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Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs

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Abstract Data on langur (*Presbytis entellus*) populations were gathered from the literature to test the importance of three selective pressures in determining group size and composition: predation pressure, inter-group resource defense, and conspecific threat. There were no detectable difference in the size of groups in populations facing nearly intact predator communities compared to those populations where predators were severely reduced in number or absent, although there was a trend for the number of adult males per group to increase in areas with nearly intact predator communities. Using population density as an indirect measure of the frequency of intrusions into a group's home range and thereby as an index of the demographic pressure favoring resource defense, we predicted that higher densities would result in larger defensive coalitions and higher numbers of females per group. This prediction was not upheld. Our third selective pressure, conspecific threat, encompasses those selective forces resulting from physical attack on females, infants, and juveniles. Our index of conspecific threat uses the number of non-group males divided by the number of bisexual groups, because in langurs, the major source of conspecific threat derives from non-group males who, following group take-over, kill infants, wound females, and expel juveniles from groups. This index of conspecific threat was strongly related to the mean number of resident females, was weakly related to the mean group size, but was not related to the number of males in the group. In addition, as predicted, populations with a high index of conspecific threat had higher levels of juvenile expulsion. These analyses were corroborated by a simulation model which used a computer-generated series of

null populations to calculate expected slopes of immatures regressed on adult females. These randomly generated populations, matched to means and ranges of real populations, allowed us to determine if deviations of the observed slopes from the expected null slopes could be explained by variation in predation pressure, population density, or conspecific threat. We found no evidence that predation pressure was associated with decreases in immature survival in smaller groups, as would be predicted by the predation-avoidance hypothesis. We found no evidence that immature survival was compromised by small group size in high-density populations, as would be predicted by the resource-defense hypothesis. However, as the index of conspecific threat increased, groups with larger numbers of females were more successful than groups with fewer females in reducing mortality or expulsion of immatures. Overall, conspecific threat received the strongest support as a selective pressure influencing langur group size and composition, suggesting that this selective pressure should be evaluated more widely as a factor influencing composition of animal groups.

Key words *Presbytis entellus* · Group living · Group size · Infanticide · Social organization

Introduction

The size and composition of social groups has been extensively discussed in terms of costs and benefits (Altmann 1974; Alexander 1974; Terborgh and Janson 1986). It is generally agreed that the presence of other individuals increases feeding competition, results in reduced food intake (Wrangham 1980; van Schaik 1983; van Schaik and van Hooff 1983; Janson 1985; Chapman 1988; Chapman et al. 1995), and has direct influences on individual fitness (Whitten 1983; Lee

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1987). In contrast, the benefits that result from group-living and the degree to which animals of different ages or sexes share these benefits, remains an area of contention (O'Brien 1991; Chapman et al. 1995). Primates are an excellent taxonomic group to address such issues, since most species form cohesive groups, but exhibit a high degree of variation in group size and composition.

Two selective pressures thought to favor group living and influence group composition have received widespread attention: predator avoidance (Alexander 1974; van Schaik 1983) and intergroup resource defense (Wrangham 1980; Moore 1984; Robinson 1986). Recently, the avoidance of conspecific attack has received consideration as a selective force influencing bonding between males and females (Watts 1989; Trumbo 1990, van Schaik and Dunbar 1990; Smuts and Smuts 1993; van Schaik and Kappeler 1993), but this factor has not been broadly evaluated and may also play a role in determining the size and composition of groups.

The predation avoidance hypothesis claims that primates live in groups to reduce the risk of predation, despite the increased cost of within group feeding competition (Alexander 1974; van Schaik and van Hooff 1983; van Schaik et al. 1983; Terborgh and Janson 1986). Group living is theorized to provide fitness benefits by lowering the per capita predation risk through cooperative vigilance, defense, and dilution of risk (Hamilton 1971; van Schaik et al. 1983). Thus, according to optimality models, group size should covary with predation pressure (van Schaik 1983; Terborgh and Janson 1986). In addition, group composition may vary with predation risk, since cooperative defense and cooperative vigilance require adult or subadult participation almost exclusively (DeVore and Hall 1965; Hauser 1988; van Schaik and van Noordwijk 1989).

The resource defense hypothesis considers competition between conspecific groups for high-quality, defendable food patches as the selective force favoring group living and the formation of female bonds (Wrangham 1980; Isbell 1990). Since in some species both sexes are involved in contests between groups, while in other species only one sex is involved (Cheney 1992), the intensity of intergroup resource competition could potentially influence both group size and composition.

The avoidance of conspecific attack, particularly infanticide, has been proposed to influence the nature of certain social organizations (primates: Wrangham 1979, 1986; Watts 1989; van Schaik and Dunbar 1990; van Schaik and Kappeler 1993; lions: McComb et al. 1993; beetles: Trumbo 1990). Infanticide has been widely reported throughout the primate order (Hrdy 1977, 1979; Hausfater and Hrdy 1984), and as new field studies are conducted, the number of species documented to exhibit infanticide continues to increase (van Schaik and Kappeler 1993). The risk of conspecific attack has primarily been used to explain the protection provided by males to females and young (van

Schaik and Dunbar 1990; Struhsaker and Leland 1987), but increasing data from lions is providing rigorous evidence for the role of female cooperation in defense against infanticide (McComb et al. 1993).

In this study we gathered data from the literature on 20 populations of Hanuman langur (*Presbytis entellus*) in order to test the importance of three selective pressures in determining langur group size and composition: predation pressure, intergroup resource defense, and conspecific threat. Hanuman langurs were selected as a focal species because they have been the focus of a number of studies investigating the functional significance of infanticide. Thus, langurs represent a species where adequate data are available to evaluate the predation avoidance, resource defense, and conspecific threat hypotheses. Since predation and infanticide events are difficult to observe, and the function of intergroup encounters difficult to interpret (i.e., defense of mates and/or food resources), we propose a number of predictions based on what one would expect to find if group composition were modified in response to variation in any of these three pressures.

Conspecific threat is considered to encompass selection resulting from various forms of exploitation by conspecifics of either sex, including infanticide (Hausfater and Hrdy 1984), expulsion and killing of juveniles (Hrdy 1979; Agoramoorthy and Mohnot 1988; Reena and Ram 1991; Rajpurohit 1991a), induced abortion (Pereira 1983; Wasser and Starling 1986; Agoramoorthy et al. 1988), sexual harassment (Tutin 1979; Wrangham 1986), lethal male raiding (Manson and Wrangham 1991), and sexual coercion (Smuts and Smuts 1993). The general heading of conspecific threat is used here rather than sexual coercion which was restricted to encompass force or the threat of force used to increase male sexual opportunities and/or to decrease the sexual opportunities of other males (Smuts and Smuts 1993). This does not clearly encompass the killing of juveniles or juvenile expulsion as mothers do not resume cycling as a result.

Methods and predictions

Study animals and populations

Hanuman langurs (*Presbytis entellus*) are found in groups of up to 118 animals (Reena and Ram 1992), with one or more adult males. Most female langurs remain in their natal groups all their lives (Hrdy 1977; but see Newton 1987), implying close kinship between female group members (Moore 1984). The social system of some langur populations is characterized by instability in male residency in bisexual groups due to invasion by non-group males which may attack residents of any age or sex (Sugiyama 1965; Hrdy 1977; Boggess 1980; Mohnot 1984a,b). These non-group males live in bands which can number up to 50 and travel between the ranges of bisexual groups (Vogel and Loch 1984; Mohnot 1984b,c; Sommer 1987). Take-overs involve non-group male(s) harassing and attacking the current resident male(s) for periods lasting up to 27 days.

When replacement of the current resident(s) by outsider(s) does occur, the newcomer(s) may commit infanticide and force juveniles to leave the group (Newton 1986, 1987, 1988, Sommer 1987; Agoramorthy and Mohnot 1988; Rajpurohit 1991b; Ross 1993). Evidence from Jodhpur, the only site where individually identified juveniles have been followed for long periods, showed that expelled juveniles joined all-male bands; however, over the course of months the juveniles disappeared, which the author ascribes to predation (Rajpurohit 1991b; Rajpurohit and Sommer 1991). Some studies have never reported infanticide, nor have they observed aggressive male replacement (e.g. Jay 1965). Although detailed data come from only a few study sites, the populations examined here derive from the entire geographic range of the species.

To test the predictions, we used population censuses if the data included at least three bisexual groups and if the researchers had made an effort to census nongroup males (Table 1). All data were collected from the literature or from personal communication with individual researchers (J. Moore, P. Newton, G. Kurup) and we used the interpretations presented in Moore (1985) and Newton (1988) when confusion arose over census data. Non-parametric tests (Spearman rank correlations and Mann-Whitney *U*-tests) are used throughout and probability levels are two-tailed. To estimate the proportion of the variance explained by certain correlations, simple linear regression is used on log-transformed data.

Predation avoidance hypothesis, prediction 1a: dilution of predation risk

Where predator pressure is high, the size of groups (or the number of males) is expected to be larger than in populations with low predator pressure.

Bishop et al. (1981) provided a four-point scale as an index to evaluate predation risk from locations having a (1) full complement of predators, (2) partial complement of predators with only a few species represented by diminished numbers of individuals, (3) where most predators were eliminated, but leopards occasionally passed through and dogs harassed the langurs, and (4) locations with no predators. These authors emphasized the action of large mammalian predators, but raptors and snakes also prey on langurs (Rajpurohit and Sommer 1991). For studies conducted after Bishop et al. (1981), we estimated predation risk following the same criteria (analyzed separately). Sample sizes were small, so the four-point scale of Bishop et al. (1981) was collapsed into locations with a nearly intact predator community (category 1) versus those with non-intact communities (categories 2–4). Our additional rankings rated populations near urban centers as non-intact (Karnataka, Bangladesh, Raipur, Jaipur, Andhra Pradesh: Table 1) and other populations as near intact (Kanha Meadow, Ambagarh, Ranthambhore; J. Moore, personal communication; Reena and Ram 1992).

Predation avoidance hypothesis, prediction 1b: juvenile loss

Survival of immatures is expected to be lower in smaller groups. Since independently locomoting immatures are considered the most vulnerable class of individuals, the number of juveniles should decrease disproportionately in smaller groups as predation risk increases.

This prediction, and a number of subsequent predictions, concern the proportion of infants and/or juveniles expected in groups of varied sizes. To address these predictions one must take account of the necessary relationship between the number of adult females and the number of immatures they produce and construct a null model specific to each real population in which group size has no effect on numbers of immatures apart from that dictated by female reproductive capacity. To do this we generated 19 sets of 50 null populations. These 19 sets formed the expected to which we compared the observed real populations (Table 2). Each of 17 real pop-

ulations (the complete data set was not used because of insufficient data; see Tables 1 and 2.) was simulated by 50 randomly generated null populations. Each null population consisted of the same number of groups as the real population. Each null group within that population was composed of a number *X* of females which varied, in a uniform random manner, between the minimum value and the maximum value observed in the real population. Each null group also contained a random number *Y* of infants and *Z* of juveniles. We allowed *Y* and *Z* to vary as follows. To start these values were generated randomly as 0–100% of the number of null group females (*X*), thereby creating a reproductive output appropriate to each simulated group. Then each value was reduced by the value *W*. This value, *W*, was calculated as the difference between the mean number of infants (or juveniles) of the null population minus the mean of the real population. If positive (the randomly generated null groups had higher reproductive output than the real populations), *W* was subtracted from the randomly generated counts of each group. This manipulation forced the null groups to conform to the average reproductive output of the real population's groups so that the null population reflected the actual one more accurately. The final step was to truncate the infant and juvenile counts for each null group so that they remained within the maxima and minima of the actual population. This resulted in no significant difference between the null and real populations in mean number of females, infants, and juveniles.

Each real population was then compared to its own set of 50 null populations. We sought deviations in the observed slope from the expected (generated with the 50 null populations). If the slope of the simple linear regression of infants on females (and juveniles on females) in the population lay within the range of 94% (47 of 50) of the slopes calculated for the 50 null populations, then we concluded that there was no additional or extraneous effect of group size on numbers of immatures (null hypothesis cannot be rejected). If however, the population's slope lay below or above 94% of the null slopes, we inferred that some demographic change should be expected in future censuses of that population. All populations were considered in subsequent tests, regardless of whether or not they were identified as likely to experience some demographic change in the future.

The method we have chosen to simulate the real populations is intended to reflect the mean and the range of the real distribution of females and immatures. The result is a distribution of null populations with high variance. The effect of high variance is to generate a greater number of null populations of extreme slope. This provides a conservative assessment of whether the real population is actually extreme. The high variance of the null populations will affect all real populations similarly. The rank order of deviations of each real slope from the mean of its 50 null slopes is not expected to differ however. To confirm this, we generated null populations using a different algorithm. This second algorithm used a binomial distribution of females and immatures based around the mean of the real population. Thus, the null regressions generated tended to lie closer to the mean (lower variance).

We then tested all hypotheses against this new set of deviations and found no differences. In fact, the second algorithm produced deviations which were significantly positively correlated with the deviations produced in our first method ($r^2 = 0.88$, $P < 0.001$).

Resource defense hypothesis, prediction 2a: intrusion reduction

More frequent competition over resources requires larger defensive coalitions and thus, the number of female per group should correlate with higher population densities.

Exclusive use of resources, whether food, water, or shelter, requires an adequate system of monitoring the home range and adequate defenses against intrusion. We propose that population density can be considered an index of the frequency of intrusion by conspecifics since density should correlate positively with the likelihood of encountering conspecifics in a given area (e.g., Newton

Table 1 The demographic characteristics of the Hanuman langur populations used to test where predators are reduced in number or absent receive a 1. The sources for the demographic data are indicated in the footnote; - indicates that the information was not available

Study site (Reference)	No. of groups sampled	Mean group size	Mean no. of females (adult+subadult)	Mean no. of males (adult)	Mean no. of juveniles	Mean no. of infants	No. of nongroup juveniles	Predation index	Density (ind/km ²)	Nongroup males per bisexual group
Abu Forest (1)	13	20	12.8	1.9	2.3	3.1	29	1	31.6	8.00
Abu Town (1)	8	20	10.0	1.8	2.9	5.0	1	1	71.8	1.75
Jodpur (1,2)	6	51	26.2	1.0	7.5	9.0	56	1	18.0	23.33
Ranthambhore ^a (1)	7	43	22.9	2.7	6.0	8.6	34	0	14.6	17.29
Kanha Meadow (3)	14	20	11.5	2.4	2.6	5.2	0	0	46.1	4.00
Deotalao (3)	4	21	10.5	1.0	6.0	5.3	0	-	-	8.50
Gir Forest (4)	9	30	18.8	3.4	4.1	4.0	0	0	121.5	0.44
Mahdavi (5)	9	20	13.3	1.0	3.2	2.8	0	1	-	3.11
Bangladesh (6)	5	16	7.6	2.0	2.2	4.0	0	1	-	0
Raipur (7)	16	29	15.7	2.8	4.6	6.1	2	1	-	1.13
Simla (8,1)	7	37	13.3	4.0	14.0	6.1	0	-	24.6	1.50
Kanha (9)	30	17	9.2	1.2	3.9	3.0	0	0	-	2.50
Dharwar (10)	38	18	8.0	1.7	- ^b	-	11	1	91.5	1.58
Mundanthurai (11)	4	37	15.8	6.0	8.3	7.0	28	-	-	4.25
Karnataka #1 (12)	14	23	12.9	1.8	3.4	4.8	0	1	-	0.57
Karnataka #2 (12)	32	14	7.1	1.4	4.3	0.9	0	1	-	0.25
Andhra Pradesh (12)	12	31	8.4	1.6	3.3	3.8	0	1	-	0.33
Junbesi (13,16)	4	19	4.9	1.5	1.9	1.6	-	1	1.5	-
Orcha Forest (14)	3	19	7.3	3.7	3.0	4.3	0	0	4.4	-
Jairpur (17)	8	33	17.8	1.0	5.5	8.0	28	1	12.5	7.63
Ambagarh (17)	5	81	40.2	1.2	19.6	18.4	27	0	66.0	6.80
Rajaji (15)	4	46	-	3.4	-	-	-	0	90.0	-

Sources of the demographic data: 1 = Moore 1985; 2 = Mohnot 1971; 3 = Newton 1987; 4 = Rahaman 1973; 5 = Kankane 1984; 6 = Khan 1984; 7 = Sugiyama 1964; 8 = Sugiyama 1976; 9 = Kankane 1980; 10 = Sugiyama 1965; 11 = Ross 1993; 12 = Kurup 1984, pers. comm.; 13 = Bishop 1979; 14 = Jay 1965; 15 = Laws and von der Haar 1984; 16 = Curtin 1982; 17 = Reena and Ram 1992

^a One group of Ranthambhore langurs with 15 adult females and 40 adult males was considered to be the result of an ongoing multi-male influx

(J. Moore, pers. comm.) and was scored as a one-male group and 39 adult males were included in the tally of outside males

^b Immatures were not listed as a separate age class in this study

Table 2 The observed slopes of the relationship between the number of infants and the number of females and the number of juveniles and the number of females in a group for each of the 19

indicated populations and the expected slope based on the 50 randomly generated “null populations” (see Methods). For the references indicating the source of the demographic data see Table 1

Study site	Infants vs. females			Juveniles vs. females			Summed deviation
	Observed	Expected	Deviation	Observed	Expected	Deviation	
Abu Forest	0.31	0.33	−0.02	0.32	0.44	−0.12	−0.14
Abu Town	0.63	0.36	0.27	0.30	0.25	0.05	0.32
Jodhpur	0.30	0.14	0.16	0.35	0.28	0.07	0.23
Ranthambhore	0.60	0.49	0.11	0.30	0.27	0.03	0.14
Kanha 1987	1.02	0.37	0.65*	0.40	0.49	−0.09	0.56
Deotalao	0.95	0.27	0.68	0.03	0.21	−0.18	0.50
Gir Forest	−0.01	0.14	−0.15*	−0.08	0.27	−0.35	−0.50
Mahdavi	0.39	0.29	0.10	0.12	0.23	−0.11	−0.01
Bangladesh	0.72	0.28	0.44	−0.89	0.37	−1.26*	−0.82
Raipur	0.38	0.41	−0.03	0.16	0.31	−0.15	−0.18
Simla	0.45	0.35	0.10	0.95	0.35	0.60	0.70
Kanha 1980	0.25	0.37	−0.12	0.13	0.28	−0.15*	−0.27
Mundanthurai	0.56	0.41	0.15	0.18	0.19	−0.01	0.14
Karnataka #1	0.31	0.33	−0.02	0.13	0.30	−0.17*	−0.19
Karnataka #2	0.11	0.15	−0.04	0.06	0.35	−0.29*	−0.33
Jaipur	0.50	0.04	0.46*	0.43	0.16	0.27	0.73
Ambagarh	0.71	0.21	0.50*	0.38	0.17	0.21	0.71
Andhra Pradesh	0.69	0.48	0.21	0.04	0.37	−0.33*	−0.12
Junbesi	0.23	0.18	0.05	0.88	0.25	0.63*	0.68

*Observed value differs significantly from expected value, $P \leq 0.05$

1992). This prediction considers only females, since females have been traditionally regarded as the most active and highly motivated resource competitors (Wrangham 1980; Cheney 1992).

Resource defense hypothesis, prediction 2b: increased birth and recruitment

If larger groups were disproportionately buffered from fluctuations in food supply or resource availability when compared to smaller groups, one would expect that birth rate and immature survival should be higher in larger groups. Therefore, larger groups of langurs are expected to have more immatures per female (statistically circumventing the biological relationship between the number of adult females and the number of immatures using the null model approach outlined for prediction 1b).

Conspecific threat hypothesis, prediction 3a: non-group male threat

In populations with higher densities of non-group males, the need for improved cooperative defense against infanticidal males is expected to lead to larger groups.

We propose that the number of non-group adult and subadult males divided by the number of bisexual groups in the study population reflects the risk of take-over and the associated probability of infanticide and/or juvenile expulsion. Similar suggestions have been made by Moore (1985) and Newton (1988). Evidence suggests that both males and females are involved in cooperative defense of the group against outsiders (Hrdy 1977; Newton 1987), however to illustrate any potential differences of strategies of male and female langurs, this analysis is done for all group-members, only males, and only females.

When applying the prediction to females, a potential problem arises with assigning the direction of causality: the pressure of outside males per bisexual group is suggested to cause females to live in larger groups, rather than the converse, that the more females exist per group, the more males are forced outside of groups. The

latter suggestion rests on the assumption that total number of females and non-group males are positively correlated. This condition did not hold (total number of females vs. non-group males $r_s = 0.23$, $P = 0.351$, $n = 19$).

Conspecific threat hypothesis, prediction 3b: small alliances suffer

Infant survival is expected to be reduced when defense is compromised by small group size, particularly when the risk of take-over is high.

The risk of infanticide should be reflected in infant mortality rates. However, there are no data on infant mortality for most of the study populations. Furthermore, birth rate may be higher in groups facing repeated infanticidal episodes (Sommer and Mohnot 1985; Butynski 1990), thus obscuring any effects detectable in a census. We therefore use counts of juveniles (relative to the reproductive capacity of the group, using the null model approach) to detect differences in infant survival. This test does not directly identify the effects of infanticide, since juvenile counts may be reduced by the expulsion of older male juveniles following take-overs (Reena and Ram 1991). However, early expulsion of juveniles is costly in terms of their survival (Rajpurohit and Mohnot 1988; Rajpurohit 1991a). Thus, low numbers of juveniles, whether dead or expelled, should reflect the history of male take-overs.

Conspecific threat hypothesis, prediction 3c: juvenile expulsion

Populations with higher risks of take-over suffer more frequent juvenile expulsion, thus the number of juveniles outside of groups should be positively correlated with the index of take-over risk.

Results

Prior to examining the predictions from these hypotheses, it is valuable to examine whether variation exists

in factors influencing group size and composition, and thus whether it is realistic to expect to find differences in the populations that could covary with the parameters proposed by the predictions. The randomly generated null populations provided us with a series of regression slopes between the number of females and the number of infants in the group with which to compare the observed regression slopes for 17 of the populations (Table 2). Thus, one can ask how many of the real populations exhibited a positive or negative effect of group size on the number of surviving infants per female. The 50 null slopes for infants regressed on females averaged 0.31 ± 0.11 (range 0.14–0.49), while observed slopes averaged 0.46 ± 0.28 (range 0.009–1.02). Deviation values were calculated simply as observed minus expected (Table 2). Only two populations unambiguously displayed group size effects on number of infants (Kanha Meadow, a significantly positive effect; Gir Forest, a significantly negative effect). Overall, populations tended to show a weak positive effect of group size (overall mean slope deviation = +0.24), although more than 35% of the populations exhibited a negative effect.

The 50 null slopes for juveniles averaged 0.31 ± 0.08 (range 0.19–0.49), while actual slopes averaged 0.20 ± 0.39 (range –0.89–0.95). Six populations displayed significant group size effects on juvenile survival and retention, yet only in Junbesi was the effect positive. Overall, 70.6% of the populations displayed negative deviations for juveniles indicating that most populations showed diminished numbers of juveniles compared to the expected.

If the deviations of infant slopes are added to those of juveniles for each of the populations, we can calculate a summed effect of increasing group size (Table 2, summed deviations). Nine populations show a negative summed slope deviations, while eight showed positive summed slope deviations. The populations with negative summed deviations (neither birth rate, infant survival nor juvenile survival/retention were improved by large group size) would be expected to show some decline in group size from the time of study to the present. The others might be expected to display an increase in group size. The population at Gir Forest displayed the strongest negative effect of increasing group size (significant both at the infant and juvenile stages). Starin (1978) re-censused Gir Forest and found a decrease in number of females and juveniles per group, suggesting a sharp demographic down-turn had occurred since the census published by Rahaman (1973).

The preceding analysis indicates that differences in group size have noticeable relationships to the reproductive outputs of different populations. The remainder of this paper attempts to identify external selective pressures which may explain this variation.

Predictions: predation avoidance hypothesis

Prediction 1a

Where predator pressure is high, the size of groups (or the number of males) is expected to be larger than in populations with low predator pressure.

Using only those populations listed in Bishop et al. (1981) and in Table 1 yielded two different populations with nearly a full complement of predators and four with incomplete complements. There were no differences in the group sizes in the two types of populations (intact mean group size = 24; non-intact mean group size = 27, Mann-Whitney $U = 4.0$, $P = 0.999$). Populations with nearly intact predator communities show higher numbers of males, although the significance was marginal (intact mean number of resident males = 3.55; non-intact mean number of resident males = 1.5, $U = 0.0$, $P = 0.064$). When we include populations studied after Bishop et al. (1981), there were still no differences in group size (nearly intact mean group size = 36.5, $n = 7$; non-intact mean group size = 24.9, $n = 11$, $U = 28.0$, $P = 0.34$), while the number of resident males was higher in populations with intact predator communities (nearly intact mean number of resident males = 2.56, $n = 7$; non-intact mean number of resident males = 1.68, $n = 11$, $U = 20.0$, $P = 0.09$).

Prediction 1b

The number of juveniles (controlled for the number of females per group) should decrease in smaller groups as predation risk increases.

This prediction requires a test for association between predation risk and the slope deviations for infants and/or juveniles. Using Bishop et al. (1981), there was only one community with a nearly intact predator community where we had corresponding data, thus no test was performed. Using the larger sample of sites, we found no difference between populations with nearly intact predator communities and those with non-intact communities (nearly intact $n = 5$, non-intact $n = 10$, infants $U = 25$, $P = 0.99$; juveniles $U = 24.5$, $P = 0.951$).

Predictions: resource-defense hypothesis

Prediction 2a

More frequent competition over resources requires larger defensive coalitions and thus, the number of female per group should correlate with higher population densities.

We found no relationship between population density and the mean number of subadult and adult females ($r_s = 0.21$, $P = 0.49$, $n = 13$).

Several authors have ascribed high rates of take-overs to high population densities (Yoshida 1968; Rudran 1973; Reena and Ram 1992), but our analysis indicates that the number of outside males per bisexual group is the relevant parameter regarding take-over. In this dataset, we found that as population density increased, there was a tendency for non-group male numbers to decrease ($r_s = -0.55$, $P = 0.098$, $n = 10$).

Prediction 2b

Larger groups reproduce more successfully. Larger groups of langurs are expected to have more immatures per female.

Population density was not related to the deviation values for infants ($r_s = -0.03$, $P = 0.93$, $n = 10$), but was marginally negatively related to the deviation value for juveniles ($r_s = -0.62$, $P = 0.061$, $n = 10$). For juveniles this finding is opposite to that predicted by the resource defense hypothesis (as density increased, the benefit of living in a large group decreased).

Predictions: conspecific threat hypothesis

Prediction 3a

As the risk of take-over increases (number of non-group subadult and adult males divided by the number of bisexual groups), either group size, the number of females (adult and subadult) per group, and/or the number of males per group is expected to increase.

The number of non-group adult and subadult males (divided by the number of bisexual groups) was weakly related to the mean group size ($r_s = 0.47$, $P = 0.045$, $n = 19$), it was not related to the number of males in the group ($r_s = -0.30$, $P = 0.188$), but it was related to mean number of resident adult and subadult females ($r_s = 0.57$, $P = 0.016$, Fig. 1).

Prediction 3b

Infant survival is expected to be reduced when defense is compromised by small group size, particularly when risk of take-over is high.

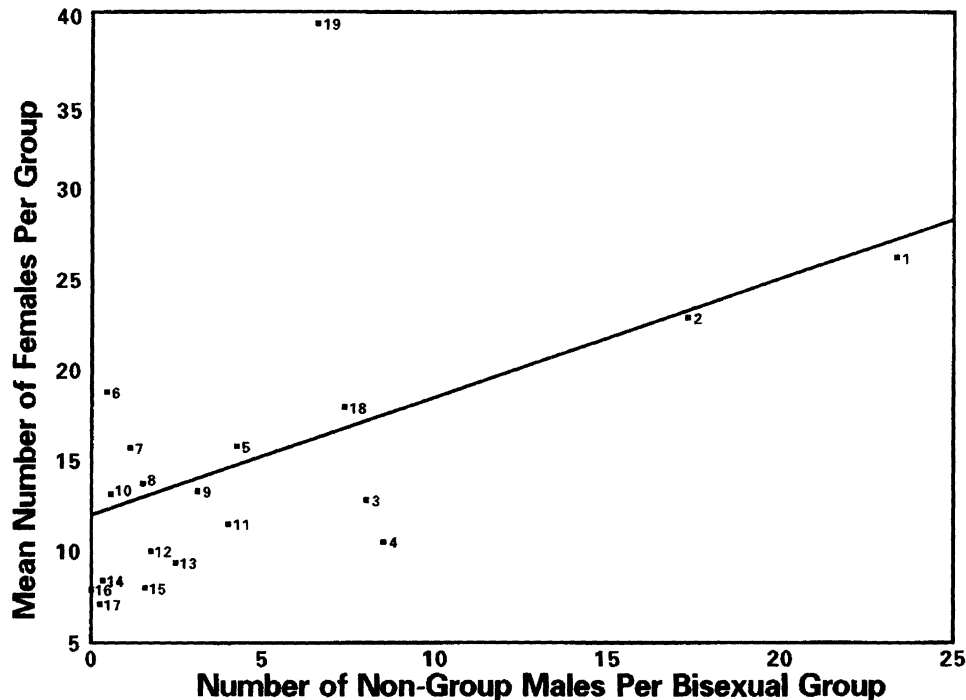


Fig. 1 The relationship between the mean number of females per group and the number of nongroup males per bisexual group for 19 populations of langurs (*Presbytis entellus*). The populations are numbered and the figures in parentheses behind the populations name are being the within-population deviations (observed-expected) of juveniles regressed on females: 1 Jodhpur (+0.07), 2 Ranthambhore (+0.03), 3 Abu Forest (-0.12), 4 Deotalao (-0.18), 5 Mudanthurai (-0.01), 6 Gir Forest (-0.35), 7 Raipur (-0.15), 8 Simla (+0.60), 9 Mahdavi (-0.11), 10 Karnataka #1 (-0.17), 11 Kanha 1987 (-0.09), 12 Abu Town (+0.05),

13 Kanha 1980 (-0.15) 14 Andhra Pradesh (-0.33), 15 Dharwar (there is no slope since immatures were not subdivided into infants and juveniles), 16 Bangladesh (-1.26), 17 Karnataka #2 (-0.29), 18 Jaipur (+0.27), and 19 Ambagarh (+0.21). The figure might be interpreted to indicate that the relationship may be driven by the extreme Jodhpur and Ranthambhore populations. However, if both axes are log transformed, these populations do not appear as outliers and the relationship is still significant (Pearson correlation $r = 0.554$, $P = 0.026$).

The slope deviation for juveniles (Table 2) was positively related to the number of non-group males per bisexual group ($r_s = 0.62$, $P = 0.011$, $n = 19$). Thus, controlling for the number of females, we find that large groups have more juveniles, especially as the threat of conspecific attack increases.

Prediction 3c

Populations with higher risks of take-over suffer more frequent juvenile expulsion. The number of juveniles outside of groups should be positively correlated with the index of conspecific threat.

As predicted, the number of non-group juveniles was strongly related to the number of non-group adult males per bisexual group ($r_s = 0.70$, $P = 0.004$, $n = 19$).

Discussion

We have attempted to identify patterns of group size and composition that would result if either predation threat, intergroup resource defense, or conspecific threat were selective forces influencing langur populations. We found that variation in mean group size did not covary with the intensity of predation between langur populations. However, the mean number of resident males tended to be greater in areas with nearly intact predator communities than in areas where predators were greatly reduced or eliminated (see also van Schaik and Horstermann 1994). Counter to what would be predicted by the predation avoidance hypothesis, the number of juveniles (controlling for number of females) was not reduced in smaller groups within populations facing higher predation risk. Based on the assumption that population density reflects the frequency of intrusion by competing conspecific groups, we found no support for the claim that increasing need for intergroup resource defense led to increased group size nor was there any evidence that larger groups had disproportionately greater numbers of infants or juveniles than smaller groups as the population density increased.

In contrast, three independent lines of evidence indicate that our index of conspecific threat influences langur group size and composition. The index was calculated as the number of adult and subadult males living outside of groups divided by the number of bisexual groups in the census. First, the mean number of subadult and adult females in langur groups was positively associated with this index. Second, the number of immatures outside of groups, which we suggest reflects the recent history of expulsion of immature males, was positively related to this same measure of conspecific threat. Finally, the greater the index, the steeper the slope relating the number of immatures to the number of females within groups, indicating that larger groups were more successful in protecting immatures from

infanticide and preventing juvenile expulsion due to attacks by non-group males than smaller groups.

Van Schaik (1983) presented a similar examination of the relative importance of the intergroup resource defense and predation threat on primate group composition. He argued that improved predation avoidance, coupled with heightened intragroup feeding competition, would reduce birth rates, but increase juvenile survival in larger groups. In contrast, the pressure of between-group feeding competition predicted higher birth rates and increased juvenile survival in larger groups (Wrangham 1980). Accordingly, he tested whether the ratio of infant to adult females increased or decreased as the number of adult females increased in groups within 28 populations of several species of primates. His insightful discussion still remains valid, however a revision of his analysis is appropriate for two reasons. First, the regression equations he used incorporated number of females on both axes (infants per female on the y and females on the x -axis). This will automatically favor a negative slope and artificially elevate the chances of obtaining significant support for the predation-avoidance hypothesis. To verify that this was true, 400 group compositions were simulated (the number of females was randomly varied from 1 to 10 and infants varied from 0 to number of females). These simulated groups were tested in sets of ten using linear regression of infants per female (y -axis) versus females (x -axis) to determine whether the null hypothesis (of no relationship) produced a negative slope. The resulting slope was negative in 32 out of 40 (significantly so in 25%) of these regressions (ranging from -0.075 to $+0.026$, with a mean of -0.0266). Since a negative slope was argued to support the predation-avoidance hypothesis, the test was biased towards its acceptance. Secondly, as Moore (1984) has pointed out, many of the sample populations did not represent female-bonded groups and another quarter of his sample represented populations which do not display female participation in intergroup encounters. Thus, the sample consisted of many populations which were not encompassed by the resource-defense hypothesis.

Our findings suggest that conspecific threat influences the size and composition of langur groups. Based on these findings it seems reasonable to speculate that this selective pressure also has the potential of influencing the nature of alliances in this species, if only simply by influencing whether particular ages and sexes are in the group and thus present to form alliances. Reports of female coalitions against males who threaten immatures come from many studies of Hanuman langurs (Yoshida 1968; Hrdy 1974, 1977; Boggess 1980; Vogel and Loch 1984; Sommer 1987; Rajpurohit 1991b) as well as other species (Smuts and Smuts 1993). Yet, cooperative defense by females has been regarded as ineffective in gorillas (Watts 1989) and langurs (Hrdy 1977), and of only limited effectiveness in lions (Packer and Pusey 1983, 1984; Pusey and

Packer 1993). Males are often considered to be more effective coalition partners (Struhsaker and Leland 1987) and have a larger genetic investment in the offspring than female coalition partners. There are two possible explanations that can reconcile the suggested ineffectiveness of female langurs in coalitionary defense of young and our findings that the number of females in a group is a function of the risk of conspecific threat. First, it could be that large numbers of cooperating females deter new males from attempting infanticidal attacks. Second, the observations of ineffective female defense may have been misinterpreted. In the earliest detailed account of female response to infanticidal attacks, Hrdy (1977) described how it took a male one month of frequent attempts to seriously injure an infant. He was faced by coalitions of females who could at times force him to retreat. The eventual success of the male could be interpreted as failure by the females, but considering the size dimorphism typical of langurs (1.6: Harvey et al. 1987), the month-long delay illustrates that males may be blocked for long periods in their attempts to kill infants. One month may be time enough for older infants to develop independence and thereby avoid future attacks (Sommer and Mohnot 1985) or for other female counter-strategies to operate such as pseudo-estrus or temporary dispersal (Hausfater 1984; Smuts and Smuts 1993). Since Hrdy's observations originated from a group of six females (Hrdy 1977), larger female coalitions may be even more successful: providing larger numbers of potential protectors at any time, as well as allowing more consistent, long-lasting, and vigilant defense against persistent attacks by a male. Sommer (1987) reports that one-third of female langur coalitions against males involve six to eight adult females not including the mother.

Our data provide several, independent lines of indirect evidence that conspecific threat can be an important selective pressure influencing the size and composition of Hanuman langur groups and may influence the advantages of female-female alliances. Past research has suggested the importance of conspecific threat with respect to female-male bonds (Watts 1989; van Schaik and Dunbar 1990; van Schaik and Kappeler 1993). If group size and female-female associations are favored by defense against conspecific threat, then a wide range of taxa may be influenced by this selective pressure.

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References

- Agoramoorthy G, Mohnot SM (1988) Infanticide and juvenicide in Hanuman langurs (*Presbytis entellus*) around Jodhpur, India. *Hum Evol* 3:279–296
- Agoramoorthy G, Mohnot SM, Sommer V, Srivastava A (1988) Abortions in free-ranging Hanuman langurs (*Presbytis entellus*): a male induced strategy? *Hum Evol* 3:297–308
- Alexander RD (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5:325–383
- Altmann S (1974) Baboons, space, time, and energy. *Am Zool* 14:221–248
- Bishop NH (1979) Himalayan langurs: temperate colobines. *J Hum Evol* 8:251–281
- Bishop NH, Hrdy SB, Teas J, Moore J (1981) Measures of human influences in habitats of South Asian monkeys. *Int J Primatol* 2:153–167
- Bogges J (1980) Intermale relations and troop male membership changes in langurs *Presbytis entellus* in Nepal. *Int J Primatol* 1:233–274
- Butynski T (1990) Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecol Monogr* 60:1–26
- Chapman CA (1988) Patch use and patch selection by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. *Behaviour* 105:99–116
- Chapman CA, Wrangham RW, Chapman LJ (1995) Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behav Ecol Sociobiol* 36:59–70
- Cheney DL (1992) Intragroup cohesion and intergroup hostility: the relation between grooming distribution and intergroup competition among female primates. *Behav Ecol* 3:334–345
- Curtin RA (1982) Range use of langurs in highland Nepal. *Folia Primatol* 38:1–18
- DeVore I, Hall KRL (1965) Baboon ecology. In: DeVore I (ed) *Primate behaviour: field studies of monkeys and apes*. Holt Rinehart and Winston, New York, pp 20–52
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Harvey PH, Martin RD, Clutton-Brock TH (1987) Life histories in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker, TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 181–196
- Hauser MD (1988) Variation in maternal responsiveness in free-ranging vervet monkeys: a response to infant mortality risk? *Am Nat* 131:573–587
- Hausfater G (1984) Infanticide in langurs: Strategies, counter-strategies and parameter values. In: Hausfater G, Hrdy SB (eds) *Infanticide: comparative and evolutionary perspectives*. Aldine, New York, pp 257–281
- Hausfater G, Hrdy SB editors (1984) *Infanticide: comparative and evolutionary perspectives*. Aldine, New York
- Hrdy SB (1974) Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol* 22:19–58
- Hrdy SB (1977) *The langurs of Abu*. Harvard University Press, Cambridge
- Hrdy SB (1979) Infanticide among animals: a review, classification and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1:13–40
- Isbell L (1990) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav Ecol* 2:143–155
- Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behav Ecol Sociobiol* 17:125–138
- Jay P (1965) The common langur of North India. In: DeVore I (ed) *Primate behaviour: Field studies of monkeys and apes*. Holt Rinehart and Winston, New York, pp 197–249

- Kankane PL (1980) Studies on the Hanuman langurs *Presbytis entellus* (Dufresne) (Primates: Cercopithecidae), at Kanha National Park, M.P. Proc Wildlife Workshop Dehra Dun, pp 61–71
- Kankane PL (1984) Research on the Hanuman langur, *Presbytis entellus*, of the Madhav National Park. In: Roonwal ML, Mohnot SM, Rathore NS (eds) Current primate researches. Department of Zoology, Jodhpur University, pp 23–31
- Khan M (1984) Ecology and conservation of the common langur *Presbytis entellus* in Bangladesh. In: Roonwal ML, Mohnot SM, Rathore NS (eds) Current primate researches. Department of Zoology, Jodhpur University, pp 33–39
- Kurup GU (1984) Census survey and population ecology of Hanuman langur, *Presbytis entellus* (Dufresne 1797) in south India. Proc Indian Natl Sci Acad 50:245–256
- Laws JW, vonder Haar Laws J (1984) Social interactions among adult male langurs (*Presbytis entellus*) at Rajaji Wildlife Sanctuary. Int J Primatol 5:31–50
- Lee PC (1987) Nutrition, fertility and maternal investment in primates. J Zool 213:409–422
- Manson JH, Wrangham RW (1991) Intergroup aggression in chimpanzees and humans. Curr Anthropol 32:369–390
- McComb K, Pusey A, Packer C, Grinnell J (1993) Female lions can identify potential infanticidal males from their roars. Proc R Soc Lond 252:59–64
- Mohnot SM (1971) Some aspects of social changes and infant-killing in the Hanuman langur, *Presbytis entellus* (Primates: Cercopithecidae), in Western India. Mammalia 35:175–198
- Mohnot SM (1984a) Research potential of Jodhpur langurs (*Presbytis entellus*). In: Roonwal ML, Mohnot SM, Rathore NS (eds) Current primate researches. Department of Zoology, Jodhpur University, pp 47–56
- Mohnot SM (1984b) Some observations on all-male bands of the Hanuman langur, *Presbytis entellus*. In: Roonwal ML, Mohnot SM, Rathore NS (eds) Current primate researches. Department of Zoology, Jodhpur University, pp 343–356
- Mohnot SM (1984c) Langur interactions around Jodhpur (*Presbytis entellus*). In: Roonwal ML, Mohnot SM, Rathore NS (eds) Current Primate Researches. Department of Zoology, Jodhpur University, pp 399–412
- Moore J (1984) Female transfer in primates. Int J Primatol 5: 537–589
- Moore J (1985) Demography and sociality in primates. PhD thesis, Harvard University, Cambridge.
- Newton P (1986) Infanticide in an undisturbed forest population of Hanuman langurs, *Presbytis entellus*. Anim Behav 34: 785–789
- Newton PN (1987) The social organization of forest Hanuman langurs (*Presbytis entellus*). Int J Primatol 8:199–232
- Newton PN (1988) The variable social organization of Hanuman langurs (*Presbytis entellus*), infanticide and the monopolization of females. Int J Primatol 9:59–77
- Newton PN (1992) Feeding and ranging patterns of forest Hanuman langurs (*Presbytis entellus*). Int J Primatol 13:245–282
- O'Brien TG (1991) Female-male social interactions in wedge-capped capuchin monkeys: benefits and costs of group living. Anim Behav 41:555–567
- Packer C, Pusey AE (1983) Adaptations of female lions to infanticide by incoming males. Am Nat 121:716–728
- Packer C, Pusey AE (1984) Infanticide in carnivores. In: Hausfater G, Hrdy SB (eds) Infanticide: Comparative and evolutionary perspectives. Aldine, New York, pp 31–42
- Pereira ME (1983) Abortion following the immigration of an adult male baboon (*Papio cynocephalus*). Am J Primatol 4:93–98
- Pusey AE, Packer C (1993) Infanticide in lions: consequences and counterstrategies. In: Parmigiani S, Saal FS von (eds) Infanticide and parental care. Harwood Academic Press, London
- Rahaman H (1973) The langurs of the Gir Sanctuary (Gujarat) – a preliminary survey. J Bombay Nat Hist Soc 70:294–314
- Rajpurohit LS (1991a) Selection of male band by male juveniles and their integration in Hanuman langur, *Presbytis entellus*. In: Ehara A, Kimura T, Takenaka O, Iwamoto M (eds) Primatology today. Elsevier, New York, pp 255–299
- Rajpurohit LS (1991b) Resident male replacement, formation of a new male band, and paternal behaviour in *Presbytis entellus*. Folia Primatol 57:154–164
- Rajpurohit LS, Mohnot SM (1988) Fate of ousted male residents of one-male bisexual troops of Hanuman langurs (*Presbytis entellus*) at Jodhpur Rajasthan, India. Hum Evol 3:309–318
- Rajpurohit LS, Sommer V (1991) Sex differences in mortality among langurs (*Presbytis entellus*) of Jodhpur, Rajasthan. Folia Primatol 56:17–27
- Reena M, Ram M (1991) Departure of juvenile male *Presbytis entellus* from the natal group. Int J Primatol 12:39–43
- Reena M, Ram M (1992) Rate of take-overs in groups of Hanuman langurs (*Presbytis entellus*) at Jaipur. Folia Primatol 58:61–71
- Robinson JG (1986) Seasonal variation in use of time and space by the wedge-capped capuchin monkey *Cebus olivaceus*: Implications for foraging theory. Smithson Contrib Zool 431:1–60
- Ross C (1993) Take-over and infanticide in south Indian Hanuman langurs (*Presbytis entellus*). Am J Primatol 30:75–82
- Rudran R (1973) Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. Folia Primatol 19:166–192
- Schaik CP van (1983) Why are diurnal primates living in groups? Behaviour 87:120–143
- Schaik CP van, Dunbar RIM (1990) The evolution of monogamy in large primates: a new hypothesis and some crucial tests. Behaviour 115:30–61
- Schaik CP van, Hooff JARAM van (1983) On the ultimate causes of primate social systems. Behaviour 85:91–117
- Schaik CP van, Horstermann M (1994) Predation risk and the number of adult males in a primate group: a comparative test. Behav Ecol Sociobiol 35:261–272
- Schaik CP van, Kappeler PM (1993) Life history, activity period and lemur social systems. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 241–260
- Schaik CP van, Noordwijk MA van (1989) The special role of male *Cebus* monkeys in predation avoidance and its effects on group composition. Behav Ecol Sociobiol 24:265–276
- Schaik CP van, Noordwijk MA van, Boer RJ de, Tonkelaar I den (1983) The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). Behav Ecol Sociobiol 13:173–181
- Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. Adv Stud Behav 22: 1–63
- Sommer V (1987) Infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan/India): recent observations and a reconsideration of hypotheses. Primates 28:163–197
- Sommer V, Mohnot SM (1985) New observations on infanticide among Hanuman langurs (*Presbytis entellus*) near Jodhpur (Rajasthan/India). Behav Ecol Sociobiol 16:245–248
- Starin ED (1978) A preliminary investigation of home range use in the Gir Forest langur. Primates 19:551–568
- Struhsaker TT, Leland L (1987) Colobines: infanticide by adult males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 83–97
- Sugiyama Y (1964) Group composition, population density, and some sociological observations of Hanuman langurs (*Presbytis entellus*). Primates 5:7–38
- Sugiyama Y (1965) On the social change of Hanuman langurs (*Presbytis entellus*) in their natural condition. Primates 6:381–418
- Sugiyama Y (1976) Characteristics of the ecology of the Himalayan langur. J Hum Evol 5:249–277

- Terborgh J, Janson CH (1986) The socioecology of primate groups. *Annu Rev Ecol Syst* 17:111–135
- Trumbo ST (1990) Reproductive benefits of infanticide in a biparental burying beetle *Nicrophorus orbicollis*. *Behav Ecol Sociobiol* 27:269–273
- Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav Ecol Sociobiol* 6:29–38
- Vogel C, Loch H (1984) Reproductive parameters, adult-male replacements, and infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan), India. In: Hausfater G, Hrdy SB (eds) *Infanticide: comparative and evolutionary perspectives*. Aldine, New York, pp 237–256
- Wasser SK, Starling AK (1986) Reproductive competition among female yellow baboons. In: Else JG, Lee PC (eds) *Primate ontogeny, cognition and social behaviour*. Cambridge University Press, Cambridge, pp 343–354
- Watts DP (1989) Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology* 81:1–18
- Whitten P (1983) Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *Am J Primatol* 5:139–159
- Wrangham RW (1979) On the evolution of ape social systems. *Soc Sci Info* 18:335–368
- Wrangham RW (1980) An ecological model of female-bonded groups. *Behaviour* 75:262–300
- Wrangham RW (1986) Ecology and social relationships in two species of chimpanzees. In: Rubenstein DI, Wrangham RW (eds) *Ecological aspects of social evolution: birds and mammals*. Princeton University Press, Princeton, pp 352–378
- Yoshida K (1968) Local and intertroop variability in ecology and social behavior of common Indian langurs. In: Jay PC (ed) *Primate studies in adaptation and variability*. Rinehart and Winston, New York, pp 217–242

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