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Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India

T R SHANKAR RAMAN*
Centre for Ecological Research and Conservation, 3076/5 IV Cross, Gokulam Park, V V Mohalla, Mysore 570002, India
*Present address: Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India

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Abstract. **Chital or axis deer (*Axis axis*) form fluid groups that change in size temporally and in relation to habitat. Predictions of hypotheses relating animal density, rainfall, habitat structure, and breeding seasonality, to changes in chital group size were assessed simultaneously using multiple regression models of monthly data collected over a 2 yr period in Guindy National Park, in southern India. Over 2,700 detections of chital groups were made during four seasons in three habitats (forest, scrubland and grassland). In scrubland and grassland, chital group size was positively related to animal density, which increased with rainfall. This suggests that in these habitats, chital density increases in relation to food availability, and group sizes increase due to higher encounter rate and fusion of groups. The density of chital in forest was inversely related to rainfall, but positively to the number of fruiting tree species and availability of fallen litter, their forage in this habitat. There was little change in mean group size in the forest, although chital density more than doubled during the dry season and summer. Dispersion of food items or the closed nature of the forest may preclude formation of larger groups. At low densities, group sizes in all three habitats were similar. Group sizes increased with chital density in scrubland and grassland, but more rapidly in the latter–leading to a positive relationship between openness and mean group size at higher densities. It is not clear, however, that this relationship is solely because of the influence of habitat structure. The rutting index (monthly percentage of adult males in hard antler) was positively related to mean group size in forest and scrubland, probably reflecting the increase in group size due to solitary males joining with females during the rut. The fission-fusion system of group formation in chital is thus interactively influenced by several factors. Aspects that need further study, such as interannual variability, are highlighted.**

Keywords. **Grouping behaviour; *Axis axis*; population density; rainfall; tropical dry evergreen forest; scrubland; grassland; seasonality.**

1. Introduction

Many species of mammals form social groups during foraging, migration, and other daily activities. The size of groups is often considered a fundamental attribute of the social organization of such species (Jarman 1974; Wilson 1975; Clutton-Brock and Harvey 1978; Clutton-Brock *et al* 1980; Wittenberger 1980; Rodman 1988), and is described using measures such as the mean group size, and Jarman's (1974) typical group size. Usually, the observed group size is explained as arising from a balance between various advantages of group-living (such as better foraging efficiency, safety from predators, or thermoregulation), and costs (such as competition for food, and susceptibility to parasites or diseases; reviewed by Pulliam and Caraco 1984; Giraldeau

*Fax, 91 80 3311280; Email, shankar@ces.iisc.ernet.in.

1988). In contrast to individuals of species that spend most of their life solitarily and form ephemeral pairs solely for mating, individuals in group-living species are faced with the choice of living in groups of various sizes versus fending for themselves alone. This is particularly so in species that form fluid groups that change in size temporally, in what is also called the fission-fusion system of group formation (Barrette 1991).

The chital or axis deer (*Axis axis* Erxleben), an endemic cervid of the Indian subcontinent, is known to exhibit a fission-fusion system of fluid group formation and dissolution (Schaller 1967; Fuchs 1977; Mishra 1982; Barrette 1991). The average size of chital groups changes over diurnal (Miura 1981), monthly, and seasonal time periods (Schaller 1967; Sharatchandra and Gadgil 1975; Mishra 1982; Khan *et al* 1995), as well as in relation to habitat (Barrette 1991; Karanth and Sunquist 1992). Based on these studies, different hypotheses have been put forward to explain the patterns of grouping behaviour in chital (see below). A simultaneous test of the competing hypotheses has not, however, been made. In this paper, predictions of these hypotheses are tested using monthly group size data from a free-ranging population of chital collected over two years from three different habitats: dense forest semi-open scrubland, and open grassland. Multiple regression models have been utilized to examine the effects of various environmental parameters on group size. The results indicate that animal density, food availability and dispersion, habitat structure, and rutting (breeding) activities interactively influence monthly and seasonal changes in chital group size.

1.1 *Hypotheses and predictions*

1.1a *Animal density*: The influence of animal density within a habitat on group size has not been proposed earlier for chital. Caughley (1977) suggested, however, that in fission-fusion group formation, given that groups have a certain probability of joining in relation to their rate of encounter, a positive relation between group size and animal density is expected.

1.1b *Food availability and dispersion*: Group sizes increase directly in relation to food availability (Graf and Nichols 1966; Schaller 1967; Sharatchandra and Gadgil 1975; Fuchs 1977; Mishra 1982; Johnsingh 1983; Khan *et al* 1995). For a given quantity of available food, the more clumped the distribution of the food, the larger is the expected group size. Conversely, if food is evenly dispersed and locally sparse, groups should break up into smaller foraging units to reduce interference competition (Jarman 1974; Sharatchandra and Gadgil 1975; Mishra 1982). These hypotheses ignore the possible confounding effect of food availability on animal density, which can influence group size as postulated above. Seasonal densities and habitat utilization by chital in the study area were found to be closely related to seasonal changes in availability of different foods, which were in turn related to rainfall (Raman *et al* 1996; see below). Thus, the effect of food availability on group size needs to be examined after removing the effects of animal density on group size, if any.

1.1c *Social behaviour and fawning*: Larger groups of chital have been noted to form in months when rutting occurs, presumably facilitating social interactions and breeding opportunities (Graf and Nichols 1966; Fuchs 1977). Alternatively, larger groups may form during the fawning season, because of the benefits in terms of better predator avoidance conferred by larger groups (Hamilton 1971; Mishra 1982). These lead to the predictions that group size will be directly related to the monthly percentage of rutting stags and fawns, respectively.

1.1d *Habitat structure*: After removing the effects of factors such as seasonal changes, the more open a habitat is, the larger the group size it should have (Barrette 1991). This is a purely structuralist explanation, claiming that open habitats permit, while closed habitats hinder, the formation of larger groups (Barrette 1991). Here I examine a prediction of this hypothesis, i.e., when other factors such as animal density are controlled, the monthly group size should be highest in open grassland, followed by semi-open scrubland, and least in closed forest.

Besides these hypotheses, predation has been proposed as a factor influencing grouping behaviour in chital (Sharatchandra and Gadgil 1975; Mishra 1982; Khan *et al* 1995). This has been ignored during this study as the study area did not have any natural predators, except for a few feral dogs (Raman *et al* 1996). It is reasonable to assume that the level of predation played a minor role, if at all, and did not vary substantially during the study to influence grouping behaviour of chital significantly.

2. Materials and methods

2.1 *Study area, vegetation, and climate*

Guindy National Park (GNP) is a 2·7 km^2 park in Madras city (13°N, 80°E). Chital were introduced in the park and occur at high densities of about 212/km^2 (estimated using line transects during 1991–92; Raman *et al* 1996). The natural vegetation of the park is tropical dry evergreen forest (Champion and Seth 1968), classified floristically as the *Albizia amara* Boiv. community (Puri *et al* 1989). Three broad habitats occur in the park: (i) Forest (occupying about 92 ha)—characterized by a closed canopy with trees such as *Acacia planifrons*, Cassia spp., *Ficus benghalensis*, *Feronia elephantum*, and *Atalantia monophylla*. The understory (1 5–2 m tall) is dense, with profuse growth of shrubs such as *Glycosmis pentaphylla* and *Clausena dentata*, but grass growth is scarce, (ii) Scrubland (occupying about 160 ha)—this semi-open habitat is characterized by scattered palmyrah palms (*Borassus flabellifer*) and few other trees. Shrubs such as *Carissa spinarum* and *Randia* spp. and over 40 species of grasses, sedges, and herbs occur, (iii) Grassland—this is an open meadow (called Polo Field) about 3.7 ha in area, where at least 67 species of grasses, sedges, and herbs are known to occur.

The mean annual rainfall is 1215 mm (based on Climatological Table of the Meteorological Dept., for Madras–Minambakkam, 1931–60). Most of the precipitation occurs during the southwest (June-September) and northeast (October-December) monsoons (figure 1). Further details about GNP are available elsewhere (Raman *et al* 1996). Four seasons were identified using a climatological table and data on rainfall collected on a daily basis for Madras (Minambakkam) during 1991–2 (figure 1): dry season (Jan–Mar), summer (Apr–May 1991 and Apr–Jun 1992), southwest monsoon (June-Sep 1991 and July-Sep 1992), and northeast monson (Oct-Dec).

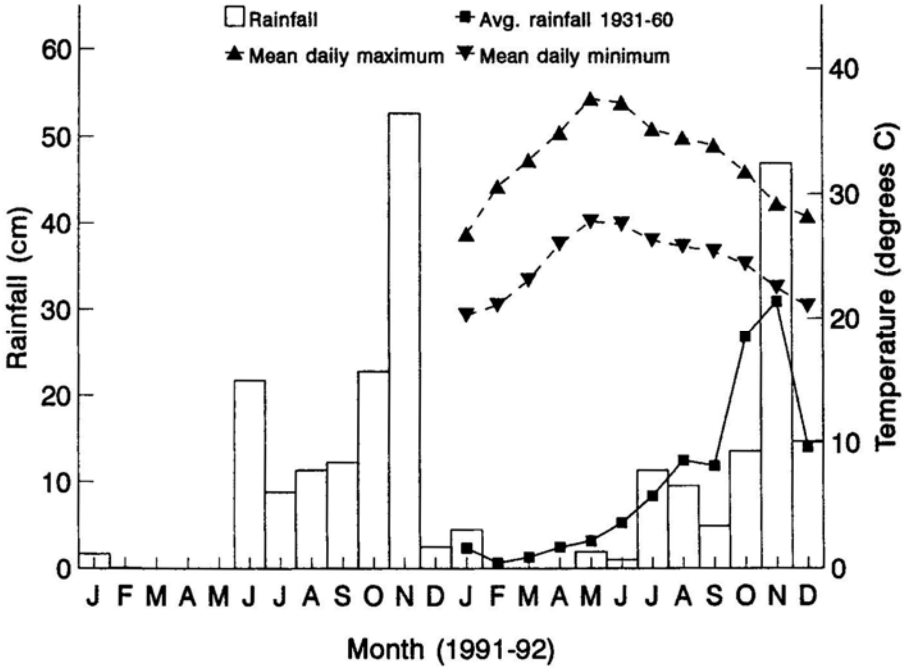

Figure 1. Rainfall and temperature data for the study area (1991–92). Average rainfall is from the Climatological Table of the Meteorological Dept. for Madras, Minambakkam (1931–60).

2.2 *Field methods*

The number of individuals and age-sex composition of groups of chital were recorded during regular line transect sampling (Raman *et al* 1996) as well as during walks along paths and animal trails in the park. A group was defined after Miura (1981,1983) as the number of individuals interacting with each other, behaving in a coordinated fashion during foraging or moving, or present in close proximity to each other (< 10 m apart) when first observed. In cases where one or more individuals occurred near the periphery of another group, the peripheral individuals were included in the group if their distance from the outer animals of the group was less than the group's approximate radius. Over 2,700 detections of chital groups were made over the two years of the study (table 1). Only groups where all the individuals could be clearly seen were tallied for group size. If movement of animals or vegetation indicated that some individuals were hidden or only partly visible in dense vegetation, or if the animals were far away (> 50 m) from the observer when detected in the semi-open vegetation, then the group was not included in the data. Although such doubtful cases occurred occasionally, the majority of detections recorded in the field were unambiguous.

The line transects, paths, and trails were sampled more or less uniformly across months in the mornings (0600–0900 h) and evenings (1600–1900 h), the time blocks of day when an average of 90% of the animals are actively foraging or moving (Miura 1981). About 7–11 field visits were made in a month, enabling observation of groups and tallying of group size on a monthly basis in the three major habitats considered here. Age-sex classification of chital observed (described in Raman *et al* 1996) was used

Table 1. Number of chital groups tallied in three habitats in Guindy National Park, 1991–92.

Month	Forest	Scrubland	Grassland	Total
1991				
January	40	71	12	123
February	35	52	9	96
March	43	44	9	96
April	74	48	3	125
May	48	30	4	82
June	33	49	19	101
July	10	38	23	71
August	12	46	20	78
September	27	54	16	97
October	12	50	23	85
November	21	47	31	99
December	29	68	22	119
1992				
January	38	97	17	152
February	48	77	3	128
March	63	50	6	119
April	73	75	2	150
May	53	79	12	144
June	65	63	9	137
July	24	90	11	125
August	15	85	32	132
September	15	75	42	132
October	16	42	17	75
November	26	90	40	156
December	21	80	26	127
Total	841	1500	408	2749

to estimate the monthly percentage of adult males in hard antler (an index of the breeding/rutting season) and the monthly proportion of fawns to females (an index of the fawning season—Schaller 1967; T R S Raman unpublished results).

Chital occur at high densities in Guindy National Park, considerably higher than most other natural areas (Raman *et al* 1996). Animal density was estimated using line transects in forest and scrubland and total counts in the grassland. Two 1 km-long transects were marked in the scrubland and a single 1 km-long transect was marked in forest to sample them roughly in proportion to their availability. Each transect was sampled twice a month, once each in the morning and evening (Raman *et al* 1996). Seasonal densities in scrubland and forest were estimated with the Fourier series model (Burnham *et al* 1980; Karanth and Sunquist 1992; Varman and Sukumar 1995) using the computer program, TRANSECT (White 1987). Monthly total counts were made in the grassland habitat, and these were pooled by season to estimate seasonal densities.

2.3 *Analyses*

Two measures of group size—the mean group size and Jarman's (1974) typical size—was estimated by habitat, month (or season), and year. A three-way analysis of variance with year, season, and vegetation type as the main factors was used to examine whether mean group sizes differed under the influence of any of the factors or interactions among factors. The mean group size is an observer-centred measurement that gives equal weightage to groups of all sizes, and may not reflect the experience of the average individual chital in the same manner as the typical group size. The typical group size is calculated by squaring the sizes of groups, summing across all groups, and dividing the sum by the total number of individuals observed (Jarman 1974). This gives a measure of the size of the group that the average individual finds itself in, and has been proposed as a more animal-centred index of group size (Barrette 1991).

Monthly sample size was low in scrubland and forest for estimating chital density using TRANSECT. A simple strip transect was therefore used to estimate monthly density in these two habitats—the number of individuals detected on a transect was divided by the total area sampled. The strip width used to calculate the area sampled was derived, for scrubland and forest separately, from regressions through the origin, following the method of Caughley (1977:15–16, and 49–50). The seasonal TRANSECT density estimate (*D*—on the y-axis) was regressed on the encounter rate (*N/L*—on the x-axis), where *N* is the total number of individuals tallied in *L* km of transect. The relationship was observed to be linear and the slope of the regression line $1/2w$, where w is the effective strip width on one side of the transect. This simplified strip transect approach is a useful measure for tracking relative changes in animal abundance from month to month. The effective strip width estimate reduces (if not removes) visibility bias for comparisons across habitats within each month. The effective strip width, w, was 37 m in the scrubland and 17 m in the forest. It must be noted, however, that the small sample size in some months may have led to imprecise strip transect density estimates. Comparing these with seasonal densities estimated with TRANSECT showed, however, that the monthly estimates were generally accurate enough to fall within the expected range (seasonal 95% confidence intervals).

Food availability is difficult to estimate for chital which are known to feed on parts of over 160 different plant species (Schaller 1967; Johnsingh and Sankar 1991). They consume predominantly grass in the wet season and browse during the dry season (Schaller 1967; Mishra 1982; Prasad and Sharatchandra 1984). As determining monthly feeding habits of chital in each habitat and measuring availability of each item of their diet was not possible during this study, an alternative index of productivity of food, namely rainfall, was used. Rainfall is known to be related to grassland and scrubland productivity in semi-arid and drier habitats (Sinclair 1977; Misra and Misra 1984). In the forest habitat in the study area, chital feed mainly on fallen leaves and fruits of trees, as grass and edible shrubs are scarce (Raman *et al* 1996). Such food was available more during the drier months as tree shed their leaves and fruits prior to rains. Monthly rainfall was, however, found to be significantly negatively correlated with the monthly number of trees fruiting in Guindy National Park ($r = -0{\cdot}61$, $df = 10$, $P = 0{\cdot}03$; phenology data from Rajasekhar 1992); most trees also shed their leaves during the drier months providing food for chital. Rainfall can thus still be used an (inverse) index of productivity of food for chital in forest.

Stepwise multiple regression using SPSS/PC + software (Norušis 1990) was used to examine the influence of monthly animal density, rainfall, percentage of rutting adult males, and fawning on the mean and typical group size within each habitat. The procedure was repeated using log (x + 1) transformed rainfall as non-linear relationships may exist in relating rainfall to food availability and group size.

Table 2. Influence of year, habitat, and season on mean group size in chital — Results of analysis of variance.

Source of variation	*df*	Mean square	*F*	*P*
Main effects	6	1048·3	55·6	< 0·001
Year	1	258·7	13·7	< 0·001
Habitat	2	1324·3	70·2	< 0·001
Season	3	567·0	30·1	< 0·001
2-way interactions	11	202·4	10·7	< 0·001
Year × Habitat	2	48·5	2·57	0·077
Year × Season	3	46·5	2·47	0·061
Habitat × Season	6	321·4	17·0	0·000
3-way interactions	6	21·0	1·12	0·351
Year × Habitat × Season	6	21·0	1·12	0·351
Residual	2725	18·87		

Table 3. Seasonal variation in mean chital group size in the three habitat types in Guindy National Park, Madras, 1991–92.

	Mean group size (SE, N)		
Year/Season	Forest	Scrubland	Grassland
Dry season '91	2·30 (0·17, 118)	2·32 (0·19, 167)	2·60 (0·44, 30)
Summer '91	2·57 (0·25, 122)	2·73 (0·27, 78)	1·57 (0·46, 7)
SW monsoon '91	2·82 (0·34, 82)	4·73 (0·40, 187)	6·35 (0·96, 78)
NE monsoon '91	1·71 (0·12, 62)	3·72 (0·28, 165)	9·99 (1·37, 76)
Dry season '92	2·02 (0·12, 149)	1·91 (0·10, 224)	2·15 (0·36, 26)
Summer '92	2·23 (0·14, 191)	1·97 (0·10, 217)	2·13 (0·39, 23)
SW monsoon '92	2·22 (0·22, 54)	3·16 (0·19, 250)	4·66 (0·81, 85)
NE monsoon '92	2·32 (0·25, 63)	4·05 (0·30, 212)	7·93 (1·27, 83)

SE, Standard error; N, number of groups tallied for group size.

3. Results

The analysis of variance (ANOVA) of group size data indicated significant effects of year, season, and habitat type on mean group size (table 2). There was also a significant interaction between habitat type and season ($P < 0{\cdot}001$, table 2). Other two-way interactions and the three-way interaction between year, habitat type, and season, were not significant.

Seasonally, mean group size and density of chital varied differently in the forest, scrubland, and grassland (table 3). In the forest, there was little variation in mean group

Table 4. Seasonal variation in chital density in the three habitat types in Guindy National Park, Madras, 1991–92.

Year/Season	Mean chital density/km^2 (SE, N)		
	Forest	Scrubland	Grassland
Dry season '91	264·7^a	150·6^a	149·4^a
	(61·8, 20)	(26·8, 52)	(24·6, 19)
Summer '91	381·4^a	110·2^a	40·5^b
	(103·3, 21)	(30·6, 24)	(13·0, 12)
SW monsoon '91		283·4^b	591·9^c
	} 90·4^b	(43·1, 68)	(119·7, 25)
NE monsoon '91		240·9^{ab}	773·0^c
	(25·6, 19)	(44·5, 60)	(118·4, 18)
Dry season '92	369·3^a	98·7^a	81·1^a
	(69·6, 33)	(20·2, 44)	(23·0, 18)
Summer '92	390·3^a	153·9^a	58·9^a
	(78·1, 25)	(24·6, 56)	(20·0, 22)
SW monsoon '92		361·4^b	499·2^b
	} 97·4^b	(62·2, 72)	(127·0, 21)
NE monsoon '92		506·3^{b*}	889·2^b
	(28·1, 21)	(84·4, 84)	(160·8, 21)

Values with the same alphabet in a column imply no significant difference (z tests, $P > 0{\cdot}05$) between them within a given year; N—In forest and scrubland: number of groups detected on transects for the density estimates, in grassland: number of total counts for grassland density estimates; *differed significantly (z tests, $P < 0.05$) from density during that season the previous year.

size with respect to season (table 3), although the density of chital more than doubled from the wet, monsoon seasons to the dry season and summer (table 4). In the scrubland and grassland, mean group size showed clearly discernible variation according to season—increasing during the southwest and northeast monsoon seasons relative to the dry season and summer. Animal density was also higher during the wet seasons in these two habitats (tables 3–4). Both, mean group size and animal density, were higher in the grassland than the scrubland during the wet seasons.

Monthly changes in mean group size, typical group size, and animal density in the three habitats are illustrated in figure 2. The monthly mean and typical group sizes over the two years were significantly positively correlated to each other in forest, scrubland, and grassland (r = 0·71, 0·83,0·92, respectively, df= 22, $P < 0{\cdot}001$). The results reinforce the patterns observed above—chital group sizes (mean and typical) and density were higher during the wet season months in scrubland and grassland, whereas, in forest, there was little change in group size although density changed substantially.

Bivariate correlations between chital density, and measures of rainfall and group size are given in table 5. Monthly chital density, and group size and rainfall measures were all significantly positively related to each other in scrubland and grassland. Both density and group size tended to be more strongly (and positively) correlated to log rainfall than rainfall in scrubland and grassland (table 5). Conversely, in the forest, chital density was negatively correlated with rainfall and more strongly with the logarithm of rainfall (table 5). No significant correlation was found between measures of

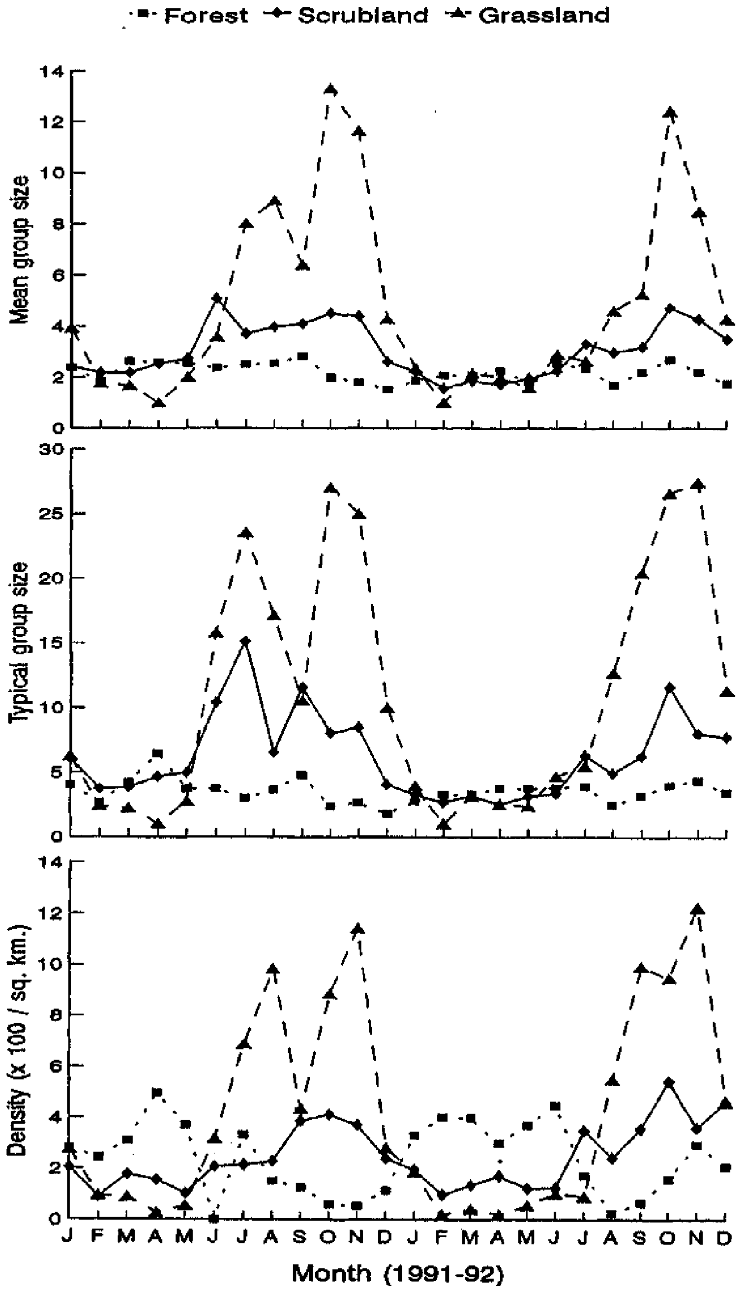

Figure 2. Monthly changes in mean group size, typical group size, and chital density in forest, scrubland, and grassland in Guindy National Park, 1991–92.

chital group size and rainfall in the forest. Forest typical group size was correlated with chital density (table 5).

The monthly changes in chital group size and animal density were also related to the monthly stage of rutting and fawning activities, but not in any consistent or intuitively

Table 5. Pearson's product-moment correlation coefficients between measures of chital group size, rainfall, and population density in the three habitat types in Guindy National Park, Madras, 1991–1992.

	Typical group size	Animal density	Rainfall	Log (x + 1) rainfall
	0·710***	0·239	−0·119	−0·048
Mean group size	0·828***	0·739***	0·736***	0·829***
	0·922***	0·885***	0·690***	0·723***
		0·453*	−0·085	−0·158
Typical group size		0·618***	0·495*	0·683***
		0·944***	0·747***	0·790***
			−0·471*	−0·644***
Animal density			0·581**	0·734***
			0·755***	0·765***

Each cell has three correlation coefficients – the uppermost gives the correlations for forest, the middle for scrubland, and the lowermost for grassland. $*P \leq 0{\cdot}05$, $**P \leq 0{\cdot}01$, $***P \leq 0{\cdot}001$; $df = 22$ in all cases.

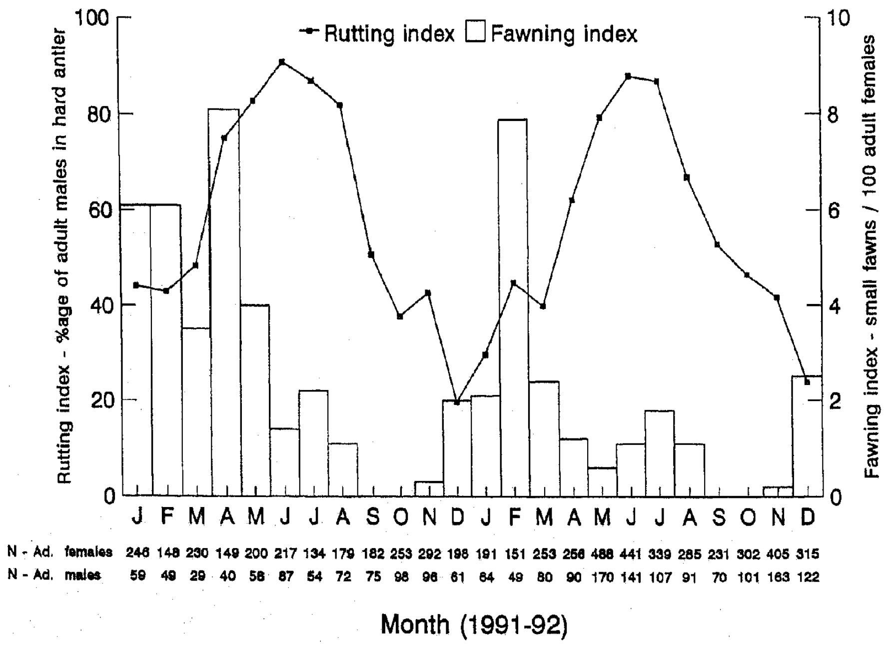

Figure 3. The rutting and fawning cycles of chital in Guindy National Park (1991–92). Data for Jan–Mar 1991 were unavailable for adult males, and therefore, data for the corresponding months of 1993 were used instead. The number of adult males and females sampled in each month is given in the data table.

obvious manner. The percentage of adult males in hard antler was used as an index of the rut, while the proportion of small fawns to adult females was used an index of fawning. The peak rut of the adult males was in May–June whereas fawning occurred predominantly between December and March (figure 3). In forest, chital mean group size was positively correlated with the rutting index ($r = 0{\cdot}50$, $df = 22$, $P = 0{\cdot}013$), while

Table 6. Results of stepwise multiple regression models of chital group size measures in three habitat types. Two classes of models were used—in Class I models, the independent variables were chital density, rainfall, the rutting index, and the fawning index (see text); in Class II models, rainfall is replaced by log (x + 1) rainfall as an independent variable.

Habitat	Dependent variable	Selected independent variables	Regression coefficient (SE)	t	R^2 (%)	F
Class I models						
Forest	Mean group size	Rutting index	0·008 (0·003)	2·69*	24·8	7·24*
		(constant)	1·747 (0·184)	9·51**		
	Typical group size	Chital density†	0·003 (0·001)	2·38*	20·5	5·68*
		(constant)	2·834 (0·344)	8·23**		
Scrubland	Mean group size	Chital density	0·005 (0·001)	4·61***	54·6	26·5***
		Rainfall	0·003 (0·001)	3·46**		
		Rutting index	0·017 (0·005)	3·23**		
		(constant)	0·593 (0·438)	1·35		
	Typical group size	Chital density	0·019 (0·004)	4·70***	38·2	13·6*
		Rutting index	0·060 (0·024)	2·49*		
		(constant)	−1·957 (2·018)	−0·97		
Grassland	Mean group size	Chital density	0·008 (0·001)	8·91***	78·3	79·4***
		(constant)	1·495 (0·519)	2·88**		
	Typical group size	Chital density	0·022 (0·002)	13·4***	89·1	179·2***
		(constant)	1·995 (0·938)	21·1*		
Class II models						
Forest	Mean group size	Rutting index	0·008 (0·003)	2·69*	24·8	7·24*
		(constant)	1·747 (0·184)	9·51***		
	Typical group size	Chital density	0·003 (0·001)	2·38*	20·5	5·68*
		(constant)	2·834 (0·344)	8·23***		
Scrubland	Mean group size	Log rainfall	0·880 (0·127)	6·95***	68·7	48·3***
		(constant)	1·896 (0·210)	9·05***		
	Typical group size	Log rainfall	2·289 (0·522)	4·38***	46·6	19·2***
		(constant)	3·185 (0·864)	3·69**		
Grassland	Mean group size	Chital density	0·008 (0·001)	8·91***	78·3	79·4***
		(constant)	1·495 (0·519)	2·88**		
	Typical group size	Chital density	0·022 (0·002)	13·4***	89·1	179·2***
		(constant)	1·995 (0·938)	2·13*		

*$P \leq 0{\cdot}05$, ** $P \leq 0{\cdot}001$; ***$P \leq 0{\cdot}001$; †density in the corresponding habitat.

density was related to the fawning index ($r = 0{\cdot}55$, $df = 22$, $P = 0{\cdot}005$). In scrubland and grassland, only the fawning index was (negatively) related with density and both measures of group size ($r < -0{\cdot}51$, $df = 22$, $P < 0{\cdot}05$ in all cases except for fawning index vs. typical group size in scrubland where $r = -0{\cdot}36$, $df = 22$, $P = 0{\cdot}08$).

To simultaneously assess the influence of rainfall, animal density, and rutting and fawning indices on chital group size, stepwise multiple regression models were used. Two classes of models were employed, one using rainfall, and the other using log rainfall (table 6). In models involving rainfall, animal density was the main predictor variable of both measures of group size in all habitats (except mean group size in forest) incorporated into the regression models (table 6). Mean group size in forest was,

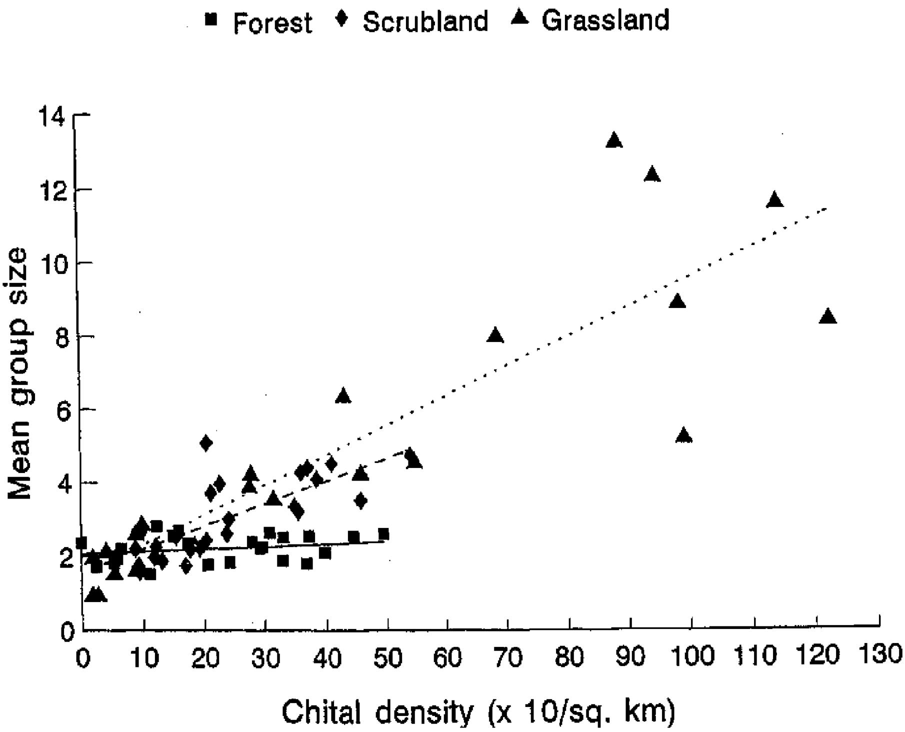

Figure 4. Linear relationships between monthly chital mean group size and density in forest (—), scrubland (---), and grassland (•••) in the study area.

however, related only to the rutting index. The rutting index was also a significant predictor variable of mean and typical group size in the scrubland (table 6). Rainfall had a significant effect only on scrubland mean group size. In models with log rainfall, the same predictor variables as above were significant for the forest and grassland habitats. In scrubland, however, log rainfall was the only significant predictor variable of mean and typical group size (table 6). Notably, the fawning index was not a significant predictor variable in any model.

Since chital density appeared to be the most significant variable influencing group size measures, the role of habitat structure was investigated by plotting mean group size against density. The prediction that grassland had the largest group sizes for a given density, while scrubland had intermediate group sizes and forest had the smallest groups, was examined (figure 4). While the intercepts of the regression lines for the three habitats did not differ significantly, there were differences in the slopes. As noted earlier (table 5), the slopes of the regression lines of mean group size on chital density were significant and positive in grassland and scrubland, whereas it was not significantly different from 0 in the forest (t = 1·16, P > 0·05). Also, the slope of the grassland regression line was significantly higher than in scrubland (F = 2·68, P< 0·05). These results indicate that at low densities mean group sizes are small (around 2–3 individuals) in all three habitats, while at higher densities the group sizes in grassland and scrubland increase, with the increase in grassland being greater than in scrubland.

4. Discussion

The results of the study clearly show that chital density and group size measures show significant seasonal and monthly changes that are closely related to monthly rainfall and type of habitat. Earlier studies have documented differences in seasonal densities of chital in different habitats (Mishra 1982; Karanth and Sunquist 1992; Raman *et al* 1996), as well as changes in mean group size of chital in relation to season or habitat (Barrette 1991; Karanth and Sunquist 1992; Khan *et al* 1995). The mechanisms and factors influencing these changes have not, however, been explicitly addressed or considered simultaneously in a single study. The present study has made such an attempt and several noteworthy results emerged.

Although chital density, rainfall, and group size measures were mostly intercorrelated, density appeared to play a predominant role in influencing group size measures as indicated by its selection in most of the stepwise multiple regression models. Chital density increased in relation to rainfall in the grassland and scrubland, but decreased in the forest. The higher availability of fresh grass and browse sprouts in scrubland and grassland is likely to have attracted chital in larger numbers into these habitats, as chital are known to be predominantly grazers during the wet season (Mishra 1982; Prasad and Sharatchandra 1984). The negative relationship between chital density in forest and rainfall is related to the fact that the main forage of chital in this habitat (fallen leaves and fruits of trees) are relatively more abundant during the drier months and summer (Rajasekhar 1992; Raman *et al* 1996). The movement of chital into grassland and scrubland areas with the rains could also have contributed to the decline in forest density. Chital density was, however, more strongly related to log rainfall than rainfall itself, indicating non-linear changes in density with rainfall. While data are unavailable, it is suggested that this is a result of a non-linear relationship between forage biomass available for chital and rainfall. One can thus assume that chital density and log rainfall (which were highly correlated) reflect changes in food availability in the different habitats more accurately than does rainfall. This is possibly why log rainfall was the only significant predictor variable for chital group size measures in scrubland, whereas in models with only rainfall, group size was more strongly related to chital density.

The fact that chital density was correlated with rainfall suggests that group size changes may occur in a two-step fashion-first, chital density in a habitat changes in relation to rainfall and food availability, and second, group size increases when density increases because of the higher encounter rate and fusion of groups (as suggested by Caughley 1977). This appears to be the case in the grassland habitat. Conversely, it is possible that groups form or fuse preferentially during high rainfall months (i.e., the probability of groups fusing per encounter increases with rainfall) because a larger number of animals can forage together at a site without interference when food availability per unit area is higher (Wilson 1975; Sharatchandra and Gadgil 1975; Khan *et al* 1995). Such a mechanism probably regulates changes in chital mean group size in the scrubland, where rainfall had a significant effect on group size, in addition to the effect of increasing animal density. Here individuals can, however, also forage on their own without incurring any cost during high rainfall months when food availability relative to density is higher. Therefore, other advantages to grouping such as social interactions, vigilance and predator detection or avoidance, need to be also invoked to explain changes in group size.

In the forest habitat, chital grouping patterns were different from scrubland or grassland. The mean and magnitude of change in chital group size measures was lower in forest than in scrubland or grassland. The seasonal mean group size varied between 1·71 (during the 1991 NE monsoon season) to 2·82 (during the 1991 SW monsoon season; see table 3). Smaller group sizes in forest habitats are presumably a consequence of food being more dispersed and scattered throughout the habitat (Jarman 1974; Mishra 1982; Johnsingh 1983; Karanth and Sunquist 1992). Thus, even though chital densities increase substantially in the forest during the dry season, individuals and groups may not coalesce to form larger groups while foraging to avoid competition for forage (Sharatchandra and Gadgil 1975). This should suggest that large groups could form in the forest if food was abundantly available in some patches. During casual observations, large aggregations of chital were in fact noticed forming to feed on locally abundant food sources such as fallen fruits under *Ficus benghalensis* trees, often in commensal association with bonnet macaques (Krishnan 1972). Thus while chital density in a habitat can be used as an index of overall food availability (as judged by its correlations with rainfall), food dispersion is not accounted for, and may be a critical aspect to measure in future studies.

An alternative suggestion has been that group sizes are smaller in forests as closed habitats hinder, while open habitats facilitate, formation of groups (Barrette 1991; Khan *et al* 1995). The influence of other factors were not controlled for in the above studies. In the present study, after controlling for the variable that appeared to have the strongest influence on group size (density), group size was found to decrease along the gradient from grassland to scrubland and forest. This result was valid only at higher densities; at low densities groups break up into small sizes (mostly 1–3 individuals, figure 4) in all habitats. These groups typically consist of a female with a fawn and yearling (considered the basic sub-unit of chital social organisation by Graf and Nichols 1966; Schaller 1967), small doe groups, and solitary males (unpublished data). The gradient in group sizes across habitats at higher densities, at first sight, provides support for the structuralist hypothesis of Barrette (1991). Nevertheless, other factors such as food dispersion, differential use of habitats by unisexual fe/male groups that differ in size, and predator avoidance may also be involved.

Social behaviour and phase of the annual reproductive cycle on grouping behaviour, also appeared to have an influence on grouping behaviour of chital. While the fawning index was not a significant predictor variable of group size in any of the multiple regression models, the rutting index was. Fuchs (1977) has remarked on the tendency of chital to form larger groups during the rut in an introduced population in Texas. Rutting males are known to join groups of females to from mixed groups more frequently during the rut (Schalter 1967; Miura 1983; Khan and Vohra 1992). This can explain why mean group size of chital in forest and scrubland was positively correlated to the rutting index during the present study. The lack of significant effect in grassland is likely to be because of two reasons: (i) low sample size of groups during the dry season months, when the rut was in progress, due to low animal density (table 1, figure 2), and (ii) during the wet season months, the effect of solitary males joining female groups (typically larger in size than in the other two habitats) may not have led to a significant change in group size, compared to scrubland and forest, where a single male joining groups of 2–4 females would increase the size of those groups by 33–20%. The mean group size is a more sensitive measure of changes in group size due to the individuals remaining solitary or joining groups (Barrette 1991), and that is probably why typical group size did not show changes in relation to the rutting index.

Another aspect that emerged during this study is the significant effect of year on mean group size. Inter-annual variability in chital group size in different habitats has not so far been studied in detail. Table 2 shows that the mean group size of chital was smaller in all three habitats during the dry season, summer, and SW monsoon in 1992. In contrast to the positive relationships between chital density and group size within a given year, it is possible that this decrease in chital group size is a result of an increase in chital density between 1991–92. Chital density increased significantly in the study area from 185·4/km^2 (SE = 15·0) during 1991 to 239·2/km^2 (SE = 19·0) during 1992 (Raman *et al* 1996). The total annual rainfall received decreased, however, from 1313mm in 1991 to 1081mm in 1992, respectively (figure 1). As chital are already maintained at high densities in Guindy National Park due to artificial feeding and low levels of predation (Raman *et al* 1996), it is likely that under the increased density in 1992, the food available per individual decreased in the three habitats. In contrast to the proximate positive relationship between density and group size within a given year, increase in density across years (rainfall remaining constant) may lead to groups fragmenting into smaller units to lessen competition over food.

This study's attempt to simultaneously examine the influence of several environmental and social variables on two measures of group size suggests that the fission-fusion system of fluid group formation in chital is strongly influenced by animal density and rainfall. Other factors such as habitat structure and social behaviour too play a role, and our ability to detect their effects may depend on the habitats and index of group size used for comparisons. A caveat that needs to be added is that the chital population in the study area is a high-density population, artificially-fed during some years and thriving in the absence of predation, and is therefore unlike many other natural habitats of chital. Comparable studies from other habitats will be required to assess the generality of these results. It is recommended that future studies also focus on the changes in probability of groups or individuals coalescing as function of animal density and rainfall, on measuring food dispersion, the effects of predator avoidance, and inter-annual variability in relation to per capita food availability, to further elucidate mechanisms driving changes in chital group size.

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