions after release

The first movement by a group member in the initial release into the enclosure occurred when UR left the outdoor run and quickly travelled out of sight, to the west of the shelter box and returned within 30 minutes. For the remainder of that day, UR remained within 1m of the cage. NO was the first to climb a tree but also stayed within 1m of the cage. In the late afternoon, AC and HI both travelled about 20m from the cage. Then HI repeatedly moved after AC and AC chattered and retreated, often out of sight of the female. HI and AC moved out of sight of the outdoor run and the observer. HI was later found approximately one hour later in a catatonic huddle (see below).

One week after the initial release HI, AC, and UR travelled to the opposite end of the enclosure (approximately 177m). These three returned to the opposite end of the enclosure after each release from subsequent recaging. NO did not travel with them but was carried down by DUPC technicians to rejoin the group.

After release into the enclosure, affiliation was observed between HI and each male (Table 1b). Each male initiated more affiliative interactions than the female. Affiliative interactions also occurred during subsequent recagings. While free-ranging, HI remained dominant to all males. The dominance relationship between NO and his eldest son, AC, was subject to reversals (Table 2b), as was that between AC and UR.

Ruffed lemurs engage in loud male-female choruses (Pereira *et al* 1988). Vocalizations were rare when caged. Vocalizations by the group as a unit began on the second day after release into the enclosure. Frequencies of initialization of group vocalizations in each phase varied between individuals (Test of Independence G=39.632, P<0.001). Vocalizations by all individuals were significantly different than expected, based on the number of hours observed in each phase. AC initiated the most vocalizations in most phases of the release (Figure 2). Vocalizations continued during subsequent recagings but vocalization rates decreased during and after oestrus.
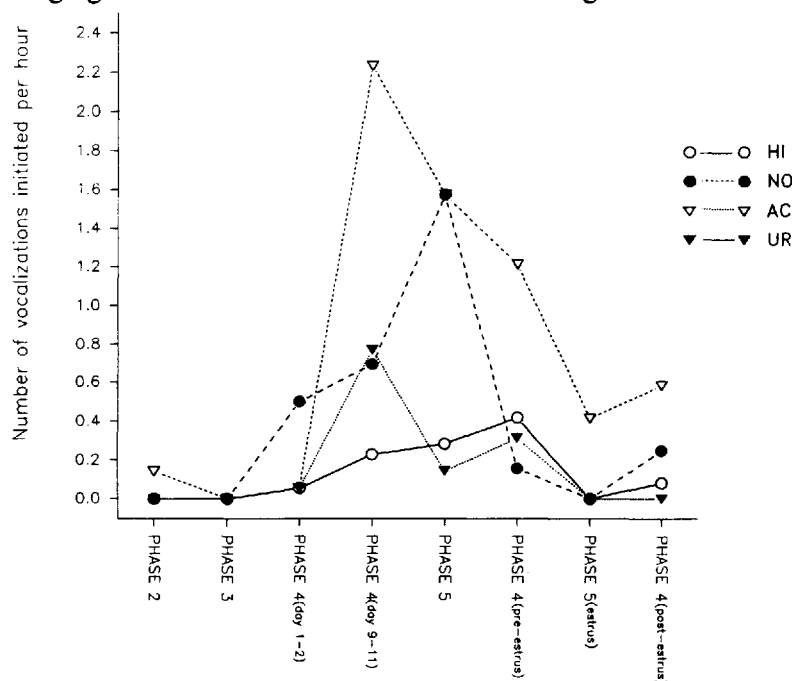

Figure 2   **Rates of initialization of group vocalizations for all group members. Vocalizations frequencies were significantly different to an expected based on equal rates and the number of hours observed in each phase (Goodness of Fit tests for HI, G=24.136, P<0.001; NO, G=23.541, P<0.001; AC, G=81.106, P<0.001; UR, G=34.090, P<0.001).**

226

Cohesion

The spacing of the individuals while free-ranging varied during phase 4 (G=51.571, P<0.05). The amount of time spent in the first two distance intervals (within 3m and 3 to 6m) formed the only non-significant subset across all free-ranging time periods (G=11.779, not significant).

The distance of the nearest neighbour to the focal animal varied between pre-oestrus release and post-oestrus release for NO and HI but not for AC and UR (Figure 3).
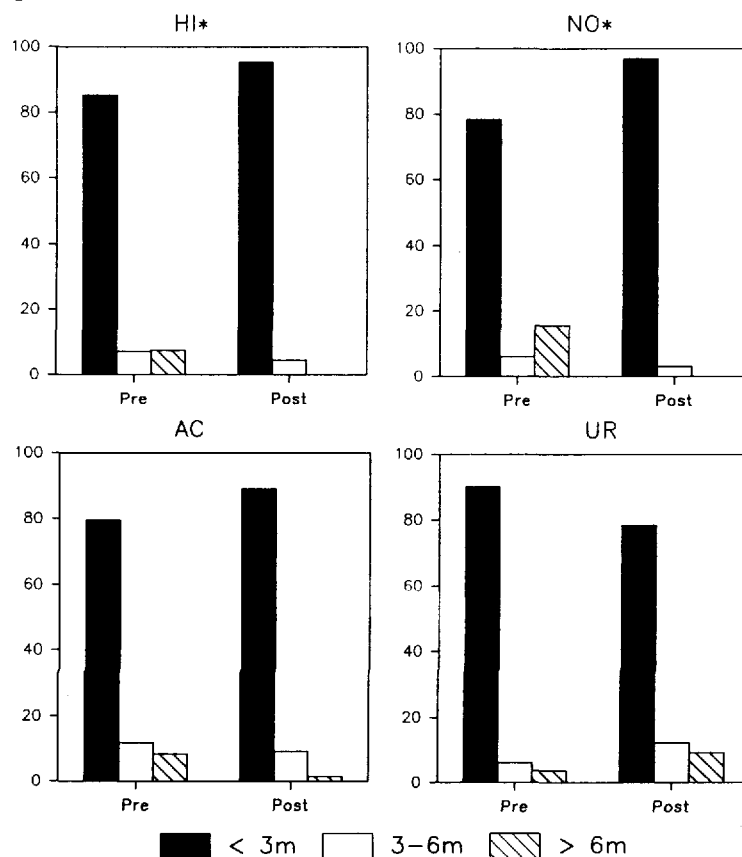

Figure 3   **Distance from focal animals to nearest neighbour for pre-oestrus and post-oestrus free-ranging periods (Test of independence HI, G=20.214, *P<0.05; NO, G=9.306, *P<0.05; AC, G=5.691, not significant; UR, G=5.227, not significant).**

Abnormal and stereotypic behaviours

Several abnormal behaviours were observed during group formation and when the animals were first released into the enclosure. Several individuals also showed stereotypic behaviours in the original cages as well as in later phases. The most frequent abnormal behaviours were male huddles and individual catatonic huddles.

a) All male huddles

Huddling is a frequent activity in many lemur species but is extremely rare in ruffed lemurs (three huddles, each involving only two individuals, during 70 hours of observation of black-and-white ruffed lemurs, Pereira *et al* 1988). No all male huddles were observed during Stages 1 and 2, but once the partition was opened for Phase 3, all male huddles were frequent. This huddling only occurred in Phase 3[1] and not during the cold (freezing) temperatures that resulted in recaging the lemurs (Phase 5). On the first day of Phase 3, the huddles consisted of all three males. During the next two days, most huddles consisted of AC and UR, with NO joining the huddle for brief periods. All huddles began when the female either directed aggression at one of the males or, more frequently, when the female looked directly at them or passed near their position. NO was frequently in front nearest to the female with AC and UR huddled behind him. One of the two sons frequently raised his head and gave submissive chatters to the female before resuming the head-tucked position (n=16 occurrences in 38 huddles). On the first day of Phase 3, the huddles involved all the males in tight physical contact. By the third and final day of Phase 3, the males sat very close to each other (within 1 cm) but without physical contact.

Once the outdoor run was opened for Phase 4 and the animals had access to the entire enclosure, only three huddles were observed. In each of these occurrences, the huddle consisted of the two younger males and the huddle lasted less than fifteen minutes. At no point was a huddle observed between a male and the female.

b) Individual catatonic huddles

Individual catatonic huddles were first observed in Phase 4. Within an hour after AC and HI first moved away from the outdoor run, HI was found on the ground slightly over 10m east of the cage with her eyes open but fixed on one spot. Over the next five hours, the female maintained a huddled position and her eyes did not move or blink in response to the presence of the observer or being thrown raisins. The female remained totally passive when picked up and returned to the outdoor run. The female then immediately defecated and entered the shelter box. Less than fifteen minutes later the female emerged to feed.

Twenty four hours later NO was found in the same tightly curled position with his eyes oriented on one spot. NO was also passive when returned to the outdoor run where he defecated and began to feed.

Six weeks after the initial release, NO was found huddled in a gully about half-way between the outdoor run and the location of the other three individuals at the far end of the enclosure. NO's posture was identical to previous catatonic huddles but he did not hold this position. Several minutes after observers stood near him, NO moved rapidly back to the run.

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[1] The high and low temperature during Phase 3 averaged 38°F for the low and 68°F for the high (National Weather Service at Raleigh-Durham Airport)

Stereotypic behaviours

Two forms of stereotypic locomotion were observed during Phase 1 in the animals' original cages (Figure 4). AC displayed a characteristic pacing behaviour on the wire shelf over the door. This was repeated a maximum of three times in a pacing bout and the maximum number of pacing bouts observed in an hour session was 11 with an average of 2.54.
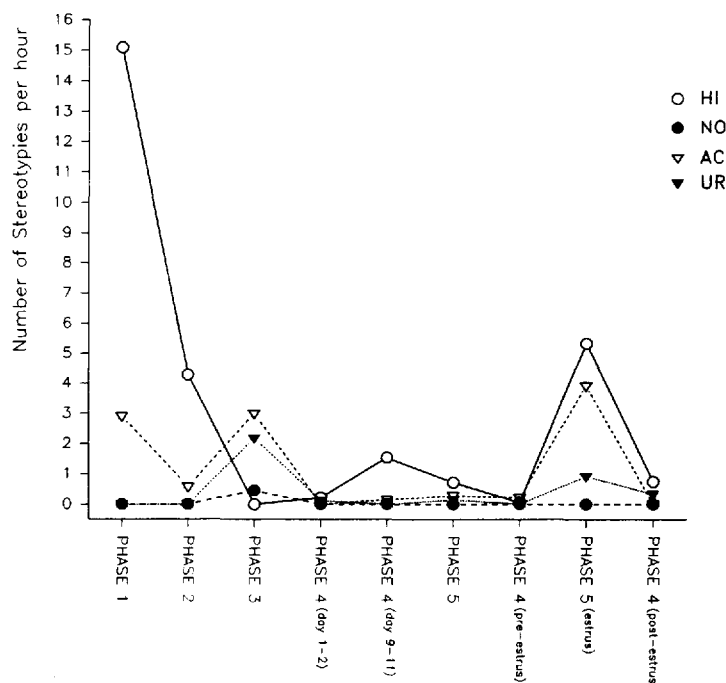

Figure 4   **Rates of stereotypic behaviours. Frequencies of stereotypic behaviours were significantly different to an expected based on equal rates and the number of hours observed on each phase (Goodness of Fit tests for HI, $G=515.213$, $P<0.001$; NO, $G=17.235$, $P<0.05$; AC, $G=172.201$, $P<0.001$; UR, $G=80.187$, $P<0.001$).**

During Phase 1, HI would repeatedly jump up and down while facing the wire of her cage. These jumping bouts were highly repetitive, frequently lasting for over 10 minutes. Interruptions between jumps were brief and infrequent and up to 30 bouts were recorded in an observation period.

During Phase 2, all three males were observed pacing. The female jumped only slightly when the partition was closed but this behaviour stopped in Phase 3 as soon as the partition was opened. During Phase 4, frequency of stereotypic behaviour by the female decreased further below the Phase 1 frequency. During Phase 5, the frequency

of jumps by the female was greater than in Phase 4. During Phase 4, only AC displayed any pacing and this level was still well below the Phase 1 frequency. During the subsequent recaging in Phase 5, UR resumed pacing when recaged between January 12 to 23. This period included the mating season. NO only paced in the outdoor run at the beginning of Phase 3.

Stereotypical behaviours for all individuals occurred at different rates in different phases (HI, G= 515.213, $P<0.001$; NO, G=17.235, $P<0.05$; AC, G=172.201, $P<0.001$; UR, G=80.187, $P<0.001$). Stereotypical behaviours were more frequent in Phases 1 and 2 for HI and AC, and decreased with release to free-ranging but did not increase during subsequent recaging except at oestrus.

Interspecific interactions

There were a total of 139 agonistic interactions between the *Varecia variegata rubra* and the *Eulemur fulvus collaris* in the enclosure. *P. v. coquereli* directed more aggression against the *Varecia* (against NO=1, UR=5, AC=11, and HI=1) than they received (from NO=0, UR=4, AC=1, and HI=0). *E. f. collaris* received more aggression from the *Varecia* (from NO=11, UR=2, AC=104, and HI=7) than they directed (against NO=0, UR=0, AC=2, and HI=0). AC was the most aggressive towards the *E. f. collaris*, whereas the other *Varecia* only started to aggress during the last days of the study.

Discussion

Due to the timing of events of group formation, release into a novel situation, and the onset of the breeding season it is not possible to ascribe any of the effects observed to any single factor. Any conclusions, therefore, about the effects of a particular factor remain tentative. In future studies, it may be possible to examine the effects of factors separately, and also to examine for potential interactions between factors.

The social organization of this free-ranging *Varecia variegata rubra* is similar to that described for *Varecia variegata variegata* (Pereira *et al* 1988). The female was clearly dominant to the males and there was a lower level of inter-individual cohesion than observed in other diurnal prosimians. It was noticeable that tight physical contact between the related males rapidly decreased to the point that physical contact was avoided. The frequent huddling by the males during the first three days was highly unusual and most likely a result of the stresses of group formation. Levels of cohesion among individuals are, however, slightly higher than described for the black-and-white subspecies, with 80 per cent of focal animal sampling being within 0 to 3 metres of the nearest neighbour in this study group compared to 50 per cent between 0 and 5 metres in the free-ranging *Varecia variegata variegata* (Pereira *et al* 1988). Cohesion levels for some individuals vary with time of year (White 1991, this study) as once HI and NO mated, their nearest neighbour distances decreased significantly whereas those of the unmated sons did not. The compositions of this study group and the *V. v. variegata* group, however, were markedly different and this may have affected the levels of cohesion observed among individuals.

Agonistic interactions among the males indicate that the relative dominance rank among the males was subject to reversals. If HI and NO had not been secluded for mating, NO might have lost his dominant position to his son AC. After mating, NO maintained his dominant position. It is interesting that there were no attempts by any male to forcibly evict or exclude either of the other males from the group. Among captive females, dominance rank between mothers and daughters reverses at or before maturity, with daughters coming to out-rank their mothers at two-years of age (White 1991). The same does not appear to be true of males as NO, despite his difficulties in adjusting to the environment, was able to maintain his dominant position during this study.

There was obvious competition among the related males for access to the female. It is interesting to note that subsequent to this study, when the female gave birth to a litter of three female infants, AC attacked an infant. The female was confined to the outdoor run and the males were free-ranging in the enclosure. AC managed to pull the arm of one of the litter through the narrow caging of the run and bit it severely enough to warrant amputation. This supports suggestions that infanticide by non-parental males may be a social strategy in ruffed lemurs (White *et al* in press).

There was no affiliation between the female and the males until all were released into the enclosure. This appears to mark the point of group formation since they started to vocalize as a unit and affiliation between the sexes continued when the group was recaged. Release, and the associated opportunities to escape from aggressive interactions can, therefore, help in the formation of groups under captive conditions.

Mating also greatly enhanced the ability of the least adjusted male, NO, to adapt to the free-ranging environment. NO displayed a catatonic huddle six weeks into the release and did not range as fully as other group members. Once released after mating, however, NO immediately ranged as fully as other group members and his cohesion with others, as reflected by the distribution of nearest neighbour distances, increased.

The catatonic huddle observed during the release has also been observed during releases of the black-and-white subspecies into an enclosure at the DUPC (Balko, personal communication). This catatonic posture appears to be analogous to the still posture assumed by *Varecia* infants when their mother leaves the nest to forage.

Stereotypic behaviours can be directly affected by space restrictions (Draper & Bernstein 1963, Paulk *et al* 1977). In the present study frequencies of stereotypic behaviours by AC did increase in the outdoor run, and the other two males displayed pacing behaviours for the first time when the partition was opened, but the female's stereotyped behaviours decreased, probably because of her interest in and aggression towards the males. Stereotypic behaviours were infrequent when the animals were in the large enclosure. When the group was recaged, stereotypic behaviours remained low, except during oestrus. Free-ranging may, therefore, be an important management tool in decreasing the frequencies of stereotypic behaviours.

Animal welfare implications

Natural habitat enclosures are important tools in the psychological well-being of captive primates. The stresses involved in release and group formation can, however, temporarily produce new aberrant behaviours. Normal behaviours, however, soon become apparent. After the social group was formed the stereotypic behaviours remained low during subsequent recagings except during the added stress of oestrus. Timing of the release relative to the breeding season was important in this case such that the male that showed the poorest adjustment rapidly adapted to the new environment and changed in behaviour from hesitant to assertive after mating.

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