

## REVIEW

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## The number of males in primate social groups: a comparative test of the socioecological model

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**Abstract** As applied to polygynous mammals, the socioecological model assumes that environmental risks and resources determine the spatial and temporal distribution of females, which then sets male strategies for monopolizing fertile matings. The effects of female spatial distribution (i.e., female number) and temporal overlap (female mating synchrony) have been examined in comparative studies of primates, but the relative influence of these two factors on male monopolization potential (the number of males) remains unclear. One particular problem is that female synchrony is more difficult to estimate than female number. This paper uses multivariate statistical methods and three independent estimates of female synchrony to assess the roles of spatial and temporal effects in the context of a phylogenetically corrected dataset. These analyses are based on sensitivity analyses involving a total of four phylogenies, with two sets of branch length estimates for each tree, and one nonphylogenetic analysis in which species values are used (because male behavior may represent a facultative response to the distribution of females). The results show: (1) that breeding seasonality predicts male number (statistically significant in six out of nine sensitivity tests); (2) that expected female overlap, after controlling for female group size using residuals, also accounts for the number of males in primate groups (significant in eight out of nine tests), and (3) that actual estimates of female mating synchrony predict male number, again after correcting for female group size (significant in five out of nine tests). Nonsignificant results are in the predicted direction, and female group size is significant in all statistical tests. These analyses therefore demonstrate an independent influence of fe-

male temporal overlap on male monopolization strategies in mammalian social systems.

**Key words** Primates · Mating synchrony · Group composition · Phylogeny · Comparative methods

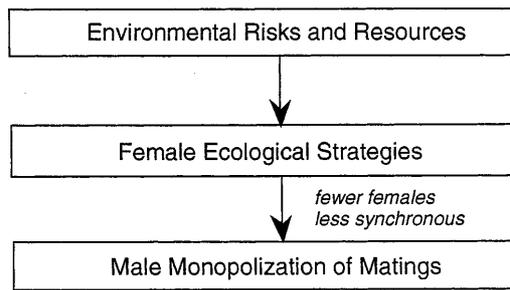
### Introduction

A primary goal of mammalian socioecology is to understand the selective factors that drive variation in social systems (Crook and Gartlan 1966; Eisenberg et al. 1972). The causality and interactions among the important factors can then be represented as a general model and tested using experimental (Ims 1988) and comparative (Clutton-Brock and Harvey 1977; Mitani et al. 1996) approaches.

As applied to polygynous mammals, the socioecological model proposes that environmental risks and resources determine the spatial and temporal distribution of fertile females; this “spatiotemporal” distribution of females then structures male options for monopolizing fertile matings (Fig. 1; Emlen and Oring 1977; Clutton-Brock 1989). Spatial distribution involves the “clumping” of females in space. Temporal distribution refers to overlap in female fertile periods (i.e., mating synchrony). This model has been studied extensively in primates, where information is available to test this framework. In primates, male monopolization of female groups is thought to increase (resulting in fewer males in the group) when there are fewer females in the group (the spatial effect) and when females are less synchronously receptive (the temporal effect).

Within-species variation supports both spatial (Altmann and Altmann 1970; Newton 1988; Alberts and Altmann 1995) and temporal (Cords 1984; Srivastava and Dunbar 1996) effects. In cross-species analyses, spatial effects have been convincingly demonstrated. For example, Andelman (1986) showed that male number is

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**Fig. 1** The standard socioecological model in which environmental risks and resources impact the reproductive success of females more than males (i.e., mammalian females bear gestation and lactation costs, and they protect offspring from predators). In contrast, male reproductive success is more dependent on access to fertile mates. Thus, environmental factors are thought to structure female options, and the resulting spatiotemporal distribution of females sets male options for maximizing mating opportunities. Males are better able to successfully monopolize a group of females when there are fewer females and when these females are less synchronous in their mating. Although not shown here, males may also manipulate females directly, for example, through infanticide or herding of females during fertile periods (see Discussion)

correlated with female number across species of cercopithecine primates. The effect of female number is not generally disputed (Dunbar 1988; Altmann 1990; Mitani et al. 1996).

More debated are temporal effects as an explanation for variation in male number across species. One particular problem is that female mating overlap is difficult to estimate, and this forces researchers to use relatively crude “proxies” for overlap. For example, Ridley (1986) used breeding seasonality as a proxy for female overlap, based on the logic that female overlap should be more common, simply by chance, when females mate in a shorter window of time. Under this assumption, Ridley (1986) provided evidence for a temporal effect by showing a correlation between breeding seasonality and multimale social systems (i.e., a single male is less able to monopolize a group of seasonally breeding females). Altmann (1990) criticized Ridley (1986) on a number of issues, maintaining that female number probably plays the more important role in determining male number. In addition to Ridley’s (1986) study and a more general approach by Dunbar (1988, 1999), two studies in macaques provide some evidence for a temporal effect at the species level: Oi (1996) showed that social groups of seasonally breeding macaques have fewer females per male, while Paul (1997) showed that seasonal species exhibit a weaker relationship between male rank and reproductive success.

Mitani et al. (1996) attempted to resolve this issue by performing a phylogenetic comparative test to differentiate between spatial and temporal effects, concluding that female number, but not breeding seasonality, determines the number of males in primate groups. According to them, the primary linkage in the socioecological model (as it applies to primates) involves female spatial distribution.

Mitani et al.’s (1996) study is a clear improvement on previous studies, and their research has helped refocus attention on this important issue. However, there are several reasons why their methods may have missed more subtle temporal effects, and it is therefore premature to dismiss the role of female overlap in the socioecological model. First, instead of assuming that spatial and temporal effects are mutually exclusive, the two effects should be examined simultaneously. Thus, multivariate statistical methods are more appropriate (e.g., Srivastava and Dunbar 1996; see also Quinn and Dunham 1983). Alternatively, male number could be compared to a composite measure that incorporates both spatial and temporal effects (e.g., Dunbar 1988, 1999; see also Mitani et al. 1996, p. 326). However, this would make it difficult to examine the relative roles of the two effects.

Second, more sensitive statistical tests are possible. For example, the independent variables in Mitani et al.’s (1996) analysis are continuous (breeding seasonality and female group size), yet the authors dichotomized their continuous measures into binary traits for most analyses (seasonal versus nonseasonal, and small versus large female groups; see also Ridley 1986), unnecessarily reducing the statistical power for phylogenetic comparative tests (Garland et al. 1993). A related concern involves their choice of comparative methods. To avoid problems of ancestral state reconstruction (e.g., Omland 1997; Cunningham et al. 1998), Mitani et al. (1996) used pairwise comparisons that only examined evolutionary transitions on branches connecting extant species (e.g., Møller and Birkhead 1992). While this approach will tend to be conservative and may be appropriate in some cases (Deaner and Nunn 1999), pairwise comparisons reduce the degrees of freedom from the maximum available; thus, more subtle effects might be missed. In any case, results based on independent contrasts may not be overly sensitive to errors in character state reconstruction (Schluter et al. 1998; T. Oakley, personal communication).

A final problem is not limited to Mitani et al.’s (1996) study but deserves serious attention in future comparative research on the socioecological model. Following other researchers (e.g., Ridley 1986; Newton 1988), Mitani et al. (1996) used reproductive seasonality as a proxy for overlap in female receptivity. Another measure of overlap calculates expected female overlap based on mating and life history traits (Dunbar 1988, 1999). As with breeding seasonality, expected overlap assumes that ovulation is a chance event among females.

A third way to quantify the temporal effect is to estimate actual female overlap. This measure does not assume that ovulation is random among females, and it takes into account socially mediated synchrony, where a female’s sexual state is dependent on the sexual behavior of other females in her group (see McClintock 1981, 1983). Female mating periods can be “underdispersed,” where females are more synchronous in their mating than expected by chance, or sexual behavior can be

“overdispersed,” where females are less synchronous than expected by chance. Pereira’s (1991) research on ringtailed lemurs (*Lemur catta*) provides an example of how socially mediated synchrony can lead to problems in previous estimates of the temporal effect. Ringtailed lemurs are assigned the shortest breeding-season duration in Mitani et al.’s (1996) dataset (38 days), rendering it the most “synchronous” among the 49 listed. However, Pereira (1991) has shown that within their relatively short mating season, ringtailed lemur fertile periods rarely overlap, and so they may actually have the least synchronous cycles in that dataset. Coupled with the problems discussed above, cases of socially mediated synchrony may explain why Mitani et al. (1996) found no support for the temporal effect.

In this paper, I reexamine the socioecological model in primates to determine whether female temporal overlap explains variation in the number of males across species (i.e., male monopolization potential). In particular, I reanalyze Mitani et al.’s (1996) data using multivariate statistical methods and more sensitive phylogenetic comparative tests, and I expand on their data by including two additional estimates of female mating overlap. Primates are the focus because they provide the best available information for this test (although the sample used here is composed almost exclusively of anthropoid primates). However, these conclusions should also hold for mammals more generally.

## Methods

### Proxies for temporal overlap

In this paper, temporal overlap refers to within-group mating synchrony. Three independent proxies, each of which are sensitive to different sources of error, were used to quantify female temporal overlap (summarized in Table 1). Three different sets of comparative tests are therefore reported below. In the multiple regression model, female group size and one of the three proxies for temporal overlap served as independent variables, while male group size served as the dependent variable. To facilitate comparison with Mitani et al.’s (1996) analysis, continuous values for male and female number and for breeding seasonality were taken directly from that paper (see Table 2).

### Test 1: breeding seasonality

The first set of analyses uses breeding-season duration as the proxy for female overlap. Breeding season is treated as a continuous variable (i.e., birth season duration in days, which should be correlated with mating season duration; see Mitani et al. 1996). As

noted above, breeding seasonality is not a perfect proxy for female overlap. However, use of this proxy allows comparison to the results of Mitani et al. (1996) using a continuous measure and different statistical and phylogenetic methods.

### Test 2: expected female overlap

The second set of analyses uses life history and social variables to calculate the probability that two or more females are synchronously receptive. Calculations are based largely on Dunbar’s (1988, 1999) approach: female synchrony is assumed to be a chance event based on the average number of mating (“estrous”) days by individual females per ovulatory cycle, the duration of the breeding season, and the number of females in the social group. Expected values are calculated using the binomial theorem (see below).

One issue in this analysis involves whether synchronized ovulation is the relevant factor or whether synchrony in female mating activity is more important. I argue that overlap in female mating activity matters most, as females will probably be able to blur the boundaries of the actual timing of ovulation to some degree (i.e., through “probabilistic” signals of fertility, such as exaggerated swellings; Nunn 1999b). Thus, I assume that a male mates because he has some nonzero probability of fertilization success. For this reason, I assume that female reproductive condition is judged by males as a binary state: fertile or infertile. This is obviously an oversimplification, but, by making this assumption explicit, I hope to stimulate further discussion of this issue.

Another simplifying assumption is that females cycle every year and that each female experiences two cycles prior to conception. The assumption of a yearly cycle may not be ideal, given the variability in primate interbirth intervals (Harvey and Clutton-Brock 1985; Dunbar 1999). However, Dunbar (1999) provides an alternative analysis that uses the most up-to-date information on interbirth intervals (but assumes mating durations are constant), complementing the present analysis. In any case, the assumption of a fixed interbirth interval may be preferred if females of larger-bodied species (which tend to have longer interbirth intervals; Harvey and Clutton-Brock 1985) use deceptive mating tactics more often, such as mating during pregnancy (van Schaik et al. 1999), or if they obscure the exact timing of ovulation, e.g., through exaggerated sexual swellings (Nunn 1999a). In these cases, males should perceive more overlap, which is the same as underestimating the interbirth interval.

The binomial theorem is used to calculate the probability that a certain number of females mate simultaneously (see Dunbar 1988, 1999; Sokal and Rohlf 1995):

$$P(Y) = \frac{k!}{Y!(k-Y)!} p^Y (1-p)^{k-Y}$$

In the present context,  $P(Y)$  is the probability that  $Y$  females are mating simultaneously, and  $k$  is the number of females in the group (rounded to nearest integer). The variable  $p$  reflects the probability that an individual female is mating and is calculated as twice the duration of mating divided by the duration of the breeding season ( $2 \times$  reflects the assumption of two cycles to conception). These parameters were used to calculate the probability of zero or one female mating per day, which was subtracted from 1 to give the probability that two or more females mate on a given day (because probabilities must sum to 1).

This measure is used to estimate total expected overlap. However, expected overlap is a function of female number

**Table 1** Summary of comparative tests

Test number	Measurement of temporal overlap	Sources of data
1	Breeding season duration (days)	Mitani et al. 1996
2	Expected percent time that more than one female is in estrus	Mitani et al. 1996; van Schaik et al. 1999
3	Observed percent time that more than one female is in estrus	Literature search and personal communications (see Table 2)

**Table 2** Raw data used in the comparative analyses. *Breeding season duration*, *Number of females*, *Number of males*: information taken from Mitani et al. (1996). *Duration of mating*: number of days mating per ovulatory cycle (from van Schaik et al. 1999; blank cells indicate no information was available). *Expected overlap*:

calculated following methods in Dunbar (1988, 1999) as outlined in Methods (blank cells indicate no data was available for test 2). *Observed overlap*: calculated as explained in Methods (blank cells indicate no information was available for test 3)

Species	Breeding season duration (days = birth season)	Number of females	Number of males	Duration of mating (days)	Expected overlap	Observed overlap	References for observed overlap
<i>Alouatta caraya</i>	365	2	1	3	0		
<i>Alouatta palliata</i>	365	8	2	3	0.7	7.5	K. Glander, personal communication
<i>Alouatta seniculus</i>	365	2.5	1.5	3	0.1	2.5	C. Crockett and T. Pope, personal communications
<i>Ateles belzebuth</i>	365	11.5	4				
<i>Ateles paniscus</i>	365	15.5	5	6	9.6		
<i>Brachyteles arachnoides</i>	153	9	7	2	2.2	14.9	K. Strier, personal communication
<i>Callithrix jacchus</i>	365	2	2	28	2.4	0	Digby and Ferrari 1994; L. Digby, personal communication
<i>Cebus apella</i>	92	2.25	2	5	1.2	9.5	Janson 1984
<i>Cebus capucinus</i>	212	4	5.5			15.8	S. Perry and L. Rose, personal communications
<i>Cebus olivaceus</i>	124	6	1				
<i>Cercocebus albigena</i>	212	6	3	4	1.9		
<i>Cercocebus galeritus</i>	59	6	2				
<i>Cercopithecus aethiops</i>	92	4.25	3	33	92.9		
<i>Cercopithecus ascanius</i>	182	9.5	1	3	4.1		
<i>Cercopithecus campbelli</i>	62	4	1				
<i>Cercopithecus mitis</i>	120	18	1	2	12	1.5	M. Cords, personal communication
<i>Cercopithecus neglectus</i>	90	3	1				
<i>Colobus badius</i>	244	9.5	3.5	5	6.1		
<i>Colobus guereza</i>	365	3	1				
<i>Erythrocebus patas</i>	62	12.5	3	2	20.3	47.7	Harding and Olson 1986
<i>Gorilla gorilla</i>	365	3	1	2	0	0	D. Watts, personal communication
<i>Lemur catta</i>	38	4	4.5	1	1.5	0	Pereira 1991; Sauther 1991
<i>Macaca fascicularis</i>	123	6.75	4	15	54	66.6	van Noordwijk 1985
<i>Macaca fuscata</i>	46	9	3	11	97.4	56.5	Okayasu 1992
<i>Macaca mulatta</i>	82	9	2.5	9	62	39.8	Gordon 1981
<i>Macaca nemestrina</i>	365	22	3	13	47.1	41.7	Oi 1996
<i>Macaca radiata</i>	92	9	7	5	25.5		
<i>Macaca silenus</i>	365	7	1.75	18	14.6		
<i>Macaca sinica</i>	66	9.5	5	14	96.7		
<i>Macaca sylvanus</i>	76	10.5	9	14	95.3	35.9	J. Kuester, personal communication
<i>Macaca thibetana</i>	89	9.5	4.5				
<i>Miopithecus talapoin</i>	59	27	13	11	100		
<i>Nasalis larvatus</i>	62	5	1			0	Yeager 1990
<i>Pan paniscus</i>	365	8	8	15	13.6		
<i>Pan troglodytes</i>	365	35	10	14	76.1	7.8	D. Watts, personal communication
<i>Papio anubis</i>	365	34	14	6	30.8		
<i>Papio cynocephalus</i>	365	13	8	9	13.2	22.6	Hausfater 1975; Noë and Sluijter 1990; see also Altmann 1999

**Table 2** (contd.)

Species	Breeding season duration (days = birth season)	Number of females	Number of males	Duration of mating (days)	Expected overlap	Observed overlap	References for observed overlap
<i>Papio hamadryas</i>	365	2	1	5	0.1		
<i>Papio ursinus</i>	365	14.5	7	9	16.7		
<i>Presbytis entellus</i>	365	12	1	6	5.7	4.2	V. Sommer, personal communication (with C. Borries and A. Srivastava)
<i>Presbytis pileatus</i>	120	4	1				
<i>Presbytis senex</i>	153	5	1				
<i>Procolobus verus</i>	89	2	1.25				
<i>Saguinus fuscicollis</i>	151	1	1.88	10	0	0 <sup>a</sup>	
<i>Saguinus mystax</i>	153	2	2			0	Garber et al. 1993
<i>Saguinus oedipus</i>	122	1	2	11	0	0 <sup>a</sup>	
<i>Saimiri oerstedii</i>	59	16	10	2	29.6	11.9	Boinski 1987b
<i>Saimiri sciureus</i>	61	23	7	2	45.1		
<i>Theropithecus gelada</i>	365	4	1	9	1.4		

<sup>a</sup> Only one female in Mitani et al. (1996), so no overlap is possible (see Methods)

(Dunbar 1988, 1999; see below). To estimate overlap independent of the spatial effect, I therefore partialled out female number using a residual approach. Details on these calculations are presented below.

### Test 3: empirical measures of female overlap

In a third analysis, I used empirical data on female overlap to assess the possibility that female mating behavior is socially mediated within groups. Much of this information comes from personal communications, although some data could be obtained from the published literature (e.g., estimated from figures showing female mating patterns over time). As in test 2, I used as a measure of synchrony the percentage of days on which two or more females are sexually active within a social group, and calculations were limited to the breeding season (when this could be determined). Species with a single female in the Mitani et al. (1996) dataset were assigned a value of 0% overlap. When an expert on a given species provided a range of values, I took the midpoint of this range for the comparative tests. Likewise, when different researchers provided more than one estimate, I used the mean of these estimates (see Table 2).

This dataset represents the first attempt to compile information on this notoriously difficult variable. Future comparative tests will certainly have better information from more species and so it is worth examining several complicating factors. First, definitions of "estrus" differ among researchers (e.g., Nadler 1994). In general, I favored data based on observations of mating; however, in some cases, when this more detailed information on matings was not available, estimates were based on physical signs, such as sexual swellings. Related to this, not all copulations are fertile (Hrdy and Whitten 1987; Manson et al. 1997; van Schaik et al. 1999). However, as in the second proxy, I assume that males perceive a nonzero probability of fertilization success when they choose to copulate with a particular female.

Second, copulations will be more readily observed in some species than in others. In addition, values reported here most likely underestimate true synchrony, as matings will be missed because of "sneak" matings away from the core of the social group (Smuts 1987) or when matings occur outside regular or planned observation hours (at night, or when the group cannot be found).

Third, populations and groups within populations may differ in the degree of synchrony owing to variation in social factors (such as the number of females, varying relatedness, seasonal ecological

factors, or female proximity; Wallis 1985, 1992, 1995). I dealt with this problem in several ways. I preferred sources of information on female synchrony that matched references and study populations in Mitani et al. (1996). When this was not possible, I obtained data from social groups with approximately the same number of females as the Mitani et al. (1996) dataset. For example, gorillas (*Gorilla gorilla*) are here classified as having no overlap, but there are times when females are synchronously receptive (Watts 1990); however, this female synchrony tends to occur at female group sizes larger than those examined here (D. Watts, personal communication). To control for possible effects that males have on female receptivity, I also preferred data on overlap that matched the number of males in Mitani et al.'s (1996) dataset. For example, I used data from groups with male influxes in patas monkeys (*Erythrocebus patas*), as Mitani et al. (1996) list this species as having three males. For several species, I nevertheless used information from different wild or captive populations when no other information was available and when this alternative information matched social situations in Mitani et al. (1996) reasonably well. The effect of including values in which social conditions differ is to introduce error variance; thus, in the few cases where references differ from those used by Mitani et al. (1996), trends should be obscured rather than strengthened (Clutton-Brock and Harvey 1984).

Finally, even if social conditions are matched precisely, the number of females mating will be a function of female group size. Thus, as in test 2, I partialled out the effect of female number to examine pure overlap effects (see below).

### Phylogenetic comparative methods

When comparative analyses do not explicitly incorporate phylogeny, the degrees of freedom may be overstated, leading to incorrect statistical conclusions (Harvey and Pagel 1991; Martins and Hansen 1996). Here, I used the phylogenetic comparative method of independent contrasts to examine the relationship between continuous traits. In particular, I used a variant of Felsenstein's (1985) original method (as implemented by the computer program CAIC; Purvis and Rambaut 1995) because this method makes use of more of the data than pairwise comparisons (Felsenstein 1985). It calculates evolutionary changes, or "contrasts," over branches of the phylogeny such that each contrast is fully independent of other contrasts and is thus suitable for standard statistical analysis (see Felsenstein 1985; Harvey and Pagel 1991; Martins and Hansen 1996). These contrasts represent evolutionary change. Hence,

compared to nonphylogenetic analyses, the questions become more explicitly evolutionary: how do evolutionary changes in the number of females, or changes in the temporal overlap among these females, relate to evolutionary changes in the number of males?

Phylogenetic comparative tests make a number of assumptions regarding phylogenetic information. To assess how violations of these assumptions affect the results, I performed a series of sensitivity tests in which each analysis was run using four different phylogenies, each with two sets of branch lengths. These sensitivity tests are not subject to the problem of multiple comparisons because the same prediction is examined using the same dataset, but under different phylogenetic assumptions; hence, statistical corrections for multiple comparisons are not needed (e.g., the Bonferroni correction; Sokal and Rohlf 1995; see also Donoghue and Ackerly 1996).

In these sensitivity tests, I used the three phylogenies employed by Mitani et al. (1996) to compare our results. In addition, I ran analyses a fourth time using Purvis' (1995) composite estimate of primate phylogeny. For each tree, the analysis was run under two assumptions: once with equal branch lengths (a speciation model; Garland et al. 1993) and another time where branch lengths were estimated (a gradual model). Purvis (1995) provides estimates of divergence times for a model of gradual evolution; to obtain branch lengths for the three non-Purvis (1995) trees taken from Mitani et al. (1996), I used the estimation method proposed by Grafen (1989), where divergence dates (i.e., the ages of internal nodes) are estimated as 1 minus the number of descendent species. Four topologies and two sets of branch length estimates for each tree gives a total of eight sensitivity tests for each of the three comparative tests summarized in Table 1. As suggested by intraspecific variation (see above), male number may represent a facultative response to changes in female spatiotemporal distribution; therefore, a ninth sensitivity test was conducted that examined the data without controlling for phylogeny.

The method of independent contrasts also makes a number of statistical assumptions that were tested in two ways (see Garland et al. 1992; Purvis and Rambaut 1995). First, the absolute values of contrasts from each of the three variables were regressed on nodal estimates output by CAIC. Second, the absolute values of contrasts for each variable were regressed on the square root of the contrast variance. In no cases were the assumptions violated when using breeding season in days, and so this variable was not transformed. However, the assumptions were regularly violated when using raw values for female and male group size. Logarithmic transformations of branch lengths and raw data (number of males and females) improved the assumptions for most, but not all, of the analyses; to make all tests comparable, however, these variables were always transformed. In transforming branch lengths, logarithms were taken of branch length + 1; then, to conform to the requirements of CAIC (Purvis and Rambaut 1995), these values were rescaled so that all branch lengths were > 2. Logarithms were also taken on percentages + 1, as this fit the assumptions better (in a subset of data) than straight percentages or arcsine-square root transformations (Sokal and Rohlf 1995).

The number of females was identified as the independent variable for CAIC when calculating contrasts used in the multiple regression analyses (i.e., these contrasts were all made positive; Garland et al. 1992; Purvis and Rambaut 1995). The contrasts calculated for each trait were then entered into a stepwise regression model (using JMP, SAS Institute, Cary, N.C.; default settings of 0.25 to enter a variable and 0.10 to leave). I performed all regressions through the origin (Harvey and Pagel 1991; Garland et al. 1992). All *P*-values are two-tailed and considered significant at *P* < 0.05.

#### Controlling for female number

In tests 2 and 3, the measures of overlap are expected to be a function of female number (Dunbar 1988). The data in Table 1 (after appropriate statistical and phylogenetic transformations) confirm the existence of this problem: expected overlap in test 2 is

an increasing function of female number ( $b = 1.01$ ,  $P < 0.001$ ,  $n = 33$ ), as is observed overlap in test 3 ( $b = 0.657$ ,  $P = 0.017$ ,  $n = 22$ ; using the Purvis phylogeny under a gradual assumption). Thus, the unambiguous relationship between female and male number found in previous studies (Andelman 1986; Mitani et al. 1996) probably also involves aspects of female overlap. Unless corrected in some way, this collinearity among the two predictor variables (female number and female overlap) makes it difficult to estimate the influence of each on the dependent variable (the number of males).

I controlled for this problem by calculating residuals from the regression of female overlap on female number, and used these residuals as the measure of overlap in the analyses. Thus, a positive residual for a particular species means that these females are expected to be (test 2) or actually are (test 3) more synchronous than predicted based on the number of females in the group. Least-squares regression was used so that residuals would be perfectly uncorrelated with female group size (Harvey and Pagel 1991). The same procedure was used to control for female number in tests 2 and 3 so that measures would be comparable.

This analysis is more complicated than it first appears, however, because the regression line used to calculate residuals must also be free of phylogenetic effects. The following procedure was therefore implemented. First, I entered information on female number and overlap into CAIC to calculate contrasts for these traits; this was repeated for each phylogeny-branch length combination (eight in total). Second, contrasts in the relevant measure of overlap were regressed on contrasts in the number of females; this was again repeated for each phylogeny-branch length combination. Third, these eight regression coefficients were forced onto the raw data to calculate residuals for each species, which then served as estimates of excess overlap. As least-squares residuals, these estimates are independent of female number and thus remove the effect of collinearity in the multiple regression model; however, as species estimates, these residual values still have the potential for phylogenetic nonindependence. Thus, in the fourth and final step, residuals for each species were entered into CAIC, along with female and male group size, to calculate the contrasts used in tests 2 and 3.

## Results

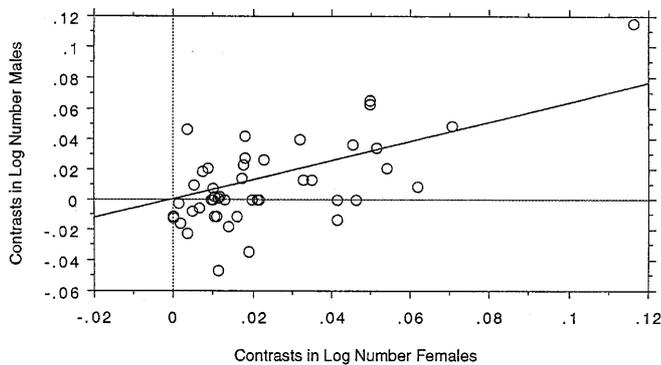
### Test 1: breeding seasonality

The results of the stepwise multiple regression analyses for test 1 are presented in Table 3. In all eight phylogeny-branch length combinations, female group size was entered into the model, and this variable was highly significant in all cases ( $P < 0.0001$ ). Thus, male number is tightly linked to female number (Fig. 2), consistent with spatial effects in the socioecological model (Andelman 1986; Altmann 1990; Mitani et al. 1996). However, this test is correlational, and so causality cannot be unambiguously assigned in this case: it is possible (but unlikely) that more males lead to more females, rather than vice versa (Mitani et al. 1996).

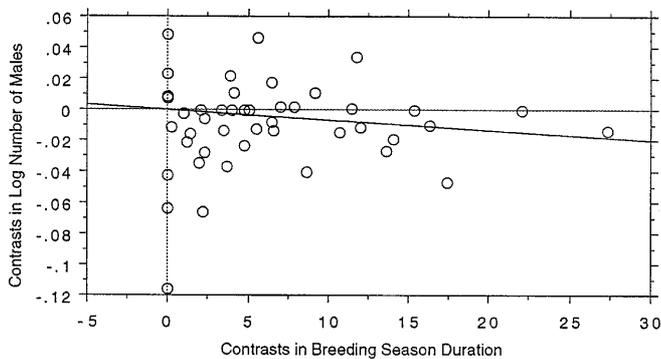
Male number is also independently linked to breeding season duration, although this association was not as strong (Table 3, Fig. 3). Thus, in no case did *P*-values approach the highly significant results involving female group size. Nevertheless, breeding season duration was entered into the stepwise regression model in all phylogenetic analyses, and in the two cases where this variable was not statistically significant, *P*-values approached

**Table 3** Results of test 1: breeding seasonality. *Phylogeny*: Mitani-1 to -3 refer to the phylogenies in Fig. 1 of Mitani et al. (1996). *Model/branch lengths*: Gradual refers to Grafen's (1989) "arbitrary" estimate of branch lengths for the phylogenies from Mitani et al. (1996), or to the branch lengths provided in Purvis' (1995) tables

Phylogeny	Model/branch lengths	Sample size	Number of females			Breeding seasonality		
			$b_{\text{females}}$	F-ratio	P	$b_{\text{breeding season}}$	F-ratio	P
Mitani-1	Gradual	42	0.61	45.69	<0.0001	-0.00063	3.67	0.06
	Speciational	42	0.64	49.21	<0.0001	-0.00081	7.22	0.011
Mitani-2	Gradual	43	0.67	29.40	<0.0001	-0.00086	5.74	0.021
	Speciational	43	0.65	54.81	<0.0001	-0.00090	7.80	0.008
Mitani-3	Gradual	42	0.63	48.94	<0.0001	-0.00062	3.61	0.06
	Speciational	42	0.63	47.99	<0.0001	-0.00077	6.75	0.013
Purvis	Gradual	46	0.67	51.19	<0.0001	-0.00095	7.55	0.0087
	Speciational	46	0.61	36.41	<0.0001	-0.0010	8.42	0.0058
None		49	0.60	29.37	<0.0001	-0.00023	0.52	0.47



**Fig. 2** Relationship between female number and male number. Axes are independent contrasts in the number of females and the number of males (raw data logarithmically transformed). Contrasts were calculated based on Purvis' (1995) phylogeny assuming a model of gradual evolution



**Fig. 3** Relationship between breeding seasonality and number of males in primate groups. Axes are independent contrasts in breeding seasonality (days, untransformed), and independent contrasts in the number of males (log transformed). Contrasts were calculated based on Purvis' (1995) phylogeny assuming a model of gradual evolution

significance ( $P = 0.06$  in both cases). The causal arrow in the case of breeding seasonality is relatively more straightforward: changing the number of males should not change the duration of the breeding season, strongly

for that phylogeny. Branches in both cases were transformed by taking the logarithm of the estimates + 1. In *Speciational* models, branch lengths were all equalized. *Sample size*: these differ among the phylogenies due to different numbers of polytomies (see Purvis and Rambaut 1995)

suggesting that causality runs from breeding season duration to the number of males (Ridley 1986).

Phylogenetic sensitivity can be examined using the results in Table 3. Slopes are consistently in the predicted direction and fall within a remarkably narrow range, indicating that these conclusions are generally robust to alternative phylogenetic topologies and branch lengths. If male number is a facultative response by individual males to the spatiotemporal distribution of females (see above), then it may be appropriate to examine these cross-species patterns without controlling for phylogeny. In nonphylogenetic analysis, log number of females is significant and positive and breeding seasonality remains in the predicted direction, but not significantly so (Table 3).

#### Test 2: residual expected female overlap

The results of test 2 are also consistent with the socioecological model: both female group size and female residual expected overlap significantly predict male number (Table 4, Fig. 4). As in test 1, female group size is relatively more important, but eight out of nine tests give significant  $P$ -values for this proxy of female overlap (with the one exception at  $P = 0.09$ ). Partial regression coefficients for residual expected overlap differ in sign from slopes in test 1 because a different proxy is used: in test 1, higher values of the proxy (breeding season) should result in less overlap and therefore fewer males; in test 2, higher values for the proxy (residual expected female overlap) indicate more overlap and therefore more males.

As noted in the Methods, female number and overlap are highly correlated, and the residual measure of overlap used here represents overlap in excess of that expected based on the number of females. Thus, what is usually considered a spatial effect actually also involves the effect of female overlap. I therefore also examined the relationship between male number and expected overlap itself (i.e., prior to taking residuals). In seven out of eight phylogenetic analyses, expected female overlap

**Table 4** Results of test 2: residual expected female overlap. See legend to Table 3 for further explanations

Phylogeny	Model/branch lengths	Sample size	Number of females			Residual expected female overlap		
			$b_{\text{females}}$	$F$ -ratio	$P$	$b_{\text{residual expected}}$	$F$ -ratio	$P$
Mitani-1	Gradual	32	0.61	33.85	<0.0001	0.29	7.31	0.011
	Speciational	32	0.64	36.53	<0.0001	0.34	9.84	0.0038
Mitani-2	Gradual	33	0.65	40.38	<0.0001	0.21	3.07	0.09
	Speciational	33	0.66	37.24	<0.0001	0.28	5.94	0.021
Mitani-3	Gradual	32	0.64	37.43	<0.0001	0.31	6.83	0.014
	Speciational	32	0.64	36.83	<0.0001	0.34	9.62	0.0042
Purvis	Gradual	33	0.69	44.52	<0.0001	0.32	9.05	0.0052
	Speciational	33	0.65	40.42	<0.0001	0.38	13.87	0.0008
None		36	0.54	21.78	<0.0001	0.20	4.26	0.047

has a lower  $P$ -value than female number in a stepwise regression (e.g., for the Purvis phylogeny under a gradual assumption:  $b_{\text{females}} = 0.37$ ,  $P = 0.019$ ,  $b_{\text{expected overlap}} = 0.32$ ,  $P = 0.005$ ). This result is confirmed in nonphylogenetic analysis ( $b_{\text{females}} = 0.28$ ,  $P = 0.10$ ,  $b_{\text{expected overlap}} = 0.20$ ,  $P = 0.047$ ). These results agree with Dunbar's (1999) analysis, which also found that expected overlap explains more of the variance than female number alone. Hence, the conclusions from test 2 are not sensitive to assumptions regarding interbirth intervals.

### Test 3: residual observed female overlap

The results of Test 3 also support the existence of temporal effects in the socioecological model: both spatial and temporal effects were entered into the stepwise regression model in all cases, and regression coefficients were all positive (Table 5). Residual observed overlap was significant in five of the nine tests, and in the four nonsignificant tests,  $P$ -values were less than 0.10. Patterns are more clearcut when examined graphically

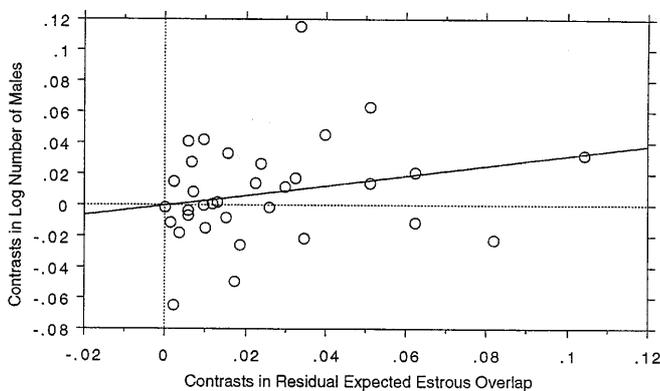
(Fig. 5), possibly because the proxy used in test 3 incorporates the effects of socially mediated synchrony.

The relationship between male number and observed overlap (prior to taking residuals) is also strong: six out of eight phylogenetic tests give lower  $P$ -values for observed overlap than female number in a stepwise regression (e.g., for the Purvis phylogeny under a gradual assumption:  $b_{\text{females}} = 0.25$ ,  $P = 0.17$ ,  $b_{\text{observed overlap}} = 0.36$ ,  $P = 0.011$ ). In fact, in only one case is female number significant in stepwise regression analyses that also include observed female overlap as an independent covariate. In nonphylogenetic analysis, female number is not even entered into the regression model, while observed overlap is highly significant ( $b_{\text{observed overlap}} = 0.26$ ,  $P = 0.009$ ). Thus, as expected, a composite estimate that captures both female number and overlap explains more of the variance than female number alone (Mitani et al. 1996; Dunbar 1999).

## Discussion

These results show that the number of males in primate social groups is positively related to both female number and female temporal overlap. The three proxies for temporal overlap (breeding seasonality, residual expected overlap, and residual observed overlap) were obtained using independent methods and information; these tests therefore serve as independent evidence for temporal effects in the socioecological model. Furthermore, regression coefficients fall within a remarkably narrow range in sensitivity analyses, indicating that these results are relatively insensitive to phylogenetic error. The residual measures reflect excess overlap from that expected by female number alone; hence, results concerning female overlap are independent of spatial effects.

In test 1, breeding seasonality is not significantly correlated with log number of females ( $r = 0.19$ ,  $P = 0.20$ ; phylogenetic analysis based on the Purvis phylogeny under a gradual assumption). Thus, test 1 offers a means to estimate the relative roles of spatial and temporal effects. Results from this test show that female number is more important (Table 3). Results



**Fig. 4** Relationship between residual expected number of mating females and male number. Axes are independent contrasts in residual expected mating overlap (percentage of time with two or more mating females + 1, log transformed) and independent contrasts in the number of males (log transformed). Contrasts were calculated based on Purvis' (1995) phylogeny assuming a gradual model of evolution

**Table 5** Results of test 3: observed residual female overlap. See legend to Table 3 for further explanations

Phylogeny	Model/branch lengths	Sample size	Number of females			Residual observed female overlap		
			$b_{\text{females}}$	$F$ -ratio	$P$	$b_{\text{residual observed}}$	$F$ -ratio	$P$
Mitani-1	Gradual	21	0.63	20.33	0.0002	0.32	4.47	0.048
	Speciational	21	0.58	13.70	0.0015	0.29	4.30	0.052
Mitani-2	Gradual	22	0.61	21.92	0.0001	0.28	4.02	0.059
	Speciational	22	0.57	14.55	0.0011	0.25	3.45	0.08
Mitani-3	Gradual	21	0.64	23.32	0.0001	0.33	4.92	0.039
	Speciational	21	0.58	14.84	0.0011	0.31	4.72	0.043
Purvis	Gradual	22	0.49	10.48	0.0041	0.36	7.86	0.011
	Speciational	22	0.60	18.03	0.0004	0.32	5.27	0.033
None		23	0.33	5.14	0.035	0.22	3.41	0.08

from tests 2 and 3 also show that spatial effects explain more of the cross-species variation in male number (Tables 4, 5). However, the relative importance of female number and overlap cannot be fully evaluated in these tests because overlap estimates were sometimes taken from different populations than those used by Mitani et al. (1996) for female number.

Spatial and temporal effects are difficult to separate for another reason. Past studies distinguished between the effect of female number and female overlap (Altmann 1990; Mitani et al. 1996). However, as shown above, one effect of more females is increased overlap (see also Dunbar 1988). Excess overlap was examined here (Tables 3, 4, and 5); nevertheless, the spatial effect in these tests still involves aspects of female overlap. Hence, the strong and well-established relationship between male and female number in this and previous studies (Andelman 86; Mitani et al. 1996) likely also reflects an increase in female overlap that accompanies additional females.

Male decisions might be facultative responses to changes in female distribution, in which case phylogenetic tests are not needed. In addition, it might be possible to use comparative data to determine the proximate

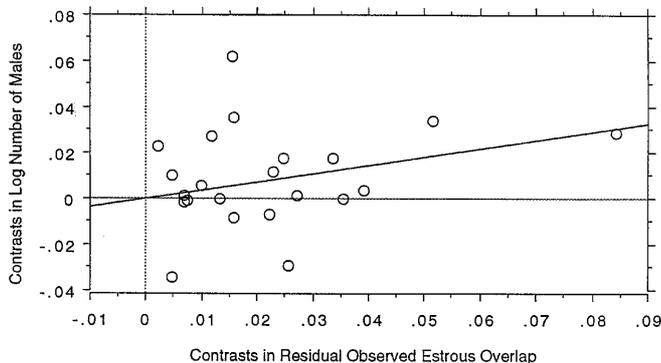
cues that males use in mapping onto females. The stronger relationship between female and male number suggests that female number plays the more important role in this proximate mechanism. I return to these male decisions below.

#### The socioecological model

The socioecological model presented in Fig. 1 is an oversimplification. In particular, intersexual conflict, and the resulting counterstrategies implemented by both sexes, complicates this picture (van Schaik 1996). Males need not simply “map onto” the distribution of females, but may instead manipulate females directly with the goal of increasing mating opportunities (e.g., herding females away from other males, or committing forced copulations; Smut and Smuts 1993). Females are expected to respond to this selection with counterstrategies, which then lead to a new round of strategies on the part of males. The result is a cycle of escalated intersexual interactions (Wrangham 1979; Rice 1996). Below, I investigate two relatively unexplored perspectives that bring more realism to this simple model: mating synchrony in females and the factors influencing male strategies of monopolizing females.

#### Mating synchrony: the female perspective

In many cases, female synchrony probably allows females to break the monopoly of a single male; hence, synchrony may encourage the formation of multimale social groups. Females might benefit from multimale social groups if this reduces the risk of infanticide (van Schaik et al. 1999) or predation (DeVore and Hall 1965; van Schaik and Hörstermann 1994). Synchrony is probably especially easy to achieve when breeding is already seasonal, as females are more likely to overlap simply by chance (e.g., Rowell and Dixon 1975). In addition, a longer duration of mating activity, as occurs in species with exaggerated sexual swellings (Nunn 1999b), will tend to increase synchrony. Consistent with this possibility, exaggerated swellings are associated with



**Fig. 5** Relationship between residual observed mating overlap and male number. Axes are residual observed mating overlap (percentage of time that two or more females are simultaneously receptive + 1, log transformed) and independent contrasts in the number of males (log transformed). Contrasts were calculated using Purvis' (1995) phylogeny under a model of gradual evolution

multimale social systems (Clutton-Brock and Harvey 1976; Nunn 1999b). Exaggerated swellings are also associated with nonseasonal breeding, possibly because this is where additional mechanisms are needed to increase overlap among females (van Schaik et al. 1999).

Pheromonal or other social mechanisms can be used to increase or decrease female overlap from that expected by chance alone (McClintock 1983). As expected, then, several instances of socially mediated synchrony have been reported in species with exaggerated sexual swellings, where selection for overlap likely exists (e.g., hamadryas baboons, *Papio hamadryas*: Kummer 1968; Zinner et al. 1994; savanna baboons, *P. cynocephalus* and *P. anubis*: Wallis 1989; common chimpanzee, *Pan troglodytes*: Wallis 1985). However, the evidence for socially mediated synchrony in anthropoid primates is presently disputed (Strassmann 1997, personal communication).

Having multiple males in the group also comes with costs. One cost will be increased feeding competition. In addition, synchronous females may experience more female-female competition for mates, and thus less mate choice (e.g., Knowlton 1979). However, increasing the number of males may also have some positive effects on female choice, in that synchrony would at least increase female proximity to multiple potential mates (Cords 1984).

Additional theoretical research on the effects of female synchrony is needed. However, before theory advances too far, a common terminology is required to discuss the different levels and patterns of female synchrony. This terminology should be statistically based, because if socially mediated synchrony is of interest, there needs to be some assessment of whether the observed patterns differ significantly from those expected by chance (e.g., Wallis 1985; Pereira 1991). The terms under- and overdispersed could be used to refer to patterns of synchrony and asynchrony, respectively.

To quantify female synchrony, one could regress observed on expected overlap and use the residuals as an estimate of under- and overdispersion. When the data in Table 2 are analyzed in this way, patterns are about as expected based on indications of synchrony in the published literature (Table 6): all the macaques and baboons are underdispersed (Wallis 1989; Okayasu 1992; cf. Noë and Sluijter 1990), ringtailed lemurs are overdispersed (Pereira 1991), as are species with long life histories (gorillas and common chimpanzees, possibly because interbirth intervals were underestimated), and patas monkeys are underdispersed (data on female number taken from a male influx, when females might have been more synchronous). Several other quantitative measures of synchrony have been proposed recently (Rhine 1995; Engel and Lamprecht 1997; Schank 1997), but these measures have not yet been used widely. Comparisons across species will be complicated by variation in female group size, ecological and social conditions, nonreproductive mating, and identification

**Table 6** Residuals as a measure of over- and underdispersion. Values are listed from smallest to largest. The regression line was calculated from regressing contrasts in log-transformed measure of observed overlap on contrasts in log-transformed measure of expected overlap (based on the Purvis phylogeny under a gradual assumption). Residuals were calculated by forcing this regression line on the raw data such that residuals sum to 0. Negative values indicate overdispersion (i.e., asynchrony), while positive values represent underdispersion (i.e., synchrony)

Species	Residual
<i>Callithrix jacchus</i>	-0.684
<i>Lemur catta</i>	-0.611
<i>Cercopithecus mitis</i>	-0.607
<i>Pan troglodytes</i>	-0.487
<i>Gorilla gorilla</i>	-0.391
<i>Saguinus fuscicollis</i>	-0.391
<i>Saguinus oedipus</i>	-0.391
<i>Presbytis entellus</i>	-0.131
<i>Saimiri oerstedii</i>	-0.1
<i>Macaca sylvanus</i>	0.082
<i>Alouatta seniculus</i>	0.13
<i>Macaca mulatta</i>	0.228
<i>Macaca fuscata</i>	0.27
<i>Macaca nemestrina</i>	0.312
<i>Papio cynocephalus</i>	0.346
<i>Alouatta palliata</i>	0.411
<i>Cebus apella</i>	0.441
<i>Macaca fascicularis</i>	0.479
<i>Brachyteles arachnoides</i>	0.532
<i>Erythrocebus patas</i>	0.564

of “estrous” behavior (see above); hence, the most productive research on mating synchrony may be performed within species.

Another important issue concerns the patterning of synchrony within versus between groups. Here, I focused on within-group synchrony; however, between-group patterns likely also exist (e.g., Boinski 1987a; Rowell and Dixson 1975). Between-group synchrony can have ecological benefits, such as predator swamping during the birth season (Estes and Estes 1979). Between-group synchrony can also have social functions. For example, synchrony among spatially divergent females (i.e., between-group underdispersion) should make “roving-male” strategies less successful, and could thus force males to be monogamous if females are solitary (van Schaik and Kappeler 1993). In contrast, between-group asynchrony (overdispersion) might increase female choice if this enables females to mate with the best males in the population (rather than just the group; e.g., Pereira 1991; Pereira and Weiss 1991).

#### *Strategies of monopolization: the male perspective*

Male reproductive success increases with number of mating partners, and males should therefore be attracted to groups with more fertile females. This goal may be hindered by several factors that are not usually incorporated in these models, and these factors may therefore explain deviations from patterns expected within and across species (Altmann 1999).

Perhaps the most important factor involves males' imperfect knowledge of breeding opportunities in other groups. If males are assumed to follow an "optimal foraging approach" to mating strategies (Dunbar 1999), where they move around a population according to mating opportunities, imperfect information will exist at two levels in the decision to transfer: first, regarding the benefits and second, regarding the costs (see also Alberts and Altmann 1995).

In terms of the benefits, males will not be able to perfectly assess the relative benefits of joining alternative groups of females, mainly because males will not have perfect information regarding breeding opportunities elsewhere. Even when females are observed to be cycling in other groups, males will be unable to predict with certainty the number of fertilizable females because not all cycling females are fertile (e.g., Hausfater 1975) and females may cycle multiple times prior to conception (e.g., Harcourt et al. 1980; Wallis 1997). A related problem involves female strategies to blur the precise timing of fertility (e.g., through deceptive signals, exaggerated swellings, or concealment of ovulation; Hrdy and Whitten 1987; Nunn 1999b; van Schaik et al. 1999). An additional problem is ignored in optimal-foraging models of male monopolization decisions: females who are observed cycling may refuse matings. Thus, transfer into a group with more cycling females does not ensure a male's future mating success.

In terms of costs, males will not be able to perfectly assess the costs of entering a new group because resident males will attempt to restrict their entry to varying degrees (Cheney 1987). Immigration into single-male groups should be more difficult than into multimale groups, as male extragroup defense is more of a "private good" in this case, where a single male gets all of the benefits, and so is willing to put more effort into defense (Nunn 1999a; Nunn and Lewis 1999). In addition, males will be unable to perfectly assess their future dominance rank (and thus breeding position) in a multimale group, as the resource-holding potential of resident males will not be known perfectly prior to entering the group. Finally, males face risks in transferring between groups (e.g., predation, unknown food sources) and may therefore remain in their present groups despite possibilities of better breeding opportunities elsewhere (Alberts and Altmann 1995; Altmann 1999).

These sources of uncertainty should have important influences on a male's assessment of risk, and thus on his breeding strategy. When risk is high, a male may prefer to remain in his present group rather than transferring to a group with better breeding opportunities. In this scenario, the number of males may not be as tightly linked to fluctuations in the spatiotemporal distribution of females (Alberts and Altmann 1995; Altmann 1999). In a similar line of reasoning, Brotherton and colleagues (Brotherton and Manser 1997; Komers and Brotherton 1997) have argued that monogamous males may prefer a risk-averse strategy in which they intensely guard a single female rather than "roving" for females.

## Conclusions and future research

This paper has shown that both the spatial and temporal distribution of fertile mates affects male monopolization potential; hence, the socioecological model, as it applies to primates, should incorporate both effects. Socioecological models may also benefit from a more explicit consideration of female synchrony, risk aversion (Komers and Brotherton 1997), imperfect information (Altmann 1999), and the economic costs and benefits of mate defense (especially in the context of shared gains; Nunn 1999a; Nunn and Lewis 1999). In addition, the spatial cohesion of females (not just their number) should influence male monopolization potential (Emlen and Oring 1977; van Schaik and van Hooff 1983), as should the visibility of females by males attempting to monopolize these females (Rowell 1988). These factors could be examined in future cross-species comparative studies of primates, for which abundant information is available.

Finally, as noted by Ridley (1986) and Mitani et al. (1996), methods are needed to demonstrate the causality of the relevant factors in the socioecological model. Some comparative methods may be able to demonstrate causality in this case (e.g., Pagel 1994). Causality may also be a problem in comparative studies within species, where authors have noted the difficulty of determining whether multiple mating females cause male influxes, or vice versa (Cords 1984; Okayasu 1992). However, longitudinal studies of single groups may be able to address causality by showing that increases in the number of fertile females lead to subsequent increases in the number of males. Multiple approaches, including experiments (e.g., Ims 1988), will therefore be needed to fully test the causality in the socioecological model.

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