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Population Density, Social Pathology, and Behavioral Ecology

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"At a population this dense, man would be extinct."*

INTRODUCTION

One criticism of sociobiology has been that advocates can "explain anything" by recourse to a combination of adaptive story and, when a suitable story cannot be found, dismissing the observation as nonadaptive or pathological "noise." Other critics have argued that behaviors such as infanticide by males, which have generated elaborate adaptive stories, are in fact pathological and so not in need of evolutionary explanation (BARTLETT et al., 1993). While few behavioral ecologists would argue that *all* behavior is adaptive, it is clear that the importance of a socioecological perspective for helping understand the world is weakened to the degree that large classes of "pathological" behavior either must be ignored or remain mysterious to an adaptive framework.

In this paper I address two classic examples of "social pathology" − apparently maladaptive social behavior − and suggest that they can be understood to a great extent (perhaps entirely) when viewed from the perspective of competitive individuals acting according to the principles of economic defendability models. These are based on the simple assumption that territorial or possessive behavior is favored only when benefits exceed costs; while initially sounding trivial, this perspective challenges widespread typological thinking − "species X is/is not territorial" gives way to "individuals of species X should be territorial under some conditions and not others." Such models have had considerable success at explaining variation in territorial behavior of birds (MYERS et al., 1981) and may be applied to long-standing questions concerning mammalian social structure (e.g. BROTHERTON & MANSER, 1997). One of the demographic factors known to influence the cost of resource defense is the intruder pressure (normally a function of resource density, with resource-rich habitats supporting and attracting more intruders). At high intruder pressures, resource defense no longer pays off; the defender would expend more energy in agonism than exclusive possession of the resource is worth (MYERS et al., 1981; KREBS & DAVIES, 1987).

Such a perspective immediately reveals the fact that linear regressions may be inappropriate tests for the relationship between behavioral and ecological or demographic variables. For example, the relationship between age and dominance rank among male macaques is predicted to be curvilinear; males are likely to start low ranking, rise during their prime, and fall in rank as they senesce. As SPRAGUE (1998) points out, given such an inverted-U relationship, a linear regression of rank on age may find a positive, negative or no relationship depending on the age composition of the sample. A similar inverted-U pattern has been reported with respect to terri-

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*Undergraduate paper discussing CALHOUN's rat experiments, Stanford University, 1976.

toriality and intruder pressure: at low pressures defensive boundary patrols are largely wasted energy, at intermediate pressures territoriality pays off, and at high intruder pressure defenders are swamped (MYERS et al., 1981).

The first example comes from the work of JOHN CALHOUN on captive rats (*Rattus norvegicus*, Osborne-Mendel strain). He created high-density populations in which aggression, infanticide, and infant neglect became rampant; these findings were reported in an influential *Scientific American* article entitled "Population density and social pathology" (1962a). Previously unre-ported patterns in the data, discussed below, indicate that at least some of the supposedly maladaptive behavior made good adaptive sense.

The second example is that of infanticide among langur monkeys (*Presbytis entellus*). In this case, the killing of infants by male langurs has been interpreted by some as pathological (resulting from high population density) and others as adaptive (evolved via sexual selection); proponents of the adaptive interpretation have cited the absence of a correlation between popu-lation density and infanticide as a fatal flaw in the pathology hypothesis (see HRDY et al., 1995; SUSSMAN et al., 1995). However, they have had difficulty explaining intersite variation in the expression of infanticide, a problem cited by proponents of the pathology hypothesis. These conflicting interpretations are to considerable degree resolved by application of an economic defendability model, which explicitly rejects the underlying hypothesis of both camps that population density should exert linear effects on behavior.

The behavioral variation observed in these cases, which has been described as pathological by some and strategic by others, may be neither; both of those terms suggest that the behavior is somehow "located" within the individual — that is, the individual is maladjusted, or the behavior is "genetically specified" in some detail within the individual's genome (e.g. HAUSFATER, 1984). This may be a misleading way to view both situations. Instead, these apparently complex regu-larities in behavior can be derived from the interaction of a few simple tendencies (e.g. hostility toward strange males) with predictable demographic settings, rather than requiring specified mental rules or modules (cf. ALTMANN & ALTMANN, 1979). Particular sociodemographic settings reliably can lead to behavioral outcomes which are adaptive and thus seem "genetic" because of the consistency with which they appear, without in fact being genetically specified *per se* (ELMAN et al., 1996; HILL, 1999).

Both of these classic examples deal with the supposedly negative effects of high population density upon animals. Interest in the evils of crowding exploded during the mid- to late-1960s, in a climate conditioned by group selection theory, the 'population bomb,' and a dawning awareness of ecological disaster looming ahead. The University of California's on-line library catalog (MELVYL) lists two books with subject heading "crowding" published between 1960 and 1970; between 1970 and 1980, there are 38. During the early 1970s, population density was seen as threatening our very existence (as illustrated oxymoronically by the epigram above). This interest soon collapsed (only seven books since 1990), in part because it became clear that crowding *per se* did not automatically lead to pathological behavior (FREEDMAN, 1975). While population density seemed intuitively related to criminal behavior in humans and agonism in nonhumans, the relationship was neither deterministic nor systematic and so population density, as an explanatory variable, fell out of favor.

It was not altogether wrong, however. Among nonhuman primates, per-individual rates of aggression consistently rise with crowding, though this increase is not uniform across types of aggression and may not be statistically significant in individual studies (AURELI et al., 1995; JUDGE & DE WAAL, 1993, 1997). Sometimes it is not explicitly acknowledged, though present in the data (e.g. ANDERSON et al., 1977). Furthermore, species differences in the relationship between agonistic behavior and population density may have important implications for the

evolution of social systems as well as for conservation planners (YAMAGIWA, 1999). It is now clear that we cannot solve modern urban and ecological problems by merely reducing the density at which we live, but this should not be taken as evidence that population density does not contribute, in an adaptively comprehensible way, to the expression of agonistic behavior — and, through behavior, to social organization.

RATS AND SOCIAL PATHOLOGY

CALHOUN (1962a) was perhaps the seminal work suggesting a link between crowding and social pathology. He populated a room subdivided into four contiguous pens with rats and provided them with unlimited food and water; after a year, their density was high and he reported infanticide, cannibalism, homosexuality, and the formation of a "behavioral sink": the majority of the rats would congregate to feed within a small subsection of the room, increasing their real density far above that imposed by the distribution of food or size of the enclosure, and seemingly exacerbating the social pressure of numbers. The analogy with humans apparently voluntarily flocking to decaying inner cities despite high crime rates and lower quality of life compared to rural areas was compelling and the paper widely cited. CALHOUN himself promoted the analogy in papers such as "Plight of the Ik and Kaiadilt is seen as a chilling possible end for Man" (1972).

While some (e.g. HRDY, 1977: 9) noted that individual rats in what CALHOUN (1972) called "breeder pens" were doing reasonably well, simply pointing out that some individuals were better able to cope with crumbling society did not alter the general view that crowding induced pathological behavior. The image was one of a few tough individuals getting by as the world degenerated, and the conclusion that pathological behavior was rampant overall was unchallenged. I show here that there was a great deal of adaptive patterning to the supposedly pathological distribution of rats in the room. Whether other facets of the rats' behavior (e.g. the co-feeding that defined the "behavioral sink") can be interpreted adaptively is beyond the scope of this analysis, but it would be worth investigation.

METHODS

There have been few individually-oriented studies of the behavioral ecology of wild rats; the following brief natural history background is taken from CALHOUN (1963a) and BARNETT (1975). Wild *R. norvegicus* are terrestrial and live in colonies which can number in the hundreds. Within colonies, ground burrows are shared by up to about six reproductive females (often matrilineally related), each with a separate nest chamber. A burrow may or may not have one or more males associated with it and attempting (with variable success) to restrict mating access of other males to resident females. Dominance relationships among males are established at about puberty through fighting and tend to be stable thereafter; alpha males tend to be larger as adults, and hierarchies among non-alpha males are indistinct. Mortality rates are higher for subordinates of both sexes, apparently involving adrenal hyperplasia in addition to overt wounding or resource exclusion. They are multi-mount ejaculators. Males sometimes compete over receptive females, but often large groups of males will copulate sequentially with a single female, showing little if any overt competition. Nevertheless, dominant males in captivity achieve more ejaculations and continue mating with individual females longer, thereby increasing the length of postcopulatory intervals following their ejaculations; both factors contribute to fertilization suggesting that male rank is correlated with reproductive success
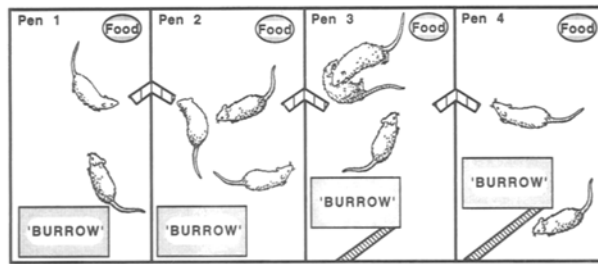
Fig. 1. Schematic diagram of CALHOUN's experiment (rats not to scale!). Each 'burrow' contains five nest boxes connected by an internal tunnel; while all burrows were elevated above the floor, those in Pens 3 and 4 were raised higher (the less-preferred condition). Both food and water were available ad lib in each pen. Actual room dimensions 10×14×9 feet; heights of burrows not given in CALHOUN (1962a).

(THOR & CARR, 1979). It is notable that conception is unlikely if the intercopulatory interval is too short; hence conceptions may be less likely under group mating conditions. Inter-colony relationships vary from tolerance to hostility. Dispersal (both within and between colonies) is male-biased, but the levels of social organization appear more permeable than among most primates and membership in a burrow or colony is flexible.

CALHOUN's experimental procedures are described in several papers (CALHOUN, 1962a, b, 1963b) and these should be consulted for details. He constructed ten by 14-foot rooms divided into four sections, with bridges connecting sections 1-2, 2-3, and 3-4; although physically arranged in a square, topologically this amounts to a line of connected rooms (Fig. 1). Each elevated "burrow" contained five nest boxes, reached via a ramp. The burrow in Pen 4 was elevated the most; Pen 3 intermediate, and Pens 1 and 2 the least. CALHOUN (1962a) states that the rats prefer lower burrows; he provides no supporting evidence but this preference would be consistent with their natural habitat. Burrow heights are not given in 1962a; CALHOUN (1962b) describes what seems to be a very similar experiment in which two burrows were elevated 3 feet and two were elevated 6 feet; the discrepancy is unexplained. Note that Pens 2 and 3 can be entered from two directions. Consequently, Pen 1 is likely to be most preferred (low burrow and single entry) and Pen 2 preferred over Pen 3 (lower burrow, both have double entries). The preference ranking for Pen 4 cannot be predicted without knowing which is more important to rats, burrow height or single entry; it is presumably least preferred on its own merits (burrow height) but equivalent to Pen 1 in ease of defense (highly relevant for the economic defendability interpretation presented here).

Three replicates were run in two series, for a total of six independent experiments. Each room was seeded with equal numbers of recently-weaned male and female rats (total of 32 in Series I and 56 in Series II). They were provided unlimited food and water and allowed to breed freely for 12 months, by which time "all the populations had multiplied and each comprised 80 adults"; thereafter weaned young were cropped to keep populations constant (CALHOUN, 1962a: 139; while it seems unlikely that all six replicates would have numbered exactly 80 before cropping, I assume at least subsequently they were kept at 80 by cropping). It should be noted that there are discrepancies between the design described in CALHOUN (1962b) and that of CALHOUN (1962a); it is not clear if they describe the same set of replicates and my analysis is restricted to that described in the *Scientific American* paper; data required for this analysis cannot be extracted from CALHOUN (1962b).

CALHOUN (1962a) presents data on usage of each pen during the 13th month in the form of bar graphs showing the percentage of animals sleeping, eating, and drinking in each pen; only the sleeping data are broken down by sex. Using this figure (bars measured to nearest 0.05 mm

Table 1. Distribution of sleeping rats.

	Series 1				Series 2		
	Pen	Males	Females		Pen	Males	Females
Room I	1	5	5	Room I	1	1	10
0.625	2	17	10	0.413	2	19	11
	3	17	10		3	8	14
	4	11	5		4	5	12
Room II	1	7	3	Room II	1	2	10
0.700	2	20	12	0.425	2	16	15
	3	18	5		3	12	15
	4	11	4		4	4	6
Room III	1	16	7	Room III	1	36	7
0.550	2	24	17	0.538	2	6	13
	3	3	8		3	1	10
	4	1	4		4	0	7

Figures are numbers of males and females sleeping in each pen, based on histograms in CALHOUN (1962a, pp. 144—145). Overall room sex ratio (italics) was then calculated from these numbers as % male.

with calipers) and the total of 80 animals per room, I calculated numbers of males and females sleeping in each pen, as well as the overall sex ratio in each of the six rooms (Table 1). All analyses were done with StatView 4.5 (Macintosh).

RESULTS

Males distributed themselves nonrandomly across the pens (Fig. 2A, Kruskal-Wallis test, $N=24$, $H=7.49$, $p<0.06$); they tended to concentrate in Pens 2 and 3 (each of which had two entrances), with Pen 1 showing markedly more variation in occupancy than the other pens. CALHOUN (1962a) notes that dominant males were sometimes able to monopolize the end pens (1 and 4), forcing subordinate males into the two central pens. This is the basis for HRDY's (1977) comment that some rats did well for themselves; as discussed above, while important one could justifiably point out that behavioral ecological theory is contributing little to our understanding if we are left with "some rats are dominant and they have an easier time of it with one entrance to guard." Ideally, we should like to understand why the pattern for Pen 1 is so different from that of Pen 4, and why in Pen 1, two replicates (marked * and # in Fig. 2) are such outliers with respect to the other four.

While the population density is constant across the rooms, the density of competing males (as measured by the sex ratio) varies from 0.41 to 0.70. I refer to this density of competing individuals as the intruder pressure. The six replicates are divided into "high," "medium," and "low" intruder pressure conditions (two rooms each); these are ordinal rankings and I know of no way to relate these intruder pressures to realistic ones experienced in the wild. Figure 2B illustrates the difference between the pen sex ratio and the overall room sex ratio, for each of the six replicates; points representing pens within the same room are connected. The two rooms with the lowest overall sex ratio (Series 2, rooms I and II) had the fewest males sleeping in Pen 1, and intermediate numbers in Pen 4. The two rooms with the highest sex ratios (Series 1, rooms I and II) had the most males sleeping in Pen 4, and intermediate numbers in Pen 1; precisely the opposite pattern. Finally, the two rooms with intermediate male densities show the greatest variation across pens, with males strongly concentrated in Pen 1 and Pen 4 having one and zero males. CALHOUN (1962a) notes that in the 0-male case, a particularly dominant male was able to establish himself at the base of the bridge connecting Pens 2 and 3, thereby monopolizing both Pens 3 and 4 (and a total of 17 females).
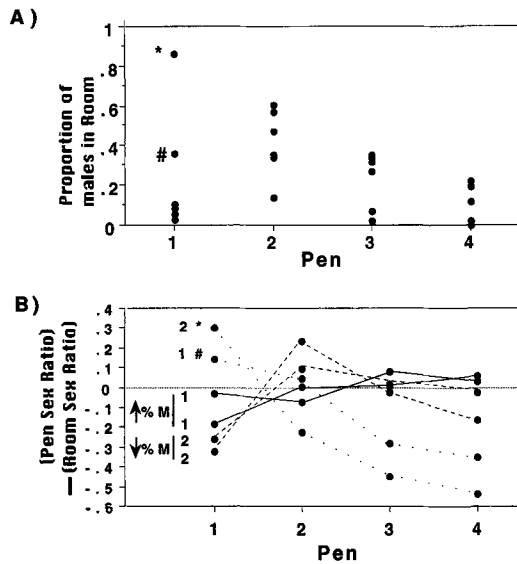
Fig. 2. Distribution of males across pens as a function of intruder pressure. There are three replicate rooms in each of two experimental series, indicated by number in (**B**). Symbols * and # indicate outliers in (**A**) and their corresponding positions in (**B**). ↓ and ↑ %M indicate rooms that ranked low and high in overall proportions of males, respectively; the remaining two rooms were intermediate. Vertical axis in (**B**) is the difference between the pen sex ratio and the room sex ratio.

DISCUSSION

I suggest the following explanation for this strong patterning in supposedly "pathological" behavior: at low intruder pressure, the males with greatest Resource Holding Power (RHP) were able to monopolize the preferred Pen 1; less dominant males "filled in" Pens 4, 3, and 2. Note that this ordering is the inverse of their quality as measured by burrow height; the preferred Pen 2 would be hardest to monopolize and Pen 4, lowest quality and easily defended, would be easiest and so held by second-tier males.

At high intruder pressure, no males could monopolize any pens and the pen sex ratio remained close to the overall room sex ratio. Finally, at intermediate intruder pressures even the highest-RHP males could not monopolize the most preferred Pen 1; however, they were able to control access to Pen 4 and the combination of controlled access, low habitat quality and high RHP permitted them to maintain absolute monopolies. Second-tier males were not able to control access to Pen 1 at all, leading to its invasion as the highest-quality pen available.

I have not attempted to address other aspects of the rats' behavior, such as the development of a behavioral sink (as defined above) or infant killing and cannibalism (though these later behaviors may be readily explicable as male competitive tactics; see below). My goal has been to demonstrate that even in the archetypal case of "crowding causes social pathology," a behavioral ecological approach that considers actors as strategic and tactical individuals operating on economic defendability principles can account for detailed variation in behavior and resulting demographics.

The insight that intruder pressure can make sense of apparent "social pathology" can be applied to another case, that of infanticide by male langur monkeys (*Presbytis entellus*).

LANGURS AND "PATHOLOGICAL" INFANTICIDE

When male langur monkeys join a troop (especially when this is done as an abrupt replacement of a single troop male), they sometimes kill young infants present (HAUSFATER & HRDY, 1984; SUGIYAMA, 1965). The stark contrast between this behavior and langurs' normally more peaceful behavior led some to suspect that infanticide represented a pathological or dysgenic response to "crowding" (it is not always clear in the literature whether a given author uses this term to refer to high population density, or the mechanism by which that density is achieved), while others see the behavior as a sexually-selected adaptation. The debate continues 30 years later (HRDY et al., 1995; STERCK, 1998, 1999; SUSSMAN et al., 1995) despite reports of infanticide from uncrowded and undisturbed sites (e.g. BORRIES, 1997; NEWTON, 1986). It is worth noting that HRDY, who formalized the sexual selection hypothesis, began her research on langur infanticide as an explicit follow-up to CALHOUN's rat work, attempting to document a crowding pathology in the wild (HRDY, 1977: 8−10).

One of the chief puzzles concerning langur infanticide is its variable occurrence; at some sites it seems to occur regularly and at others, never (CURTIN & DOLHINOW, 1978; BORRIES, 1997, suggests that with enough time it will be observed at most or all sites). In the absence of a plausible adaptive explanation for this variation, social pathology remains for some a viable alternative. In a series of publications, NEWTON (NEWTON, 1986, 1987, 1988; NEWTON & DUNBAR, 1994) attempted to explain the distribution of infanticide, and concluded that the behavior was not linearly related to population density/crowding, but instead was a function of the proportion of single-male troops in a population. Where troops contain only a single male, changes in male membership are almost inevitably abrupt and thus favor sexually selected infanticide.

The problem with this explanation is that it begs the question, why are some populations composed predominantly of single-male troops? Without an answer, one could readily argue that multi-male troops are "normal" for this species and thus single-male organization is atypical and "pathological." The question of what determines the number of males per troop in primates is of general interest; NEWTON and DUNBAR (1994) argue that it is not population density, climate, predation risk, or differential male mortality, but instead is most likely a function of numbers of adult females per troop, both within P. entellus and across colobines (see Discussion for additional alternative hypotheses). Presumably, the number of adult females per troop is determined by the variables that determine group size: NEWTON and DUNBAR (1994) suggest that small groups are favored by low predation risk and small or abundant food patches. TREVES and CHAPMAN (1996) found that conspecific threat (measured by the ratio of extragroup males: bisexual groups) explains variance in group size better than either predation threat or resource defense; however, intersite variance in that ratio remains unexplained.

NEWTON and DUNBAR's (1994) hypothesis hinges upon the existence of a strong correlation between the number of adult males and adult females per troop. While NEWTON (1988) reports such a correlation within P. entellus, it appears to be highly sensitive to methodological decisions and I find limited evidence to support it. Instead, the number of males per troop within this species, and hence the incidence of infanticide, appears to be a function of population density.

METHODS

Most populations of langurs have had some exposure to humans and are not totally wild on first contact; combined with being large, semiterrestrial monkeys this makes them ideal for

censusing and there is a great deal of demographic data available for them (more than 350 groups from at least 25 study sites). A trained observer can accurately count several groups per day under some conditions. One problem with this is that sometimes what is (accurately) counted is not a stable "group" in a socioecological sense, but an unstable phase resulting from e.g. death of a male resulting in no-male troops, or male incursions resulting in temporarily high adult sex ratios. Such incursions can last from hours to months (pers. obs.; LAWS & VONDER HAAR LAWS, 1984), and such longer "incursions" should not be dismissed as temporary − but cannot be distinguished from brief ones in a cross-sectional census survey. Rather than discount all such survey data, I have taken a statistical approach and excluded only extreme outliers from adult male/troop analyses (Table 2).

Table 2. Adult males per langur troop.

No. of males	No. of troops	
0	2	
1	172	
2	24	
3	15	
4	6	
5	3	
6	4	
7	4	
8	2	
9	4	
−		
24	1	(VOGEL, 1973)
40	1	(MOORE, 1985)
	238	

Mean=1.992, SD=3.3, range 0−40. One of the zero-male troops was known to have been single-male immediately prior to the census (male was killed by a truck: MOORE, unpubl.). The 24- and 40-male troops probably represent temporary incursions.

In addition, the data are of variable quality and there are some ambiguities in the secondary literature that can further confuse comparative analysis. NEWTON (1988) attempted, with my collaboration, to sort out some of these problems and his Table 1 is the starting point for the present analysis. However, most of our collaboration dealt with population density and proportion of unimale troops at each site; my interpretation of data on troop size and structure differs from his in several cases (Table 3). Appendix I explains the discrepancies between these data sets and those recently employed by SRIVASTAVA and DUNBAR (1996) and TREVES and CHAPMAN (1996). Relevant data from five sites have been published since NEWTON (1988): Ambagarh and Jaipur Residential (MATHUR & MANOHAR, 1992; incorrectly cited as "Reena & Ram" − the authors' first names − by NEWTON & DUNBAR, 1994), Mundanthurai (ROSS, 1993), Sariska (ROSS & SRIVASTAVA, 1994), and Ramnagar (BORRIES, 1997; KOENIG et al., 1997). I have visited both Jaipur sites with the authors and have accepted their data as given. For the other sites I contacted the primary authors directly for clarification of methodological issues; in the case of Mundanthurai, this led to significant reconsideration of the published data (below). For Polonnaruwa, one of the "older" sites, the discrepancies in the literature are large and are discussed below. All analyses have been carried out using NEWTON's (1988) data (as shown in Table 3) as well, and significant differences are noted. All analyses were done with StatView 4.5 (Macintosh).

Table 3. The langur data.

Site	Inf.	Set	Density	Percent 1-male	Adult females/troop		Adult males/troop		Males/all-male band		Disturbance rating
					Mean	Median	Mean	Median	Mean	Median	
Bhimtal	No	B	97	33.4	11.7	9	2	2	10	10	
Dharwar Forest	Yes	B	85	77	7.8	7	1.5	1	26	21.5	2.25
Dharwar Open	Yes	B	16.6	100	8.5	8	1	1	8.7	9	2.25
Hatto	No	B	17	33	19.7	14	2.7	2			
Junbesi	No	B	1.5	40	3.4	3	2	2			2
Kanha (NEWTON)	Yes	B	46.2	93	9.4	10	1.1	1	14		1.25
Kanha (KANKANE)	Yes	B	46.2	86.7	9.2	8	1.4	1	7.5	8	1.25
Melemchi	No	B	15.2	0	8	8	4	4	1	1	2
Orcha	No	B	4.4	0	6	5	3.7	3	1		1
Rajaji	No	B	90	25	13.5		3.4	3	5.5		1
Simla	No	B	24.6	42.9	11.9		2.9	2	3	2	1
Singur	No	B	12	100	5	5	1	1			3.75
Wilpattu	No	B	5.1	28.6	11.1	12	3	3			1
Ambagarh	No	R	66	90	35.2	35	1.2	1	30.5	30.5	2.5
Jaipur Residential	No	R	12.5	100	16.3	16.5	1	1	17.8	22	3.25
Rammagar	Yes	R	26	28	6.6	6	2.5	2			1.75
Mundanthurai	Yes	R/N	47.5	25	14.3	13.5	5.2	5.5	15	18	2.25
Sariska	No	R/P	30	81	33.5	33.5	1	1	21.7	13	1.4
Abu Forest	In.	N	31.6	100	10.5		1.7		8.2		2
Abu Town	Yes	N	72	87.5	8.3		1				3.75
Gir	No	N	121.5	40	13.6		2.4		2		1.75
Jodhpur	Yes	N	18	95	20		1		15.7		3
Kaukori	No	N	2.7	0	19	19	6	6	3	3	2.75
Polonnaruwa	Yes?	N	60	27	8.8		6.3	5	9	9	2.5
Ranthambhore	In.	N	14.6	66.7	21.7		7.7		16.6	17	1
Sariska	No	N	104	25	33.5	33.5	12.5	12.5	21.7	13	1.4
Abu Forest	In.	P	31.6	100	11.1	8	1	1	7.8	5	2
Abu Town	Yes	P	72	87.5	8.3	7.5	1.1	1	4.3	3	3.75
Gir	No	P	121.5	40	14	10	2.2	2	2	2	1.75
Jodhpur	Yes	P	18	89.7	16.1	13	1.2	1	12.3	10	3
Kaukori	No	P	4.8	0	19	19	6	6	3	3	2.75
Polonnaruwa	Yes?	P	145	27	8.8	7	3.8	3.5			2.5
Ranthambhore	In.	P	14.6	60	22.8	21	2.8	1	16.6	17	1

Inf.: Infanticide reported; In.: inferred; Set: the dataset used; B: both NEWTON, 1988 and the present analysis; R: recently published (since NEWTON, 1988); N: NEWTON, 1988 (recent Mundanthurai data included based on use in NEWTON & DUNBAR, 1996); P: present analysis (for Sariska I have used both recent and pre-1988 data, see Appendix 1); Density: langur population density, individuals/km^2; Percent 1-male: percentage of single-male troops. See Appendix 1, MOORE (1985), NEWTON (1988), and SRIVASTAVA and DUNBAR (1996) for sources.

Polonnaruwa

Population density estimates for this site in the secondary literature range from about 40/km² (OPPENHEIMER, 1977) to up to 200/km² (HRDY, 1977), all based on the work of RIPLEY (RIPLEY, 1965, 1967, 1979, various pers. comm. cited by secondary authors). NEWTON and I attempted to reconcile these, arriving at what was essentially a compromise density of 109/km² and 27% unimale troops (based on a pers. comm. cited in HRDY, 1977, with $N=11$ troops; NEWTON, 1988). The site density subsequently has been reported as about 60/km² by NEWTON and DUNBAR (1994: Fig. 11.5; it is 109 in Fig. 11.3) and 109/km² by SRIVASTAVA and DUNBAR (1996); in each case, the density used is that which better supports the argument being made.

In her text, RIPLEY writes that "1 square mile of dry-zone forest can support about five to seven troops with an average of 25 members each" (1967: 241), which works out to 57.9/km². However, elsewhere she estimates a biomass of about 12 kg/ha (1979; based on HLADIK, 1975, who worked at the same site at about the same time and used RIPLEY's ranging data for his analyses). At an average weight of 7.4 kg/monkey (based on troop compositions in RIPLEY, 1965; weights from ROONWAL, 1981) this works out to 160 monkeys/km². Note that if RIPLEY initially confused miles and kilometers, 5–7 troops of 25 each would be about 150 monkeys/ km², in good agreement with the biomass estimate. Which is correct? Rough calculations based on her map (1967, Fig. 1) yield a density estimate for the four troops shown of about 154 monkeys/km²; analogous calculations from HLADIK's (1977) Figure 2 yield 169/km². Finally, HLADIK (1977) notes that both langur species at Polonnaruwa occur at similar density, "(about two animals per ha), with biomasses of 10 to 15 kg per ha in maximum density locations" (p. 346); while 2/ha would be 200/km², his biomass estimate suggests an overall figure under 150/km² — but well over 60/km².

The conclusion seems inescapable that RIPLEY (1965) consistently confused miles with kilometers in reporting population density, and the true figure is likely close to 130–160/km². I use 145/km² in this paper; overall conclusions are not materially affected if the earlier compromise figure of 109/km² is used.

NEWTON's (1988) figure of 6.3 AM/troop is based on the average of four troops listed in MOORE (1985). In the course of re-examining RIPLEY's (1965) publications I noticed apparent discrepancies in the reports (Table 4). MOORE's (1985) figures were based on Table 11 in RIPLEY (1965), with troop B1 adjusted for two subadult males as indicated in her Table 6. Because age breakdowns are not given for troops B and C1, presence of subadult males cannot be checked for them; furthermore, that would not explain the discrepancy between her Tables 10 and 11 (which are consistent regarding inclusion of subadults with respect to troop B1). B1 was formed when a subgroup left troop B; if the 13 males includes subadults then the numbers are at least closer to matching (13-4 is closer to the c. 6 of RIPLEY, 1967, than is 13-2). Noting that 13 adult males/troop would be >3 SD from the mean (Table 2), I have used the figures from RIPLEY (1967) here on the assumption that most or all of the discrepancy is due to (possibly inconsistent) inclusion of subadult males.

Table 4. Males per troop at Polonnaruwa.

Troop	MOORE (1985)	RIPLEY (1967)	RIPLEY (1965: Table 10)	RIPLEY (1965: Table 11)
B1	2	2	4	4
A	3	3	3	3
C1	7	c. 4	c. 4	7
B	13	c. 6	c. 6	13

Mundanthurai

Ross (1993) estimates a population density of $47.5/km^2$ with 25% of four troops unimale (the one unimale troop experienced a takeover with infanticide during her study, and was multimale when she left). Ross worked at Mundanthurai for only 28 days. Her density estimate is based on a complete count of troops in her study area of about $4km^2$, which was on the edge of a small village into which two troops regularly entered (1993; pers. comm.). Her impression is that *P. entellus* density was lower outside her immediate study zone; further into the Park they are replaced by *P. johnii*, and further outside the Park habitat is unsuitable for langurs (pers. comm.). Thus the density of $47.5/km^2$ is based on a one-month study, in a steep ecotone at the edge of a village. Based on population density figures from Mt. Abu (density twice as high within town as in the surrounding forest; MOORE, 1985) it seems very likely that the "true" density at Mundanthurai is lower, by an amount difficult to estimate. Analyses of population density effects were carried out both with and without inclusion of this site.

Relevant analyses are based on numbers of adult females in troops rather than total troop size because (1) females are thought to be the ecological 'decision makers' among primates; (2) immatures probably do not make independent decisions about group membership; (3) demographic variables including birth seasons and infanticide can result in greater stochastic variation in number of immatures (N=234 troops, CV for adult females=63.7; immatures, 80.7); and (4) male decisions to join a troop are more likely to be a function of number of adult females, than of numbers of immatures (cf. NEWTON & DUNBAR, 1994).

RESULTS

While the number of adult males per troop (AM/t) is correlated with the number of adult females per troop (NEWTON & DUNBAR, 1994) the relationship explains very little of the variance (Fig. 3A, R^2<0.02). Furthermore (and contra NEWTON & DUNBAR, 1994), the relationship is unrelated to intersite differences (Fig. 3B; arbitrarily excluding the two 30±female sites changes the slope to +0.081, R^2=0.081, p=0.19). The difference in our results is probably due to his inclusion of troops with anomalously large number of males at several sites, thus artificially inflating site means. These figures show site means calculated with outliers excluded (as per Appendix and above); including the outliers but using site medians rather than means does not change the overall result (Y=2.18−0.01X, R^2=0.004, p=0.76, N=24). The proportion of one-male troops at a site is similarly unrelated to average number of females per troop (Y=46.03+0.72X, R^2=0.026, p=0.442, N=25).

While male membership in langur troops is unrelated to the number of females per troop across sites, both the number of adult males per troop (AM/t) and the proportion of single-male troops at a site are related to population density, *in a nonlinear fashion* (Fig. 4). There is no linear relationship between the variables (e.g. proportion single-male troops: Y=56.58−0.026X, R^2=0.001, p=0.89).

In principle the basis for this relationship could lie in general ecological variables (food distribution in space and time, predation, etc.). If so, one would expect that both the number of adult females per troop and the total size of male bands would correlate similarly with population density. While both show such a trend, it is strong only for males per male band − probably reflecting the greater numbers of extra-group males at predominantly single-male sites, though this may merit further investigation (Fig. 5, medians yield essentially similar results). Human disturbance appears unrelated to population density (Fig. 6; cf. STERCK, 1998). Repeating the analyses of Figures 5 and 6 using NEWTON's (1988) dataset yields essentially the same results.
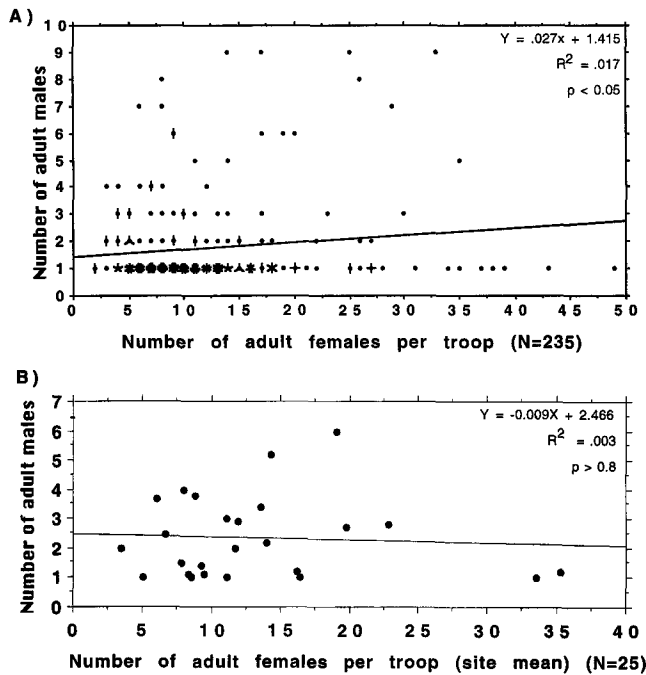
Fig. 3. Adult male membership as a function of numbers of adult females per troop. Two troops with >20 males each have been excluded as probable temporary incursions. Two troops had 0 males (Table 2); one of these (at Mt. Abu) was known to have been single-male for months prior to the census and is considered single-male here; the other (at Ranthambhore) was observed only once and is excluded from this analysis.
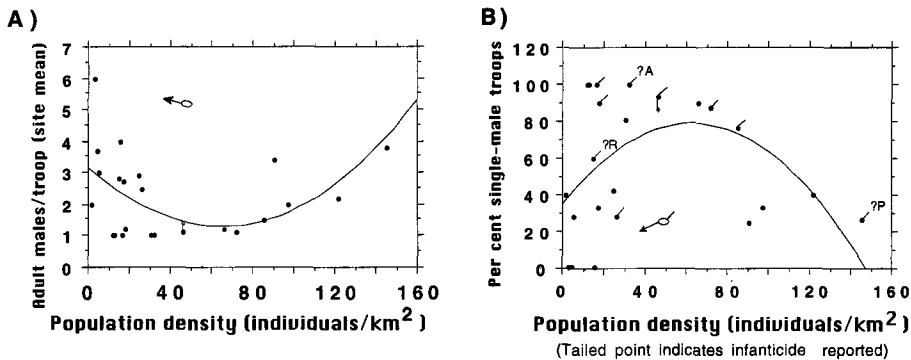

Fig. 4. Troop composition and population density: Mundanthurai (shaded, with arrow) is excluded from analysis (see text). Arrow indicates direction of probable "true" location of the point. Two Kanha studies connected by vertical line, shaded point is KANKANE (1980), not included in analysis. (A) Adult males per troop. $Y=3.16-0.06X+0.0004X^2$; $R^2=0.26$, $p=0.053$, $N=23$ (with Mundanthurai included, $R^2=0.12$, $p=0.28$; NEWTON data, $R^2=0.06$, $p=0.53$, $N=24$). (B) Per cent single-male troops. $Y=35.76+1.33X-0.01X^2$; $R^2=0.21$, $p=0.097$, $N=23$ (with Mundanthurai included, $R^2=0.16$, $p=0.171$, $N=24$; NEWTON data, $R^2=0.12$, $p=0.26$, $N=24$). For the three sites indicated by "?" and site initial in (B), infanticide is strongly suspected but unconfirmed/described: Abu forest: stalking attacks by invading males and infant disappearance, but actual wounding not observed (MOORE, unpubl.); Ranthambhore: forest guards reported dead infants in range of a recently-invaded troop, subsequent census consistent (MOORE, unpubl.); Polonnaruwa: RIPLEY (1980: 374) states that at Polonnaruwa "troop takeovers [accompanied by infant mortality and ouster of males into mostly male groups) ... (occurs) ... (RIPLEY, in prep.)]," but I have not found further description.
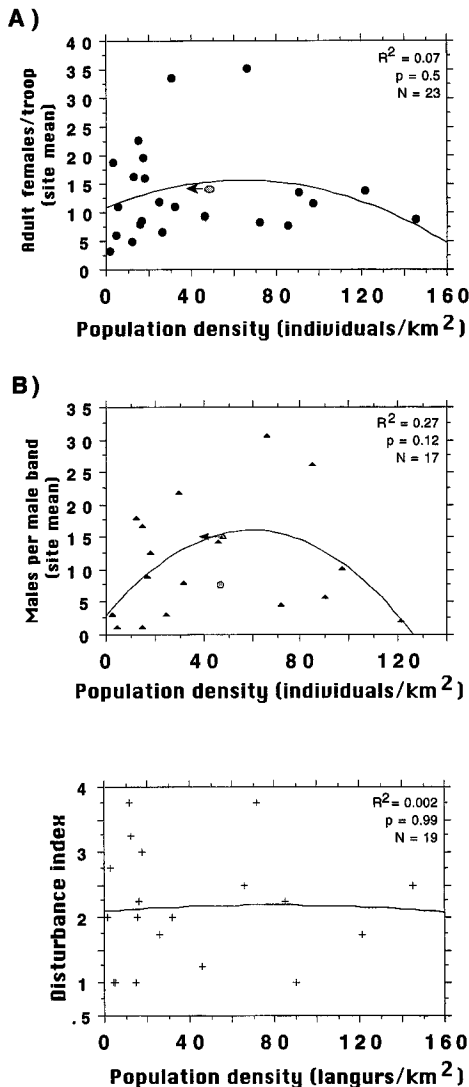
A)

B)

Fig. 5. Group size and population density. Because infants and juveniles are not demographically independent of their mothers in a bisexual troop, number of adult females (not total count) is used for troops. Because no males are born into a male band, for these total numbers are used. Shaded symbol with arrow represents Mundanthurai and shaded circle in (**B**) represents KANKANE (1980) data for Kanha; neither was used in the analyses for reasons explained in the text.

Fig. 6. Disturbance and population density. Disturbance index: Composite values from BISHOP et al. (1981) and STERCK (1998).

DISCUSSION

The finding of female monopolization at intermediate population densities giving way to multimale troops at high population densities is readily explicable in terms of economic defendability. High population densities normally lead to high intruder pressures and the inability of a single male to monopolize a troop. An exception may be local concentrations around preferred habitats, where extragroup males are excluded by males of the densely-packed unimale troops; the presence of other troops in the surrounding area gives extragroup males less-costly alternative targets (MOORE, 1985).

At first glance, the finding of multimale troops at low population densities appears inconsistent with economic defendability models; it should be easy to exclude intruders when they are rarely encountered. This neglects the tactics of extragroup males and the importance of

cost/benefit ratios for these intruders, however. First, while extragroup males do challenge troop males, these are usually perfunctory and troop males normally drive male bands away without trouble. While aggressive male replacement occurs sometimes, more often the extragroup males' strategy appears to be to "monitor a number of troops; sooner or later a resident male will fall sick or be eaten — *then* invade" (MOORE, 1985). As population density decreases, intertroop spacing tends to increase and extragroup males have farther and farther to go to monitor (and challenge) troop males. At some point range size becomes so great that the cost of monitoring several troops exceeds the benefit of having several males in the pool of "potential losers" and males who would otherwise become extragroup do better by remaining with a single troop most of the time, waiting for the resident to fail and seizing occasional chances to copulate (MOORE, 1985).

In this scenario, the presence of multiple males in a troop does not mean that it is functionally (i.e. genetically) a multi-male troop. A dominant male might be able to prevent others from breeding; the term "multi-male" obscures two very different forms of social organization (HENZI, 1988; VOGEL, 1977). Monopolization within an apparently multi-male group could be accomplished via contests over receptive females, peripheralization, or outright seasonal expulsion. All characterize low-density Himalayan sites (BISHOP, 1979) and it is clear that at least at Junbesi, troops are usually reproductively single-male (BOGGESS, 1980). The lower intruder pressure (fewer contacts with extragroup males) permits steep dominance hierarchies to arise, mediating competition as well as breeding and permitting "multi-male" organization (CURTIN, 1975). To pursue the analogy with territorial defense, resource holders no longer attempt to keep intruding male bands away from general proximity to the resource; individual rivals are allowed near and contests occur only during direct competition.

The intruder pressure hypothesis can be tested by comparing degree of skew in male reproductive success for multi-male troops at high and low population densities; skew should be high at low density non-seasonal populations (Orcha, Wilpattu, Kaukori), but low at high-density sites where troops are "truly" multi-male (Gir, Polonnaruwa). Skew at low-density but seasonal sites (Himalayas) should depend on the ability of individual males to monopolize matings against seasonal competition and should be inversely proportional to numbers of simultaneously receptive females. In large troops of synchronously breeding females, the dominant male is likely to be swamped — competitor pressure, analogous to intruder pressure, shifting the economics of monopolization (RIDLEY, 1986). While coalitions occur within all-male bands and may be important during takeovers (MOORE, 1985; SOMMER, 1988), failure to detect statistical evidence for them in troops makes the role of male cooperation in troop defense against male bands uncertain. Coalitions are likely to survive only if subordinate members benefit from them, via either kin selection or reduced reproductive skew (VEHRENCAMP, 1983).

The genetic data needed to test the hypothesis definitively are not available for most sites. However, at the moderately-low density site of Ramnagar (26 individuals/km^2) male dominance hierarchies were linear and faecal DNA paternity studies of 29 infants across ten mating seasons in three troops indicate that the alpha male of multimale troops sired on average 57% of infants (range 0–100%) — significantly greater than the 25% expected based on numbers of resident males (LAUNHARDT, 1998). Comparable data from additional sites is required before evaluating the consistency of this single point (showing moderate monopolization at a moderately low-density site) with the model suggested here.

Indirect support for the hypothesis is found in the observation by NEWTON and DUNBAR (1994: 332) that male tenure in single-male troops is shorter at higher population densities, supporting an unsurprising relationship between population density and intruder pressure.

SRIVASTAVA and DUNBAR (1996) developed an economic defendability model similar to that

presented here, in which search time (a function of range size) plays the central role in determining whether langur groups are single- or multi-male. Following MOORE (1985) they find a curvilinear relationship between population density and the distribution of single-male troops; however, they found a better fit to the data using a third-order polynomial rather than a quadratic. They interpret this as arising from the complex intercorrelations among population density, birth rate, climatic seasonality, number of females per group, and range size, with the later two the most important. Our conclusions agree in emphasizing the importance of economic defendability models and nonlinear relationships between population density and other socio-demographic variables; they differ in two respects.

First, theirs emphasizes the costs of search time, considering the problem as centered in optimal foraging theory; I emphasize the dynamics of intermale competition (a view that may better explain the presence of both unimale and multimale troops at a given site, as based on intermale variation in RHP). These two views may not be in fundamental conflict.

Second, their use of a cubic equation requires a fairly complex explanation (see SRIVASTAVA & DUNBAR, 1996: 224) relative to the one presented here, at modest gain in explanatory power (they give an R^2 of 0.330 for the quadratic and 0.57 for the cubic versions; using the numbers in their Table 1, I obtain R^2 values of 0.281 and 0.432 respectively) that relies greatly on the accuracy of several high-density estimates. (Ironically, using my density estimates instead of theirs improves the relative advantage of the cubic equation: $R^2=0.270$ and 0.459 respectively.) Figure 7 presents R^2 values for various datasets used, as a function of the order of the polynomial equation fitted. For most there is an inflection at the third-order point; I remain unconvinced of the need for more complex third-order explanations, especially given the uncertainties connected with many of the data points, but the choice is the reader's. What is clear is that primatologists need to consider nonlinearity in socioecological analyses.

This analysis suggests that the pattern of male group membership within gray langurs is not well explained by the leading general hypothesis for primates (numbers of adult females: MITANI et al., 1996; NEWTON & DUNBAR, 1994; see Fig. 3), though some readers likely will differ in
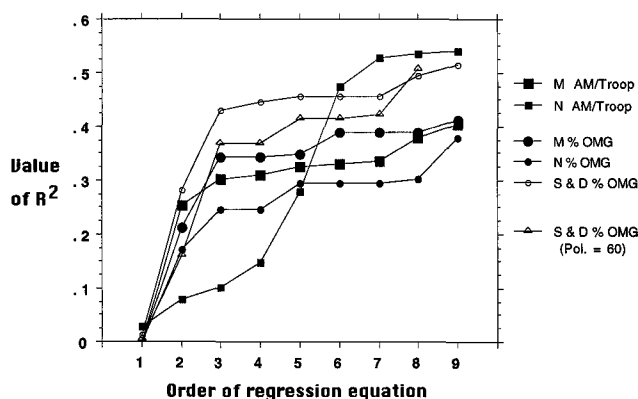

Fig. 7. Variance and polynomial choice. Amount of variance explained (R^2) by first- through ninth-order regressions of troop composition on population density in three different data sets. Large filled symbols (■, ●) and "M": MOORE dataset (present analysis); small filled symbols (■, ●) and "N": NEWTON (1988); open symbols: SRIVASTAVA and DUNBAR (1996). Squares: Adult males/troop (cf. Fig. 4A); circles: per cent one-male groups (OMG, cf. Fig. 4B); triangle: SRIVASTAVA and DUNBAR % OMG, but with Polonnaruwa population density set to 60 individuals/km². Amount of variance explained depends heavily on both the dataset used and on the order of the regression selected.

interpretation of a relationship for which the amount of variance explained is less than the associated statistical significance. Space precludes a complete analysis of the main alternative, seasonality of reproduction (RIDLEY, 1986). RIDLEY's (1986) criteria can only roughly be applied to birth seasonality information in BISHOP (1979) and MOORE (1985) [for most sites, birth months are only estimated, rendering the "75% of births" birth season criterion of RIDLEY (1986) impossible to apply strictly; RIDLEY (1986) excluded *P. entellus* from his analysis in part for this reason]. As an exploratory analysis I nevertheless have used the BISHOP (1979) and MOORE (1985) data to estimate crudely birth season lengths and to categorize sites into short (≤ 2 month) and long (≥ 5 month) birth seasons. Troop adult sex ratio [per cent males, calculated as (mean No. AM)/(mean No. AM+mean No. AF) at a site] was not significantly related to birth season length, though a quadratic equation fit an inverted-U to the data reasonably well (linear: $R^2 = 0.025$, $p > 0.5$; quadratic: $R^2 = 0.335$, $p = 0.16$; $N = 12$; calculating adult sex ratios with site medians improved the quadratic fit but only slightly). Sex ratio was not correlated with short/long birth seasonality (Mann-Whitney $U_{4,5} = 7.0$, $p > 0.4$). However, the limited and crude data here are consistent with the absence of single-male troops at sites with short breeding seasons (Table 5). Clearly, more work is needed.

Table 5. Birth seasonality and male membership in troops.

		Troop structure	
		Single-male	Multi-male
Birth season	Short (≤ 2 months)		Bhimtal
			Melemchi
			Kaukori
	Long (≥ 5 months)	Dharwar	Orcha
		Mt. Abu (town)	Polonnaruwa

The absence of single-male sites ($\geq 75\%$ troops at a site single-male) with short birth seasons is consistent with findings of RIDLEY (1986), but is here not significant (Fisher exact probability$=0.286$).

I suggest that intruder pressure, mediated by population density and possibly influenced by birth seasonality, is responsible for the distribution of multi-male and single-male troops in gray langurs.

Given this ecological basis for the distribution of single- and multi-male troops, NEWTON's (1988) account of the distribution of infanticide as a function of the prevalence of single-male troops takes on predictive value as an explanation. It should be noted that to the extent that "multi-male" troops at low density sites are genetically single-male (with high or absolute reproductive skew) sexually selected infanticide is predicted for these as well; the recent observation of infanticide at Ramnagar is a case in point (BORRIES, 1997).

If correct, this is a satisfying explanation for variation in one aspect of demography (AM/t) and infanticide in langurs, at an ultimate level. For a more proximate explanation of the ontogenetic and behavioral factors that promote aggressive takeovers and infanticide at intermediate population densities, see BOGGESS (1980, 1984) and CURTIN (1975, 1981). While BOGGESS (1980, 1984) and CURTIN (1975, 1981) interpreted the processes that prevent formation of a stable multi-male group as atypical and/or pathological phenomena deriving from human disturbance, their descriptions of the interplay amongst learning, experience, strategy and tactics among langurs can readily be seen as a starting point for a developmentally rich account of sexually-selected male langur behavior.

Caution must be used extrapolating conclusions based on this intraspecific analysis to discussions of interspecific patterns in the composition of primate groups (MITANI et al., 1996; RIDLEY, 1986), but these data support the proposition that patterns of male competition and cooperation, as they relate to population (intruder) density, are a major influence on group composition.

CONCLUSION

For two archetypal examples of crowding-induced social pathology, population density can be seen as strongly patterning the supposed "pathologies" via correlated effects on levels of intermale competition. The consequences of variation in intruder pressure change in nonlinear fashion, in various birds, captive rats, and wild langur monkeys. Models assuming linear effects seem to be grounded in the curious implicit belief that higher densities are always "worse," a view that neglects the range of behavioral options open to nonhuman primates (and other taxa) to regulate and mediate normal (i.e. non-pathological) conflict (DE WAAL, 1989, 1996).

The possibility of nonlinear density-dependent effects on competitive regimes are worth considering when trying to interpret intersite variation in other taxa. For example, SUGIYAMA (1984, 1999) has reported evidence for male dispersal among chimpanzees at Bossou. This is in marked contrast to the pattern of male philopatry documented elsewhere (MORIN et al., 1994; PUSEY, 1980) and a recent discussion of SUGIYAMA's findings notes that "the Bossou chimps live in an extremely disturbed area and ... such conditions may explain their unusual behavior" (NORMILE, 1998). The "explanation" NORMILE refers to appears (implicitly) to be that disturbance leads to "unusual" (i.e. nonadaptive, pathological) behavior via either direct psychological effects or indirectly, by interference with the operation of normative evolved behavioral mechanisms (cf. BOGGESS, 1984). Another possibility however is that the isolation of the Bossou community results in such a low intruder pressure that male xenophobia and territoriality are either uneconomical or remain unlearned [cf. the developmental arguments of POWER, 1991 (see MOORE, 1992a for a critique of this badly flawed but interesting book)]. This later interpretation implies that inter-community relationships among chimpanzees living at very low densities (<0.1/km^2: MOORE, 1992b) might "normally" be less aggressive than those at intermediate densities (the economic defendability theory could be speculatively invoked to suggest that territoriality also might break down at high densities – c.f. "carnivals," REYNOLDS, 1965). If that were so, the unusual (but not pathological) behavior at Bossou would be seen as a normal expression of chimpanzee behavior in a particular socioecological context, one of particular interest to modelers of human evolution (REYNOLDS, 1966).

Appendix 1. The data

Abu Forest NEWTON: 10.5 AF/troop, 1.7 AM/troop. These figures include two troops apparently undergoing male incursions (JLA and DW's in MOORE, 1985) when they were censused. Male band size 8.2: NEWTON apparently excluded a solitary male.

Abu Town NEWTON: 1.0 AM/troop. Census data in MOORE (1985) came primarily from a single census sweep, which took place shortly after a unimale troop male was killed by a truck. From a socioecological standpoint, this was an atypical situation and I assigned this troop 1 male for generating a site average. Male bands: MOORE (1985) lists three (plus a fourth transitory band excluded here). SRIVASTAVA and DUNBAR (1996) list just "Mt. Abu." Their mean number of females/troop and % OMG appear to come from MOORE (1985) values for Abu Town, but their figure for population density (50 individuals/km^2) is from HRDY (1977) who did not strictly distinguish habitats nor present methods of calculation.

Dharwar Forest NEWTON: Male band size 15. He evidently used only (SUGIYAMA, 1964); (SUGIYAMA, 1967) reports a band of 59 which is included here. SRIVASTAVA and DUNBAR (1996) list just "Dharwar." Their mean number of females/troop and percentage OMG resemble those of MOORE (1985) for Dharwar Forest, but their estimate of population density (13 individuals/km^2) is far closer to the 16/km^2 for Dharwar Open than to the 85 individuals/km^2 of Dharwar Forest used by MOORE (1985) and NEWTON (1988). I have no explanation; perhaps it is a typographical error in their Table 1. TREVES and CHAPMAN (1996) give the density of "Dharwar" as 91.5, citing SUGIYAMA (1965); that source states that "the population density ... in the forest part of Dharwar is from 85 to 135 animals/km^2" [MOORE (1985) and NEWTON (1988) used the lower figure for a variety of reasons; the interested reader(s) should contact this author for explanation].

Gir NEWTON: 13.6 AF/troop, 2.4 AM/troop. I used data from STARIN (1978) excluding her second, post-takeover count of Jamwadla troop, and RAHAMAN (1973) excluding Jamwadla, which STARIN (1978) had previously counted. SRIVASTAVA and DUNBAR (1996) give the density as 112 individuals/km^2 while both MOORE (1985) and NEWTON (1988) used 121 individuals/km^2; SRIVASTAVA and DUNBAR'S (1996) figure is presumably a typographical error (inspection of their Fig. 5 indicates the error was incorporated in their analysis; the consequences would presumably have been slight).

Jodhpur: I used MOHNOT et al. (1984) as it represents a near-complete census of the Jodhpur langur population. SRIVASTAVA and DUNBAR (1996) used a different but comparable census and their figures differ slightly. V. SOMMER (pers. comm.) notes that the crude population density of 15−18 individuals/km^2 is based on inclusion of rarely-used corridors and ecological lacunae, and that adjusting for such features would yield an ecologically more meaningful density for Jodhpur of about 26 individuals/km^2. This would improve the fit of the curves in Figure 4 slightly, but I have stayed with the figure of 18 individuals/km^2 for consistency with other published analyses.

Kanha: KANKANE surveyed langur populations in Kanha NP in 1977 (KANKANE, 1980) and NEWTON began work there in 1981; it is not clear how much their samples overlapped. Data from each study have been plotted but for most analyses only NEWTON's data have been used, to avoid double-counting. Considering these as independent samples would slightly increase the significance of the patterns described. SRIVASTAVA and DUNBAR (1996) appear to have used NEWTON's figures for mean number of females per troop and KANKANE's for percentage OMG.

Kaukori: SRIVASTAVA and DUNBAR (1996) give no population density for this site (and presumably did not use it in their density-related calculations); NEWTON (1988) used 2.7 individuals/km^2 (based on calculations by HRDY, 1977, from data in JAY, 1965). JAY (1965) notes that only one group of 54 was found in an area of about 8 square miles (yielding a rough density of 2.7 individuals/km^2), but JAY (1963) gives the size of this group's range as 3 square miles (for 6.9 individuals/km^2). I have used the midpoint of these two estimates, 4.8 individuals/km^2.

Melemchi NEWTON: 2.5 AM/troop. The source of this is not clear; BISHOP (1979) presents data for one troop, containing 3−5 males.

Orcha: SRIVASTAVA and DUNBAR (1996) use a population density of 6 individuals/km^2; this is the high end of a range of 2.7−6.0 individuals/km^2 calculated by HRDY (1977) from JAY (1965). NEWTON (1988) and I use the midpoint of this range, 4.4 individuals/km^2.

Rajaji: SRIVASTAVA and DUNBAR (1996) use 80 individuals/km^2, the figure given by LAWS and VONDER HAAR LAWS (1984) for bisexual troop density; as the later authors note, ecological density would be somewhat higher due to inclusion of extragroup males, and NEWTON (1988) and I use 90/km^2 for this site.

Ranthambhore NEWTON: 66.6% one-male troops, 21.7 AF/troop, and 7.7 AM/troop. I excluded a group of 15 AF and 40 AM, censused once, that was probably undergoing a male incursion. The resulting change in mean AM/troop is substantial.

Sariska NEWTON: 25% one-male, 12.5 AM/troop, and density 104/km^2. NEWTON bases percentage one-male on $N=4$ on our collaborative interpretation of (VOGEL, 1973, 1977), in which we excluded the "large mixed group" containing 24 males (with it, the figure would be 20% one-male). However, NEWTON's 12.5 AM/troop figure is the average of one unimale troop and the 24-male troop; I excluded this male count from both percentage one-male and average AM/troop calculations. Finally, ROSS and SRIVASTAVA (1994) calculated population density of 30/km^2; ROSS was able to determine number of adult males for 12 troops, all of which were one-male (pers. comm.). Neither I nor ROSS have an explanation for the dramatic density difference; I have calculated percentage one-male as the sum of ROSS' and VOGEL's data ($1/4 + 12/12 = 81\%$). SRIVASTAVA and DUNBAR (1996) base their data entirely on ROSS and SRIVASTAVA (1994); the discrepancy between their density of 28 individuals/km^2 and 30/km^2 is unexplained but presumably trivial.

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