Folia Primatol 2001;72:48-50

Received: July 24, 2000 Accepted after revision: October 22, 2000

Female Dominance in African Lorises (Otolemur garnettii)

Reinmar Hagera, Christian Welkerb

^aZoologie II, Biozentrum am Hubland, Universität Würzburg, and ^bPrimatenethologie, Universität Kassel, Germany; ^cDepartment of Zoology, University of Cambridge, UK

Key Words

Otolemur garnettii · Female dominance · Polygynous mating system

Introduction

African lorises show sexual size dimorphism and are supposed to be characterised by male dominance [1]. They have been regarded as an outgroup for comparison with Malagasy prosimians, a grouping in which female dominance has been repeatedly reported [2, 3]. Males are assumed to be dominant because measures of body weight in captive populations reveal that males are larger than females. In contrast to most polygynous haplorhine primates, in which male dominance is correlated with larger male body size [4], many polygynous lemurs lack significant sexual dimorphism [5] and instead are characterised by female dominance [3, 6]. Female dominance has been inferred from the outcome of agonistic interactions [7], that is females were able to elicit submissive behaviour patterns from males.

Here, we report from observations of captive Garnett's greater bushbabies (Otole-mur garnettii), which indicate female dominance and lack of sexual size dimorphism. Observing male/female pairs allowed us to study dominance relationships between the sexes that would be otherwise hard to investigate in a nocturnal and normally solitarily foraging species.

Materials and Methods

Three adult pairs of captive *O. garnettii* were observed between the end of December 1998 and mid-April 1999 at Kassel Primate Station. The observation period (equal for each pair) was 3 h/day for 5 days a week. We then changed the partners so that each individual could be observed with a new partner and behavioural differences depending on the partner could be recorded. To assess dominance relationships we recorded and analysed aggressive and submissive behaviour, approach and partner inspection. Aggressive behaviour patterns occurred in situations associated with conflict, and domi-

KARGER

© 2001 S. Karger AG, Basel 0015–5713/01/0721–0048\$17.50/0

Fax + 41 61 306 12 34 E-Mail karger@karger.ch www.karger.com

Accessible online at: www.karger.com/journals/fpr Reinmar Hager, Behavioural Ecology, Department of Zoology University of Cambridge, Downing Street Cambridge CB2 3EJ (UK) Tel. +44 1223 336 600, Fax. +44 1223 336 676 E-Mail rh244@cam.ac.uk

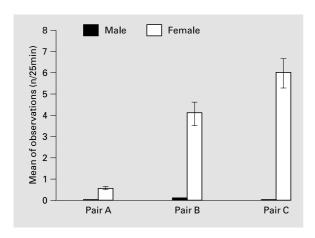


Fig. 1. Level of aggressive behaviour exhibited by members of three pairs. Error bars indicate the standard error.

nance was defined by the outcome of agonistic interactions in which one animal exhibited aggressive behaviour while the opponent displayed submissive behaviour. Aggressive behaviour patterns include threat, chase and bite. Threat behaviour is characterised by calls and, in many cases, by rearing, i.e. the individual stands on hind legs with arms flexed and facing its opponent. Submissive behaviour was characterised by retreating. Partner inspection involves body sniffing, and in particular anogenital sniffing when exhibited by males, licking and chest rubbing on the partner.

Results

Body Weights

Adult body weights were variable. Males were not significantly heavier than females (Mann-Whitney U = 15, $n_1 = 7$, $n_2 = 5$, n.s.).

Behavioural Data

Females exhibited virtually all aggressive behaviour patterns in all three pairs (fig. 1). Agonistic interactions occurred when males approached and attempted partner inspection, but we did not observe aggressive behaviour during feeding. Males exhibited significantly more partner inspection than females (Kruskal-Wallis test, p < 0.001), and even though females displayed this behaviour as well, it did not elicit agonistic interactions. Over a period of 2 weeks across all pairs we recorded a total of 238 agonistic interactions of which 232 were decided by females. These results are highly significant ($\chi^2 = 106.35$, d.f. = 1, p < 0.01). Females in pairs B and C exhibited much more aggressive behaviour than the female in pair A (fig. 1). This may be due to the fact that the males in pairs B and C both exhibited a higher level of partner inspection than male A. Males approached and followed their partners significantly more often than females did (Kruskal-Wallis test, p < 0.001). All bushbabies were paired with a new partner. The only new pair that could be established was with the male who exhibited the lowest incidence for approach and partner inspection (male A). His new partner (female B) now showed significantly less aggressive behaviour than in the first pair (Wilcoxon's

test, p < 0.05), and this male exhibited significantly less partner inspection with the new female (Wilcoxon's test, p < 0.01). All other new pairings were unsuccessful because the level of aggression led to serious biting and chasing. The males started exploring the new partner but were bitten soon after by the females and serious fighting occurred.

Discussion

The results of this study contrast with previous views on dominance relationships in Garnett's greater bushbabies. Following general assumptions from theory of sexual selection, male dominance has been inferred from sexual dimorphism [1], but evidence for this in lorises has not yet been found. In this study we could show that agonistic interactions were decided by females indicating that females are dominant.

Females exhibited nearly all aggressive behaviour patterns, which vary with levels of approach and partner inspection initiated by the males. It should also be noted that only the females started biting when placed together with a new partner.

The high level of males approaching and following females may be explained in the light of their solitary way of living and seasonal receptivity in this species [8]. When males encounter conspecifics they have to determine the sex and their mating status and thus display this behaviour. Since the outcome of agonistic encounters was previously taken as an indicator for dominance relationships amongst primates [3, 7] our findings indicate female dominance in Garnett's greater bushbabies. If female reproductive success is more dependent on environmental factors than male reproductive success, selection could favour female dominance [6].

Our findings result from a test situation that allowed us to investigate whether males or females are dominant or whether there is no dominance relationship between the sexes. Wild bushbabies are solitary foragers [8], so males and females could be expected just to avoid encounters and there does not seem to be competition between the sexes over limited nutritional resources. Our study should encourage further studies to investigate dominance relationships between the sexes in free-ranging Garnett's greater bushbabies.

References

- 1 Kappeler PM: Female dominance in primates and other mammals; in Bateson PBG, Klopfer PH, Thompson NS (eds): Behaviour and Evolution. Perspectives in Ethology. New York, Plenum Press, 1993, vol 10, pp 143–158
- 2 Richard AF: Malagasy prosimians: Female dominance; in Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds): Primate Societies. Chicago, Chicago University Press, 1987, pp 25–33.
- 3 Meyer L, Gallo T, Schultz ST: Female dominance in captive red ruffed lemurs, Varecia variegata rubra (Primates, Lemuridae). Folia Primatol 1999;70:358–361.
- 4 Mitani JC, Gros-Louis J, Richards A: Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. Am Nat 1996;147:966–980.
- 5 Kappeler PM: Patterns of sexual dimorphism in body weight among prosimian primates. Folia Primatol 1991; 57:132–146.
- 6 Jolly A: The puzzle of female feeding priority; in Small MF (ed): Female Primates: Studies by Women Primatologists. New York, Liss, 1984, pp 197–215.
- 7 Kappeler PM: Female dominance in *Lemur catta*: More than just feeding priority. Folia Primatol 1990;55: 92-95
- 8 Bearder SK: Lorises, bushbabies and tarsiers: Diverse societies in solitary foragers; in Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsacker TT (eds): Primate Societies. Chicago, Chicago University Press, 1987, pp 11–24.

50	Folia Primatol 2001;72:48–50	Hager/Welker