

STABILITY OF BREEDING AND NON-BREEDING GROUPS OF GOLDEN-HEADED LION TAMARINS (*LEONTOPITHECUS CHRYSOMELAS*)

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Abstract

Animal Welfare 2003, **12**: 251-268

*In Callitrichid primates, offspring remain in their natal group beyond the age of sexual maturity, increasing the group's inclusive fitness by cooperatively rearing their siblings. Contraception of the dominant female in these groups may alter the associated costs and benefits of this cooperative rearing in such a way that offspring themselves attempt to breed when a period longer than the normal inter-birth interval of one year has elapsed. Contraception of the dominant female may also induce changes in socio-sexual interactions between group members, which can lead to increased aggression after a short period. In this study, we investigated the occurrence of aggression in 16 captive groups of golden-headed lion tamarins (*Leontopithecus chrysomelas*) under three conditions: 1) no contraception used; 2) contraception used and offspring younger than one year present within the group; and 3) contraception used and all offspring in the group older than one year. We found that the probability of aggression occurring in the groups was best predicted by logistic regression models containing the factors 'group size' and 'overall proportion of males' or 'number of sons'. Aggression was more likely in larger groups with a high proportion of males or a large number of sons. This effect was significantly stronger for groups in which all offspring were older than one year. Absence of dispersal opportunities and differences in male and female reproductive strategies may explain the observed patterns. The increased instability of large non-breeding groups presents a problem when using long-term contraceptive methods and should be taken into account when making decisions on the most suitable population-control procedures.*

Keywords: aggression, animal welfare, Callitrichids, contraception, golden-headed lion tamarins, population control

Introduction

In Callitrichid primates, many aspects of reproductive biology, social organisation and infant care patterns are closely linked. Because dispersal of Callitrichid offspring is delayed in the wild (as well as, enforcedly, in captivity), groups typically contain several immature and mature animals that do not themselves reproduce (Goldizen 1987; French 1997). There is usually only one breeding female, reproduction in other female group-members being suppressed either physiologically or behaviourally (eg Abbott 1984; French *et al* 1984;

French *et al* 1989; Pryce & Dettling 1995; Carlson *et al* 1997; French *et al* 2002). Twinning occurs frequently (except in *Callimico* [Altmann *et al* 1988]), and infants are cared for by all group members. By helping, Callitrichid offspring contribute to the survival of their siblings, thereby increasing their inclusive fitness (Goldizen 1987; Tardif 1997). At the same time, they gain experience in rearing infants, which increases their own chances of successful reproduction later in life (Goldizen 1987; Tardif 1997).

Given their high reproductive potential, Callitrichids in captivity are frequently prevented from reproducing by the use of various contraceptive methods (Sainsbury 1997; DeMatteo 1997; De Vleeschouwer *et al* 2000a). However, preventing reproduction in Callitrichid groups may have an impact on group stability and thus group structure for two reasons. First, treatment of the dominant female with contraceptive drugs causes changes in levels of reproductive hormones, behaviour, and socio-sexual interactions with other group members. These changes are apparent within the first two months after onset of contraceptive treatment (De Vleeschouwer *et al* 2000b). As well as inducing changes in hormone levels and behaviour, contraception may influence olfactory communication. Chemical signals are an important means of communication in Callitrichids, and scents secreted from specialised gland regions contain information on species identity, gender, individual identity, social status, and reproductive status of females (eg Epplé *et al* 1993; Washabaugh & Snowdon 1998; Ziegler *et al* 1993). Scents have a very complex chemical composition (Epplé *et al* 1993) and this composition may be altered by changes in the reproductive and/or social status of females. Contraception of the dominant female may thus result in altered patterns of olfactory communication, which may influence socio-sexual interactions between group members. Current evidence (De Vleeschouwer *et al* 2000b) suggests that the normal structure of groups — with one dominant pair and several subordinate offspring — is preserved, as reproductive inhibition of offspring is maintained in groups after treatment of the dominant female with contraception. However, changes in interactions between group members may become apparent in other ways, such as through increased aggression.

A second reason for suspecting that prevention of reproduction in Callitrichid groups may alter group stability is that, when considered from the viewpoint of inclusive fitness, the absence of births could alter the costs and benefits of delayed dispersal for offspring in such a way that remaining in the group, and foregoing reproduction, is no longer the preferred strategy. If no more siblings are born, mature offspring can no longer increase their inclusive fitness through cooperative infant care, and would thus benefit from trying to reproduce themselves. Inbreeding costs do not appear to prohibit mating between close relatives in this species (Price 1998; De Vleeschouwer *et al* in press). Offspring may begin to challenge their parents and/or compete among themselves in order to attain the breeding position in the group. The parents are likely to defend their dominant position, leading to an increase in aggression and evictions of group members in groups in which breeding no longer occurs. Presumably, these effects will become apparent only after a certain period — more specifically, a period longer than the normal inter-birth interval. In Mongolian gerbils (*Meriones unguiculatus*), the occurrence of reproduction by alloparents (group members other than the genetic parents that perform infant care behaviour) is associated with an atypically long inter-birth interval in the breeding adult females (French 1984).

Thus, we might expect a higher rate of aggression in non-breeding groups than in breeding groups. If this is due to an absence of births, we would expect this higher rate to become apparent after a period that is longer than the normal inter-birth interval. If, however, it is due to changes in socio-sexual interactions resulting from the use of contraception, we would expect it to appear soon after the contraception becomes effective. In investigating this, we

need to take into account the possibility that group size and the age–sex composition of the offspring may influence the occurrence of aggression. Larger groups — or, more specifically, groups with a higher number of sexually mature offspring — will probably be less stable than smaller groups or groups with only few or no sexually mature offspring, as the former will contain more offspring that might challenge the position of their parents. Offspring might also compete among themselves. This might further depend on the sex of the mature offspring, since both sexes generally have different reproductive strategies, at least in the wild (Baker 1991; Goldizen *et al* 1996; Garber *et al* 1993; Savage *et al* 1997).

The captive population of golden-headed lion tamarins (*Leontopithecus chrysomelas*) was set up in the early 1980s as part of a conservation breeding programme that aimed to secure the survival of this highly endangered species (for further details, see Kleiman *et al* 1986; Kleiman & Mallinson 1998). Because of changing management priorities associated with the lack of potential for reintroduction, the captive population is now under severe breeding restriction, and the use of contraception is currently an important part of captive management (De Bois 1994; Ballou *et al* 1998; Leus 1999; De Vleeschouwer *et al* 2000a). A preliminary study has suggested that use of contraception in groups of golden-headed lion tamarins might render them more susceptible to group disruption than groups of other Callitrichid species (Price 1997; E C Price, unpublished observations 1997, 1998). However, the sample size of this study was very small and it was therefore difficult to assess the impact of factors such as group size, sex, and sexual maturity of offspring. The present study uses a larger database to investigate further the impact of contraception on the stability of captive groups of golden-headed lion tamarins in relation to other factors that may also affect social stability. More specifically, we asked the following questions:

- 1) Is there an increase in severe aggression in non-breeding groups of golden-headed lion tamarins compared with breeding groups, and is this related to the use of contraception or the presence of young offspring?
- 2) Do larger groups (groups with a high number of offspring) experience an increase in severe aggression compared with smaller groups (groups with a lower number of offspring)? Does this differ, depending on the sex or sexual maturity of the offspring? If it exists, is this effect more pronounced in non-breeding groups compared to breeding groups of similar size and composition, and does it differ depending on the use of contraception or the presence of young offspring?

Methods

Study animals

The study animals belonged to 16 family groups, housed at the Royal Zoological Society of Antwerp (Belgium), Chicago Zoological Society (Brookfield Zoo, USA), Jersey Zoo, headquarters of the Durrell Wildlife Conservation Trust (Jersey, Channel Islands), La Palmyre Zoo (France), Mulhouse Zoo (France), and Belfast Zoological Gardens (United Kingdom). Details on the identity of the dominant group members, location, duration of participation in the study and date of contraception onset are given in Table 1. All dominant females were implanted once with a melengestrol-acetate (MGA) implant, except in the ‘Chicago1’ group, in which the dominant female received two consecutive MGA implants.

Data collection

Data on the occurrence of aggressive events in the groups housed in Antwerp and Jersey were collected by investigating the institutions’ breeding records. Instances of animals being

removed from groups in which contraception had been used were investigated in order to identify the exact circumstances under which this removal had occurred. Data for groups housed at the other institutions were obtained in an analogous way through investigation of studbook data and the distribution of a survey. In addition, frequent personal correspondence between the International Studbook Keeper for the golden-headed lion tamarin (currently K Leus) and the institutions involved provided further details on the circumstances of removals. In cases in which the information obtained from the studbook, the survey and personal correspondence was not sufficient, we contacted the institutions involved and asked for more information. Further details on the distribution and data collection and a copy of the survey can be found in De Vleeschouwer *et al* (2000a).

Table 1 Details of the study groups.

| Group | Dominant female ¹ | Dominant male ¹ | Start date ² | Date of contraception | End date | Reason for ending |
|-----------------|------------------------------|----------------------------|-------------------------|-----------------------|----------|------------------------------|
| <i>Antwerp1</i> | 1041 | 980 | 19/10/96 | 26/03/98 | 26/05/99 | Implant removed |
| <i>Antwerp2</i> | 604 | 930 | 10/09/94 | 24/07/97 | 26/05/99 | Implant removed |
| <i>Antwerp3</i> | 961 | 652 | 20/06/95 | 20/10/97 | 01/05/98 | Split up for medical reasons |
| <i>Antwerp4</i> | 916 | 960 | 14/10/97 | 17/04/98 | 28/05/99 | Implant removed |
| <i>Antwerp5</i> | 150 | 153 | 11/04/87 | 17/03/94 | 15/07/95 | Implanted female died |
| <i>Antwerp6</i> | 152 | 151 | 24/02/87 | 10/12/93 | 15/12/94 | Implanted female died |
| <i>Belfast</i> | 199 | 367 | 09/01/93 | 07/11/94 | 07/11/96 | Implant possibly expired |
| <i>Chicago1</i> | 112 | 113 | 09/09/86 | 09/06/89 ³ | 15/10/92 | Implant removed |
| <i>Chicago2</i> | 115 | 114 | 21/12/86 | 09/06/89 | 10/03/90 | Dominant male died |
| <i>Jersey1</i> | 143 | 4 | 24/05/91 | 07/02/94 | 07/02/96 | Implant possibly expired |
| <i>Jersey2</i> | 26 | 2 | 01/02/88 | 14/05/92 | 14/05/94 | Implant possibly expired |
| <i>Mulhouse</i> | 511 | 504 | 05/01/93 | 13/03/95 | 13/03/97 | Implant possibly expired |
| <i>Palmyre1</i> | 138 | 136 | 10/07/86 | 30/11/92 | 30/11/94 | Implant possibly expired |
| <i>Palmyre2</i> | 137 | 139 | 02/04/88 | 01/04/93 | 01/04/95 | Implant possibly expired |
| <i>Palmyre3</i> | 141 | 142 | 09/05/87 | 01/12/92 | 01/12/94 | Implant possibly expired |
| <i>Palmyre4</i> | 732 | 663 | 27/05/96 | 08/11/99 | 31/07/01 | End of data collection |

¹ Studbook numbers as in International Studbook (Leus & De Vleeschouwer 2001).

² Birth date of first offspring that remained alive for one week.

³ First implant removed and replaced by another on 12/07/91.

For the analyses, we considered all aggressive events that necessitated the permanent removal of *one or more* individuals from the group. 'Removed individuals' were defined as those individuals that were removed following an aggressive event, and that were either the victim or the aggressor. Thus, if an aggressive event resulted in the removal of an individual that was either the victim or the aggressor, and if another individual was removed at the same time in order to provide company for the first animal, we considered only the first individual as being a 'removed individual'. Equally, individuals removed to reduce tension in the group, for breeding purposes, or for export, without actually being evicted, were not considered 'removed individuals'. Furthermore, we excluded individuals that were evicted after being hand-reared and reintroduced, or individuals evicted during periods when a breeding adult was temporarily removed.

In some groups, several individuals had to be removed over a short period. We considered such removals not to be independent of one another, and counted all of them as one aggressive event occurring on one day — namely, the day on which the first individual had to be removed. This was the case for the group Jersey1, where five individuals had to be removed over a period of nine days, and for the groups Jersey2, Palmyre1 and Mulhouse,

where four, two and two individuals, respectively, had to be removed on two consecutive days.

Recalculation of data

The start date for each group entering the study was the birth date of the first offspring that remained alive for at least one week. The end date of participation in the study was determined by the death of one of the dominant adults, the splitting up of the group for medical reasons, the removal or possible expiration of the MGA implant, or the date on which data-collection ended (31/07/01). MGA implants are recommended to be replaced after being in position for two years (DeMatteo 1997). This estimated minimum longevity is supported by records of conception dates from females that resumed breeding without their implant having been removed or replaced (De Vleeschouwer *et al* 2000a). The respective reasons for the groups' end dates of participation are listed in Table 1.

In captivity, females frequently give birth twice per year, whereas in the wild they normally have only one litter per year (French *et al* 1996; Raboy *et al* 2001; De Vleeschouwer 2000). We used the latter, more conservative birth-rate criterion to divide the observation period into three (hereafter referred to as 'conditions'):

- 1) *No contraception used, offspring younger than one year present in group (Ncon-<1yr)*: period beginning at the start date, when the dominant female is not treated with a contraceptive and the group is breeding regularly.
- 2) *Contraception used, offspring younger than one year present in group (Con-≤1yr)*: period starting on the day when the dominant female is treated with a contraceptive, and ending when the last-born offspring is/are one year old. Analysis of steroid hormone levels in urine collected from females on the day after contraceptive implantation reveals very low levels of oestrogens (Van Elsacker *et al* 1994; De Vleeschouwer *et al* 2000b), indicating that the contraceptive becomes effective within a few hours (24 h at most).
- 3) *Contraception used, all offspring older than one year (Con->1yr)*: period during which the dominant female is treated with a contraceptive, starting when the last-born offspring is/are one year old, and ending on the end date.

For a fourth condition, '*No contraception used, all offspring older than one year*', information was available for only one group. Therefore, these data were excluded from the analyses. Note that the categorisation of groups based on the age of the last-born offspring is not related to the age of sexual maturity (which is, on average, 17 months), but instead is used here to indicate whether the last-born offspring have reached the age when normally the next litter would already have been born. The number of years for which groups were studied, and the number of aggressive events and removed individuals for each group under the three conditions, are summarised in Table 2.

We subsequently determined the number of days for which each group remained at a certain group size and composition (in terms of *overall* numbers of sons and daughters present) and whether or not an aggressive event occurred during this period. Changes in group size and composition occurred when infants were born that survived for at least one week, or when individuals died or were removed for breeding purposes elsewhere, for export, or because of aggressive events. In a similar way, we constructed another data file, in which, in addition to group size, we considered group composition in terms of the number of *sexually mature* sons and daughters present. Females are considered physiologically mature

at 17 months of age (French *et al* 1989; French *et al* 2002; M Heistermann & K De Vleeschouwer, unpublished observations 1996, 1997). For males, no data exist on the onset of physiological fertility; however, data on the age at which they first sire offspring suggest that they reach sexual maturity at an age similar to females (*L. chrysomelas*: K Leus, unpublished studbook data 2001).

We further calculated three parameters:

- 1) *Overall proportion of males in the group*: number of males divided by total group size.
- 2) *Proportion of mature males*: number of mature males divided by total group size.
- 3) *Proportion of mature females*: number of mature females divided by total group size.

The breeding male and female were included in these proportions. We used these parameters instead of the overall, or 'operational', sex ratio (no. mature males/no. mature females), because the latter might produce distorted results: female-biased sex ratios have values between 0 and 1, whereas male-biased sex ratios vary between 1 and n (where n = total group size). Thus, particularly for large group sizes, data points for groups with male-biased sex ratios are more dispersed over the x-axis, and this increases the chances of finding a significant positive effect of sex ratio. The proportions indicated above all have values between 0 and 1.

Table 2 Number of years for which groups were studied, number of aggressive events, and number of removed individuals for the groups under three conditions of contraception and breeding: Ncon-<1yr = no contraception used, offspring younger than one year present; Con-≤1yr = contraception used, offspring younger than one year present; Con->1yr = contraception used, all offspring older than one year.

| Group | Ncon-<1yr | | Con-≤1yr | | Con->1yr | |
|---------------------|-----------------|------------------------------------|-----------------|------------------------------------|-----------------|------------------------------------|
| | No. group years | No. aggressive events ¹ | No. group years | No. aggressive events ¹ | No. group years | No. aggressive events ¹ |
| <i>Antwerp1</i> | 1.43 | 0 | 0.98 | 0 | 0.18 | 0 |
| <i>Antwerp2</i> | 2.39 | 0 | — ² | — | 1.84 | 1 |
| <i>Antwerp3</i> | 2.34 | 0 | 0.53 | 0 | — ³ | — |
| <i>Antwerp4</i> | 0.51 | 0 | 0.97 | 0 | 0.14 | 0 |
| <i>Antwerp5</i> | 6.94 | 1 | 0.99 | 0 | 0.34 | 0 |
| <i>Antwerp6</i> | 6.80 | 2(3) | 1.01 | 0 | — ³ | — |
| <i>Belfast</i> | 1.83 | 0 | 1.23 | 0 | 0.77 | 0 |
| <i>Chicago1</i> | 2.75 | 0 | 0.79 | 0 | 2.56 | 0 |
| <i>Chicago2</i> | 2.47 | 2 | 0.75 | 1(2) | — ³ | — |
| <i>Jersey1</i> | 2.71 | 0 | 1.09 | 1(5) | 0.89 | 2 |
| <i>Jersey2</i> | 4.28 | 1 | 1.31 | 1(4) | 0.69 | 1 |
| <i>Mulhouse</i> | 2.18 | 1 | 0.33 | 0 | 1.67 | 1(2) |
| <i>Palmyre1</i> | 6.40 | 0 | 0.55 | 1(2) | 1.45 | 0 |
| <i>Palmyre2</i> | 5.00 | 0 | 1.12 | 0 | 0.88 | 1 |
| <i>Palmyre3</i> | 5.57 | 1 | 0.78 | 1 | 1.22 | 0 |
| <i>Palmyre4</i> | 3.45 | 0 | 0.50 | 0 | 1.23 | 1 |
| Total | 57.05 | 8(9) | 12.93 | 5(14) | 13.86 | 7(8) |
| Total (for size ≤9) | 54.39 | 5(6) | 11.62 | 3(5) | 13.86 | 7(8) |

¹No. in brackets indicates no. removed individuals, if different from no. aggressive events.

²Last litter in this group was born more than one year before the date of contraception.

³End date for these groups was less than one year after birth of last litter.

Statistical analysis

We excluded group sizes higher than nine from the analysis, because these did not occur under all three conditions and were generally rare. Table 2 lists the number of years for which groups of sizes less than or equal to 9 were studied, and the number of aggressive events. We subsequently used a logistic regression model to determine which factors affected the occurrence of aggressive events (binary variable: no aggressive event coded as 0; aggressive event coded as 1). Using this technique, binary data are converted into probability values, by fitting a logistic curve through the available data points (Wauters *et al* 1993). The logistic model is described by:

$$P(Y_i = 1) = e^{g(x_i)} / (1 + e^{g(x_i)}) \quad \text{and} \quad g(x_i) = b_0 + b_1x_{i1} + b_2x_{i2} + \dots + b_jx_{ij}$$

where $b_0, b_1, b_2 \dots b_j$ are constants and $x_{i1}, x_{i2} \dots x_{ij}$ are the factors included in the model. $P(Y_i = 1)$ indicates the probability that $Y_i = 1$ (ie that a removal will take place) for a given value of x_i .

Models fitted using logistic regression are sensitive to colinearity among the independent variables, and this might produce incorrect results (Hosmer & Lemeshow 1989). In our case, one can suspect correlations to exist between group size, number of (mature) sons and number of (mature) daughters. Variance inflation factors (VIFs) represent the factors by which the standardised unexplained variance is inflated because of the pattern of intercorrelations among the independent variables (Sokal & Rohlf 1995). VIF values equal unity if the independent variables are not correlated (Sokal & Rohlf 1995). If VIF values are higher than 10, serious intercorrelation exists, which reduces the accuracy of the results obtained (Neter *et al* 1990). We therefore investigated only models for which all VIF values were lower than 10, while maintaining as many independent variables as possible and using models that were meaningful in terms of our research questions. Following these criteria, we tested the following models:

- 1) Model I, including the factors 'condition', 'group size' and 'overall proportion of males' (VIF: group size = 1.01, overall proportion of males = 1.01).
- 2) Model II, including the factors 'condition', 'number of sons' and 'number of daughters' (VIF: number of sons = 1.00, number of daughters = 1.00).
- 3) Model III, including the factors 'condition', 'group size', 'proportion of mature males' and 'proportion of mature females' (VIF: group size = 1.19, proportion of mature males = 1.06, proportion of mature females = 1.06).
- 4) Model IV, including the factors 'condition', 'number of mature sons' and 'number of mature daughters' (VIF: group size = 1.22, number of mature sons = 1.16, number of mature daughters = 1.11).

'Group identity' was defined as a random effect, and its interaction with 'condition' was included in the model. Data were analysed using the procedure GLIMMIX in SAS[®]. The value for α was set at 0.05. The goodness-of-fit of the models was assessed by comparing their respective deviances, which play a similar role to that of the residual sum of squares in linear regression (Hosmer & Lemeshow 1989). Thus, smaller deviances indicate that less of the variance in the data set is left unexplained by the relationship between the dependent and the independent variables in the fitted model.

The fact that, for many removed individuals, we could not determine whether they were the victims or the instigators of aggression precluded the use of logistic regression to investigate the probability that particular individuals would be evicted in relation to the

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Table 3 Significance of factors and interactions and parameter estimates for two logistic regression models determining the probability of aggression in groups of golden-headed lion tamarins under different conditions of contraception and breeding. NS, not significant.

| Factor | Parameter estimate | <i>t</i> | <i>P</i> |
|-------------------------|--------------------|----------|----------|
| <i>Model I</i> | | | |
| Intercept | -17.19 | -5.64 | <0.0001 |
| Condition | | | |
| Ncon-<1yr | 0 | — | — |
| Con-≤1yr | 0.92 | 0.82 | NS |
| Con->1yr | 3.96 | 3.57 | <0.005 |
| Group size | 1.05 | 4.54 | <0.0001 |
| Overall number of males | 9.15 | 3.69 | <0.0005 |
| <i>Model II</i> | | | |
| Intercept | -10.79 | -6.29 | <0.0001 |
| Condition | | | |
| Ncon-<1yr | 0 | — | — |
| Con-≤1yr | 1.04 | 0.85 | NS |
| Con->1yr | 4.37 | 3.63 | <0.005 |
| Number of sons | 1.85 | 5.38 | <0.0001 |
| Number of daughters | 0.14 | 0.58 | NS |

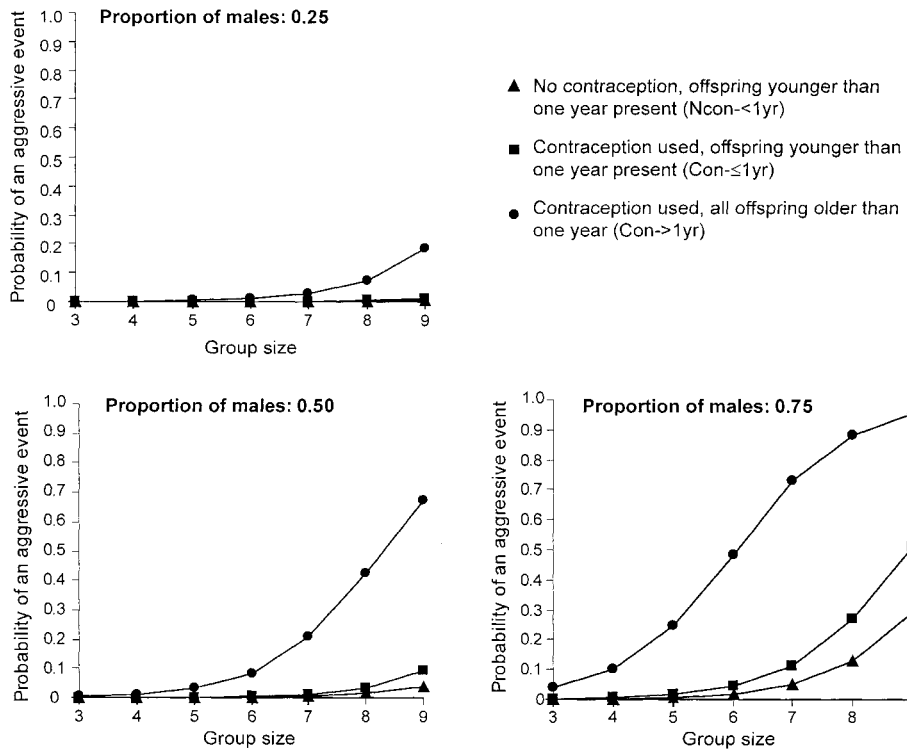


Figure 1 Logistic curves, representing the probability of occurrence of an aggressive event as a function of group size, for different proportions of males in the group and under different conditions of contraception and breeding.

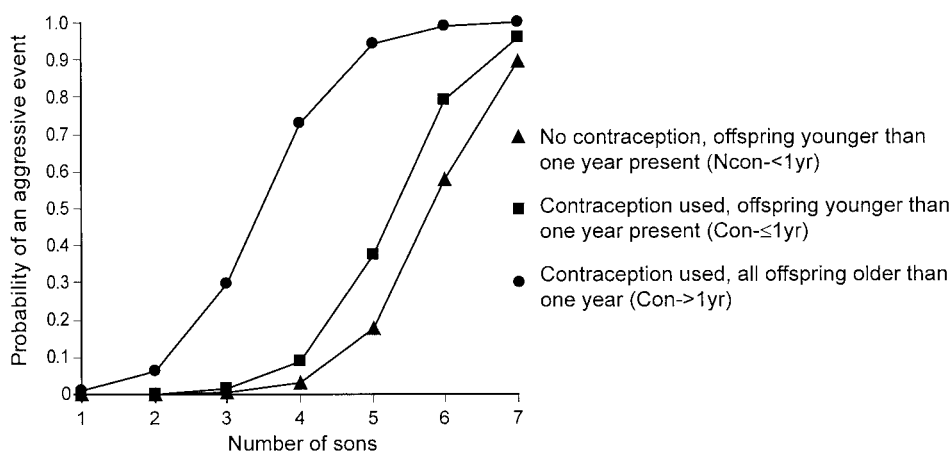


Figure 2 Logistic curves, representing the probability of occurrence of an aggressive event as a function of the number of sons in the group and under different conditions of contraception and breeding.

Table 4 lists the sex of ‘individuals at risk of removal’ and ‘removed individuals’ under the three conditions. Individuals explicitly reported to be the victims of aggression are indicated separately. Most individuals removed under the Ncon-<1yr and Con-<=1yr condition were males, in accordance with the bias in sex ratio observed for all individuals at risk. Individuals removed under the Con->1yr condition were predominantly females. The difference in sex ratio between the individuals at risk and the individuals actually removed was almost significant for the Con->1yr condition. When only individuals identified as victims were considered, no trend was apparent.

Table 4 Sex ratio (males:females) of individuals at risk of removal and individuals removed from groups under the three conditions. NS, not significant.

| | Ncon-<1yr | Con-<=1yr | Con->1yr |
|---|-------------------------|-----------------------------------|-------------------------------|
| Individuals at risk of removal | 86:66 (NS) ¹ | 59:38 ($P < 0.05$) ² | 34:23 (NS) |
| Individuals removed | | | |
| - total | 5:4 (NS) | 11:3 ($P < 0.05$) ³ | 2:6 (NS) |
| - explicitly reported to be victims | 3:3 (NS) | 7:3 (NS) | 2:5 (NS) |
| G-test with Williams' correction ($df = 1$) | | | |
| - all individuals | | | |
| - individuals reported to be victims | $G_{adj} = 0.002$; NS | $G_{adj} = 1.71$; NS | $G_{adj} = 3.26$; $P = 0.07$ |
| | $G_{adj} = 0.09$; NS | $G_{adj} = 0.32$; NS | $G_{adj} = 2.29$; NS |

¹ Based on χ^2 test with one degree of freedom.

² $\chi^2 (1) = 4.55$

³ $\chi^2 (1) = 4.57$

Discussion

Following implantation of a contraceptive device, changes in socio-sexual behaviour of formerly breeding adults and their eldest female offspring do occur, although these do not have an effect on reproductive inhibition of daughters or on group stability in the short term (Van Elsacker *et al* 1994; De Vleeschouwer *et al* 2000b). The present study shows that overall, when contraception is used in groups of golden-headed lion tamarins, group stability

is negatively affected, but only after a period longer than the normal inter-birth interval (ie one year) and predominantly at larger group sizes.

Four main findings emerge from this study. First, models containing the proportion or number of sexually mature males and females do not allow accurate prediction of the probability of severe aggression; this indicates that it is the overall number of animals and their sex, rather than the number and sex of sexually mature animals, that determine the occurrence of severe aggression. Second, group size, the proportion of males, and the number of sons in the group significantly affect the probability that severe aggression will occur: larger groups and/or groups with a predominance of males are less stable than smaller groups and/or groups that contain relatively more females. Third, the effects of group size, of the proportion of males, and of the number of sons in the group are significantly stronger in groups in which the dominant female is treated with a contraceptive and that contain only offspring older than one year. In groups that still contain offspring younger than one year, the effects are comparable whether contraception is used or not. Fourth, in groups that still contain offspring older than one year, more males than females are removed because of aggression, in accordance with the bias in sex ratio of individuals at risk. In groups where the female is treated with a contraceptive and that contain only offspring older than one year, there is a trend toward more females being removed, in contrast to the observed sex ratio of individuals at risk. When only individuals explicitly reported to be victims are considered, no trends are apparent.

The results of this study thus confirm preliminary results by Price (1997; E C Price, unpublished observations 1997, 1998) which also indicate that Callitrichid groups are less stable when contraception is used than when they are normally breeding — particularly groups of golden-headed lion tamarins. The present study, however, provides a more differentiated approach. The increased instability of groups in which contraception is used is not related to changes in socio-sexual interactions between group members associated with the contraceptive treatment *per se*. Rather, it is the absence of *births* that seems to be responsible for the effects observed.

What could be the proximate cause for this observed instability? In cotton-top tamarins (*Saguinus oedipus*), parturition by the dominant female leads to reduction in oestrogen levels in the eldest female offspring, compared to hormonal levels measured before parturition (Ziegler *et al* 1987; Snowdon *et al* 1993; Savage *et al* 1997). This may prevent the latter from competing with the dominant female during her post-partum oestrus (Snowdon *et al* 1993). These findings suggest a physiological mechanism by which an absence of births might result in an increased rate of severe aggression. When the dominant female no longer breeds, this cyclical reduction of oestrogen levels in the eldest female offspring will no longer occur, and may affect their reproductive behaviour in the long term. This will not necessarily result in the female offspring giving birth. Instead, if these females are no longer reproductively inhibited, they might attempt to attain the breeding position and mate with males in the group. This will probably increase the level of reproductive competition between males on one hand and the dominant female and her female offspring on the other hand, and result in an increase in aggression and evictions. In *Leontopithecus*, the eldest female offspring frequently show normal ovarian cycles when housed in their natal group (French *et al* 1989; Van Elsacker *et al* 1994; Chaoui & Hasler-Gallusser 1999; De Vleeschouwer *et al* 2000b; French *et al* 2002). Whether they also show a reduction in oestrogen levels after parturition of the dominant female remains to be investigated. De Vleeschouwer *et al* (2000b) did not find consistent changes in socio-sexual interactions between dominant females and their eldest female offspring after contraception, at least not in the first two months. Affiliative

interactions did not change, while aggressive interactions either decreased or did not change following contraception. At that stage, however, three of the four groups in the study still contained offspring of less than one year and thus, according to the results of the present study, signs of increased instability were not yet expected. A detailed study investigating changes in behaviour and hormones over the entire contraceptive period would be necessary in order to identify the exact physiological causes of the increased group instability.

Group size, the proportion of males in the group and the number of sons all provide good estimates of the probability of aggression, whereas the proportion of sexually mature males and females, and the number of sexually mature sons and daughters, prove to be only poor predictors. Larger groups are less stable, and even more so if they contain a high proportion of males or a large number of sons. It is possible that space limitations in zoos present a problem for bigger groups, resulting in evictions. However, this does not explain why groups containing many males are less stable than other groups of similar size but containing more females, or why groups that contain offspring older than one year are less stable than groups that contain offspring of younger ages.

In golden lion tamarins (*Leontopithecus rosalia*) and cotton-top tamarins (*Saguinus oedipus*), groups with a male-biased sex ratio also suffer from a higher rate of aggression (Inglett *et al* 1989; Snowdon & Pickhard 1999). The particular problem of males might be explained by looking at the potential reproductive strategies available to individual males and females for increasing their reproductive success. Published data on reproductive strategies and immigration patterns are unavailable for wild golden-headed lion tamarins, but there is substantial information on wild golden lion tamarins. Baker (1991) tested different adaptive hypotheses for explaining infant-carrying patterns of male and female helpers in wild golden lion tamarin groups, and found that these varied in accordance with the associated benefits. Male golden lion tamarins frequently co-disperse and enter new groups together with related males (Baker & Dietz 1996). As expected, male helpers more readily carry related male infants, which are their potential co-emigration partners (Baker 1991). Females, however, usually disperse alone (Baker & Dietz 1996) and thus do not benefit from preferentially carrying related female infants. On the other hand, the acquisition of adequate parental skills is particularly important in order for females to raise infants successfully (French *et al* 1996); accordingly, although female helpers show no preference for carrying related infants, younger females without rearing experience are more likely to carry infants than older, experienced females (Baker 1991). Maternal, but not paternal, rearing experience is an important determinant of infant survival in golden-headed lion tamarins as well as in golden lion tamarins (De Vleeschouwer *et al* in press). Data on immigration patterns in golden-headed lion tamarins have not been published, so currently it is not possible to fully evaluate whether male and female helpers might experience similar costs and benefits as golden lion tamarins. Assuming for now that the costs and benefits are similar for both species, why would male offspring be more likely to cause or experience aggression, resulting in their removal? In 'two-male' golden lion tamarin reproductive groups, both males have the opportunity to copulate with the breeding female. However, the dominant male is responsible for 94% of the copulations with the female during her fertile period (Baker 1991; Baker *et al* 1993). Subordinate males gain indirect fitness benefits if they are related to the dominant male. Although their expected lifetime reproductive success is lower than that of the dominant male, it is higher than if they remain in their natal group as helpers because of the prospect of acquiring the dominant position over time (Baker 1991; Baker *et al* 1993). Given this effect of dominance on male lifetime reproductive success, male co-emigrants may benefit if dominance relationships between them are already firmly established before they

enter a new group. Dominance fights and interference with matings soon after entering a group may result in delay in the onset of reproduction, loss of a breeding attempt (if the female fails to conceive during that breeding season), or offspring being born during a period when environmental conditions for lactating and weaning are less than optimal. Male siblings may thus be more likely to cause or suffer from aggression in their natal group because of attempts to establish dominance relationships with their siblings. In groups containing more males, such dominance fights are more likely, particularly between males or twins that are close in age, which are most likely to be co-emigrants. Severe aggression would then occur if individuals refuse to accept their subordinate status.

Females usually disperse alone (Baker & Dietz 1996). However, they still benefit from establishing firm dominance relationships with their siblings in case the reproductive female dies, when the most dominant daughter may attain reproductive status. In females, however, this may involve physiological mechanisms rather than overt aggression. In a large group housed in Antwerp, the eldest daughter showed normal ovarian cycles, while two adult-aged but lower-ranking female siblings did not. The death of the group's mother did not alter this pattern, suggesting that the factor suppressing normal ovarian function in the low-ranking females was still present. One suggestion is that inhibition of ovarian cycles in the younger females results from the presence of the eldest daughter (M Heistermann & K De Vleeschouwer, unpublished observations 1995).

This effect of offspring sex on the likelihood of aggression can be expected regardless of whether the group is still breeding or not. When the group is not breeding, both male and female offspring lose the indirect fitness gains associated with the production of non-descendant kin. Even in breeding groups, the benefits to older offspring of assisting in the rearing of yet another litter are probably small, as older males are unlikely to co-emigrate with infants that are not close in age, and females that are already experienced may gain little from additional performance of parental skills (Baker 1991). Older offspring may benefit only through increased survival of the infants and possibly the breeders. In larger groups, on the other hand, where many helpers are available, the relative surplus value of older offspring is probably small. However, for female offspring there is an additional factor. If the dominant female no longer breeds, successful reproduction might become more feasible for subordinate females: if the subordinate females' infants no longer have to compete with the dominant female's for care by the helpers, their survival chances will probably increase. Even though, as in our groups, inbreeding is the result, this might still be a valid option as the subordinate female is familiar with the 'natal territory', has several experienced and related helpers at her disposal, and dispersal and breeding elsewhere is not an option (as in a zoo situation).

Breeding by subordinate females in wild golden lion tamarin groups does not lead to dominance reversal, but these subordinate females frequently leave the group after one or two years, sometimes forcibly being evicted (Dietz & Baker 1993). Analysis has further revealed that although dominant females may tolerate reproduction by subordinates if no inbreeding is involved, they will always benefit from evicting the subordinate female if her reproduction would result in inbreeding (Dietz & Baker 1993). The same rule seems to apply for cases of polygyny in captive groups of golden-headed lion tamarins (De Vleeschouwer *et al* 2001). In the Mulhouse group in our study, eviction of the daughter in the Con->1yr condition occurred after she had delivered twins (inbreds sired by either her father or a male sibling). Aggressive events appeared closely related to this fact, with the dominant female killing the daughter's infants and evicting the daughter (De Vleeschouwer *et al* 2001). In the other study groups and in non-breeding groups, as a rule, polygyny does not occur more

frequently than in normally breeding groups (De Vleeschouwer *et al* 2000b). However, dominant females might actually intervene earlier, at the time when subordinate females attempt to mate. This argument might explain the increased rate of removals of female offspring from their natal group seen in groups in which all offspring are older than one year.

Our analysis is somewhat hampered by the fact that for most aggressive events, we could not actually witness the circumstances leading to the removal of individuals. Animals found crouching on the floor and continuously attempting to escape from other group members while uttering distress vocalisations are usually considered victims. In some cases, these individuals could actually have been the initial instigators of the aggression (K De Vleeschouwer, personal observations 1994–1998). More detailed information on the actual circumstances of the aggression is needed in order to understand the exact causes of aggression and the probability of eviction in relation to characteristics of the individual.

Animal welfare implications

The fact that large non-breeding groups of golden-headed lion tamarins become less stable after one year presents a management problem for institutions holding such groups. At the time when the conservation breeding programme for this species was being established (early 1980s) the captive population was required to grow (Kleiman & Mallinson 1998). The use of contraception was therefore rare, and offspring were frequently taken from their natal groups for breeding purposes shortly after reaching sexual maturity. Currently, severe restriction on the breeding pairs in the world's captive population necessitates the frequent use of contraception (De Vleeschouwer *et al* 2000a). Offspring also remain in their natal groups for a longer period because they are required for breeding less frequently. While this allows animals to remain in social groups, it also leads to larger and thus less stable groups. The degree to which the increase in aggression presents a management problem depends on the frequency, size and composition of non-breeding groups in the captive population, and thus varies over time along with changes in group composition and use of contraception. Regardless of this, large non-breeding groups need to be watched closely and, if signs of aggression occur, animals may need to be removed in order to prevent escalation and possible deaths. Alternatively, institutions may prefer to wait until an eviction actually occurs. The results further indicate that it is particularly important to monitor closely groups with a large number of males. While mandatory from a welfare point of view, the (preventative) removal of more animals from their natal group will only add to existing demographic problems with placing surplus animals (Ballou *et al* 1998).

Given that an increase in the likelihood of aggression has more to do with the absence of births in the dominant female than with the method of contraception itself, consideration should be given to restricting the duration of each bout of contraception, for example by removing the contraceptive device sooner or by using short-term contraceptive methods such as Depo-Provera injections. These injections would be easier to administer, as animals could be returned to the group immediately (whereas insertion and removal of MGA implants requires anaesthesia, surgery and removal of animals from the group for several hours). Information on the use and safety of contraceptive methods other than MGA implants is still scarce, however, and further studies are required (De Vleeschouwer *et al* 2000a). In captivity, multiple litters per year are a frequent occurrence (De Vleeschouwer 2000). Restoring the pattern of one litter per year, which is observed in wild groups (Raboy *et al* 2001), would still ensure the continued presence of offspring younger than one year, but might also reduce the likelihood of aggression occurring. This reduced breeding rate might

also be sufficient for meeting the objectives of the conservation breeding programme (depending on the objectives for, and reproductive rates achieved by, individual females).

These population-control methods depend on reliable reversibility of the contraceptives used. MGA implants appear not to be fully reversible in golden-headed lion tamarins (De Vleeschouwer *et al* 2000a; De Vleeschouwer *et al* in press). Other population control methods that have been suggested include euthanasia and the establishment of single-sex groups (Sainsbury 1997; Glatston 1998; De Vleeschouwer *et al* 2000a). If some male offspring are allowed to breed, the formation of polyandrous groups with related males also allows more animals to be housed in a social group while retaining the same reproductive output. Although rarely formed, long-term stable polyandrous groups do exist in captivity (K De Vleeschouwer & K Leus, unpublished studbook data 2001) and are a natural type of group formation in the wild (Dietz *et al* 1996). Ultimately, the decision on the most appropriate population-control method has to be based on an evaluation of all possible side-effects, in combination with consideration of the animals' well-being, ethical issues, the educational value of the captive population, the roles of individual animals in the survival plan for the species, and public opinion.

Acknowledgements

First, we thank the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA) for permission to conduct this research on the captive population of golden-headed lion tamarins. We also thank V Sodaro (Brookfield Zoo), L Lorca (ZooParc de Beauval), N Lindsay (Whipsnade Wild Animal Park), P Moisson (Zoo de Mulhouse), P Stifman (Newquay Zoo), M Challis (Belfast Zoological Gardens), and T Petit (La Palmyre Zoo) for providing us with further details on the occurrence of aggression in their groups of golden-headed lion tamarins. E Price is gratefully acknowledged for providing data on groups from Jersey Zoo and useful comments on earlier drafts of this manuscript. Thanks also go to Stefan Van Dongen for statistical advice. K De Vleeschouwer was supported by doctoral and postdoctoral grants provided by the Centre for Research and Conservation of the Royal Zoological Society of Antwerp. We thank the Flemish Government for structural support to the Centre for Research and Conservation of the Royal Zoological Society of Antwerp.

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