Group size, sex ratio and seasonality of the sambar (*Cervus unicolor*) of the Yala Protected Area Complex, Sri Lanka

Mangala de Silva*

Department of Zoology, University of Peradeniya, Peradeniya, Sri Lanka.

Abstract

The sambar population in the Yala Protected Area Complex (YPC) was studied by monthly observations for 14 months. During the study, 538 sightings were made. The frequencies (%) of different categories were as follows: adult male-37.5, adult female-48.3, yearling male-2.8, yearling female-4.1, juvenile-4.7 and fawn-2.6. The sambar were found mostly (about 60% of the observations) as solitary individuals. The largest group observed consisted of 14 individuals. The average group size was 2.2, but it was higher during the rainy season (2.5) and lower during the dry season (1.8). The average group sizes in grassland, scrub and forest habitats were 2.9, 2.3 and 1.2, respectively. The percentage of solitary animals was 26.8%.

Sambar are active only during late evenings and early mornings and in the night. From about 0800 to 1600 hours they were almost always found resting either standing or lying down in the shade of a tree. Feeding was observed only after 2000 hours in grassland habitat and after 1600 in the sand-dune habitat.

Sambar breed during most months of the year in YPC, except the peak drought months of July and August. However, there appears to be an enhanced birth period from October to January, which is the main rainy season in YPC. The observed overall female to male ratio of the adults was 1:0.82, but in monthly samples the deviation of the sex ratio from the expected ratio of 1:1 is not statistically significant.

Introduction

The Sambar (Cervus unicolor Kerr, 1792), which is distributed in south and south-east Asia from India to South China including Taiwan and southwards to Sumatra and Borneo, is the largest member of the Family Cervidae in Sri Lanka, the other three species being the spotted deer (Axis axis), the barking deer (Muntiacus muntjak) and the hog deer (Axis porcinus). It is distributed from the sea level to the highest elevations and is still found in most forest areas including the Horton Plains National Park and environs at over 2,000 m a.s.l. (Fig. 1). At present its habitats of lowland and highland forests continue to dwindle as these forest areas are being developed for human settlements and agriculture. This human interference leads to fragmentation and reduction in extent of its habitats. The sambar has already disappeared from most of its former range and is gradually becoming confined to such protected areas as

National Parks and Wildlife Sanctuaries. The fragmented small populations in the non-protected areas are highly vulnerable to poaching and habitat destruction and will become nonviable within a short period of time.

Very little work on the ecology of sambar has been done in Sri Lanka. The sambar are nocturnal and very elusive deer and are very well concealed in their preferred habitat of dense forest (Phillips, 1984). Eisenberg & Lockhart (1972) were the first to make a detailed ecological study of sambar in Sri Lanka during their study of large mammals in Wilpattu National Park. Santiapillai et al. (1981) studied the sambar in the Block I of the Ruhuna National park, a component of the Yala Protected Area Complex (YPC). In India, the ecology of sambar has been studied by Johnsingh (1983) in Bandipur Sanctuary, Karanth & Sunquist (1992) in Nagarhole Sanctuary

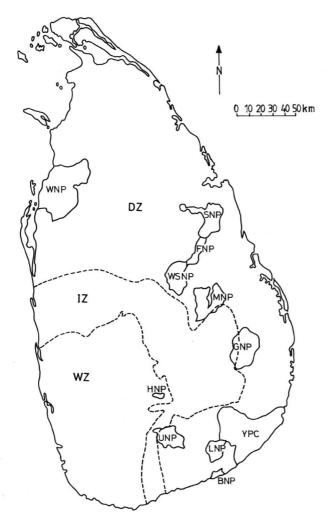


Figure 1. The location of Yala Protected Area Complex and the Eco-climatic zones of Sri Lanka. Major Protected Areas are also indicated. (DZ-dry zone, IZ-intermediate zone, WZ-wet zone; FNP-Flood Plains National park, GNP-Galoya National Park, HNP-Horton Plains National Park, MNP-Maduru Oya National Park, SNP-Somawathiya National Park, UNP-Udawalawe National Park, WNP-Wilpattu National Park, WSNP-Wasgomuwa National Park, YPC-Yala Protected Area Complex.)

and Varman & Sukumar (1993) in Mudumalai Sanctuary in the southern region and by Shaller (1967) in Kanha National Park in the northern region. Mishra & Wemmer (1982) studied the breeding ecology of sambar in Royal Chitwan National Park, Nepal, while Ngampongsai (1987) studied its habitat use in Thailand.

Yala Protected Area Complex is the largest of the contiguous forest areas with little human interference available to sambar and other wildlife in Sri Lanka and the ecological studies of large mammals in YPC are of great importance to future conservation and management of these species.

The present work deals with the observations on sambar during a study of large mammals of the YPC.

Study area and habitats

Yala Protected Area Complex (YPC) is situated in the south-eastern part of Sri Lanka, and consists of a group of contiguous Protected Areas (Fig. 2). These include a Strict Natural Reserve (Yala Strict Natural Reserve), two National Parks (Ruhuna National Park and Yala East National Park) and three Sanctuaries (Kataragama, Katagamuwa and Kudumbigala Sanctuaries). This group of Protected Areas is situated in the lowland Dry Zone, one of the three major eco-climatic zones characterised by low and seasonal rainfall, the other two zones being the Intermediate Zone and the Wet Zone (Fig. 1). The YPC has an area of 1,518 km² (Table 1) and is bordered by the sea on the south and east. Its vegetation consists mainly of Moist Deciduous forest, Dry Evergreen forest, thorn-scrub and grasslands. A few natural waterholes and several man-made seasonal reservoirs are scattered within the park. The two rivers, "Menik" and "Kumbukkan", and a number of streams, which are mostly seasonal, drain the area. The mean annual rainfall is about 1,300 mm of which the major part (about 64%) falls in late October to early January during the north-east monsoonal rains and the most of the rest (about 27%) in April and May (south-west monsoonal rains) (Fig. 3). The dry season extends from June to September. However, rainfall can vary considerably between years. There is a north-south gradation of rainfall, being high in the northern part and low in the southern part. Northern part may get over 1,600 mm of annual rain, whereas the southern part may get only less than 1,000 mm. The monthly mean temperature in the area varies between 26° and 29°C (Müeller-Dombois, 1968).

Materials and methods

The present study was carried out during the months of January, February, March, May, June, July, August, September, November and December 1995 and January, April, July and October, 1996, each study session lasting 5-10 days of field work. Different Protected Areas within YPC were visited, and the different habitats in each Protected Area were studied by moving along roads by vehicle or along transects on foot. During the study, the number and the categories of sambar observed were recorded. Various habitats in the component Protected Areas of the YPC were visited during different times of the day and

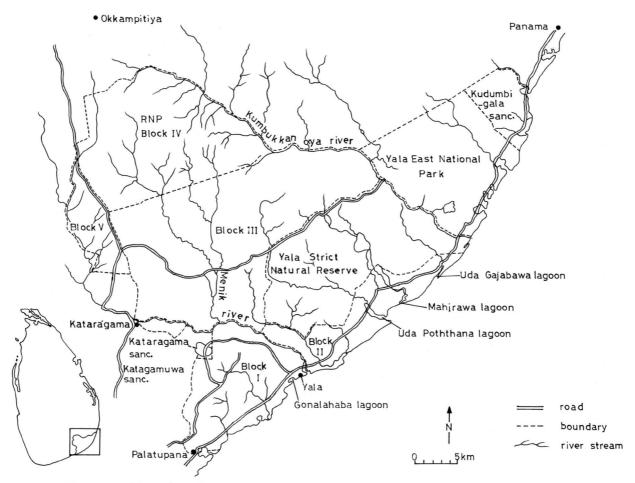


Figure 2. Yala Protected Area Complex.

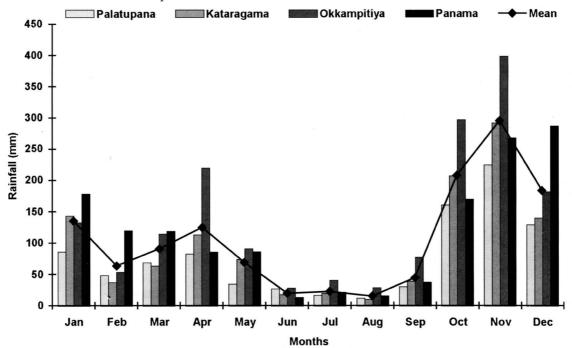


Figure 3. The mean monthly rainfall at different locations near YPC of the 15 year period of 1980 to 1994. The locations of rainfall stations are shown in Fig. 2.

Vol. 4, No. 1.

precautions were taken not to disturb wildlife as much as possible while walking along the transects. The study was carried out mainly during the daylight hours but a few night searches were also made by vehicle. The following categories of sambar were recognised according to Eisenberg & Lockhart (1972): adult males with hard antlers, antlers in velvet and antlers shed, yearling males with hard antlers and antlers in velvet, adult females and yearling females, juveniles, and fawns. The category of yearling included second year (e.g. spike males) and third year (e.g. "prong" males with brow tine) individuals.

Yala East National Park and Kudumbigala sanctuary could not be visited because of the prevailing terrorist activities and security situation in those areas, but observations of other parts of the YPC should apply to these areas as well.

Results

A total of 538 sightings of sambar were made during the 14 months of study. The frequencies of various categories observed are given in Fig. 4. The highest number of individuals observed, after eliminating repeat observations, in any sampling period was 39 in January 1995. This contained 20.5% hard antlers, 15.4% velvet antlers, 41.0% of adult females, 15.4% yearling females, 2.6 juveniles and 5.1% fawns, and included 20.5% solitary individuals (10.2% hard antlers and 10.2% velvet antlers). The largest aggregation observed was 14 animals near the Meynert reservoir in the Block I of Ruhuna National Park (RNP) (Fig. 2) during the same month. The animals were lying down under the shade of trees in the morning hours. The composition of this group was three hard antlers, three velvet antlers, five adult females, two yearling females and one yearling male. A mixed group of 11 was also observed near the Meynert res-

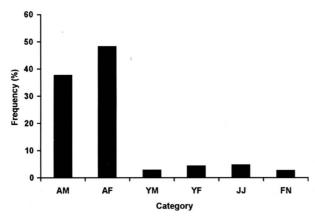


Figure 4. Frequency of various categories of sambar observed during the study period. (n=538). (AF-adult female; AM-adult male; FN-fawn; JJ-juvenile; YF-yearling female YM-yearling male;)

ervoir in March 1994. The other two large groups containing 9 and 8 individuals were also mixed groups and were observed during different months near seashore at Uda Poththana in Block II of RNP (Fig. 2). The observed group structure is given in Fig. 5. There were 144 solitary animals, most of which were adult males (Table 1). The pairs consisted mainly of all males, all females, or male+female (Table 1). The frequencies of individuals in different size groups are shown in Fig. 6. This shows that only 26.8% individuals are solitary. There were 26.3% individuals in groups of size 3-5 and 25.6% in groups of size 6-10. These groups contained mostly females and their progeny.

According to the pattern of rainfall (Fig. 3), three seasons are recognised in this study, the rainy season, the wet season and the dry season. The rainy season lasts from October to January. During this period about 64.3% of the annual precipitation occurs from the north-east monsoonal rains. The vegetation (scrub and grassland) that dried up during the dry season grows and the waterholes and seasonal streams fill up and flooding may occur. The wet season is considered to last from February to May. About 27.5% of the rainfall occurs during this period. The vegetation (scrub and grasslands) remains green during this season. The dry season lasts from June to September. Only about 8.2% of the annual rainfall is received during this period. July and August are drought months but the drought period may sometimes extend to September and even October. During the dry season, the seasonal waterbodies begin to dry up. During prolonged drought periods almost all the waterholes and streams dry up, and water remains available only in the two major rivers Menik and Kumbukkan, of which even the former may dry up.

The highest number of sambar per sampling session was observed during the wet season and the

Table 1. Composition of solitary and pair categories. (AF-adult female; AH-hard antler; AS-antler shed; AV-velvet antler; FN-fawn; JJ-juvenile; YF-yearling female; YH-yearling hard antler)

| Solitary | Frequency (%) | Pair | Frequency (%) |
|----------|---------------|-------|------------------|
| | (70) | | (70) |
| AH | 56.3 | AH | 15.3 |
| AV | 8.3 | AH+AV | 6.9 |
| AF | 20.8 | AH+AS | 5.6 |
| YH | 5.6 | AH+AF | 30.6 |
| YF | 9.0 | AF | 22.2 |
| | | AF+JJ | 13.9 |
| | | AF+FN | 5.6 |
| (n) | 144 | | 72 |

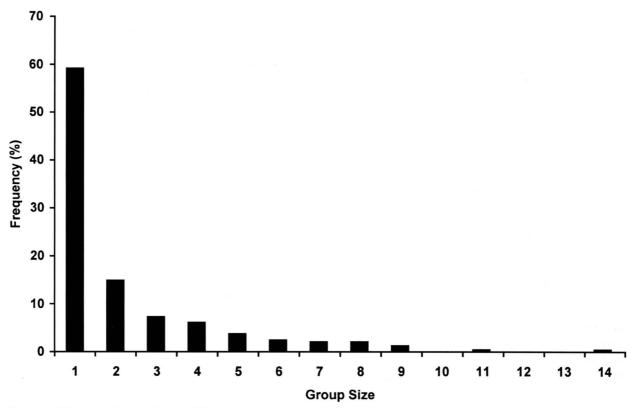


Figure 5. The grouping tendency of the sambar.

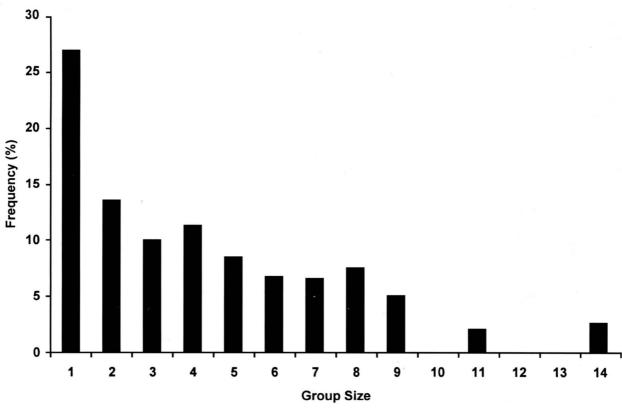


Figure 6. Frequency of individuals in different size groups.

least number during the dry season. The frequency of solitary animals was high in the dry season and low during the wet and the rainy seasons (Table 2). The average group size (including solitary and pairs) was highest during the rainy season and lowest during the dry season (Table 2). The average group size (including solitary individuals and pairs) for the entire study period was 2.2. However, if solitary individuals were discounted, the group size was 4.0. The average group size in the grassland, scrub and forest habitats were 2.9, 2.3 and 1.2, respectively. In the forest habitats, the sambar observed were either solitary individuals (mainly adult males and a few adult females) or adult female+juvenile or yearlings.

The sambar were not observed to come to water during the survey hours which on a few occasions went up to 2200 hours. However, they were observed to feed in the grasslands associated with waterholes by about 2000 hours. During daytime they were almost always found resting either standing or lying down in the shade of a tree. The sand-dunes is a favourite habitat of sambar. They were observed in the sand-dunes from about 1600 hours into the night, in most instances feeding.

The female to male ratio of adults was 1:0.82 and that of yearlings was 1:0.68. However, it must be noted that if the spike antlers were not visible in yearling males they would have been classified as yearling females. The observed monthly adult sex ratios did not significantly deviate from the expected 1:1 ratio in a Chi-squared test (c^2 =8.3320, d.f.=27). The sex ratios during the rainy, wet and dry seasons were 0.89, 0.84 and 0.69, respectively, but did not significantly deviate from the expected ratio of 1:1 (c^2 =4.6558, d.f.=5).

The variation of frequencies over the months of various categories of male (hard antlered, velvet antlered and antlers shed) is shown in Fig. 7. Velvet antlered males were more common during the major rainy season and the hard antlered males were more common during the dry season. The velvet antlers observed in July, August and September were in growing stages, whereas those observed in December and January were full-grown antlers. Males

Table 2. The seasonal variation of the average number observed (per day), frequency of solitary individuals and average group size.

| Duration | Average no. per day | Frequency % solitary animals | Average group size |
|-------------------|-------------------------------------|---|--|
| October - January | 6.7 | 25.7 | 2.5 |
| February - May | 7.7 | 40.0 | 2.1 |
| June-September | 4.2 | 60.0 | 1.8 |
| | October - January February - May | per day October - January 6.7 February - May 7.7 | per day % solitary animals October - January 6.7 25.7 February - May 7.7 40.0 |

with shed antlers were more common during April to July than during other months.

Fawns were observed during the period November to May, more commonly from December to February (Fig. 8). The juveniles were observed from November to July but they were more common from February to April.

The main predator of sambar in YPC is the leopard (*Panthera pardus*). The two species of crocodiles (*Crocodilus palustris* and *C. porosus*) present in the YPC, particularly the larger *C. porosus*, may also predate on sambar that come to water at night. The jackal (*Canis aureus*), although present, may be able to attack, if at all, only fawns. During the study, three individuals of sambar killed by leopard were observed, one yearling female, one yearling male and one adult female. In addition, a skeleton of a newly killed adult male sambar with antlers shed (patches of meat were still present on bones) was also found. Eight skulls (cause of death unknown), three of adult females, one of a male with antlers shed and four with antlers intact, were also found.

Discussion

The sambar, unlike the spotted deer (*Axis axis*), are often solitary (Phillips, 1984). In YPC, 26.8% of the observed sambar were solitary in contrast to 1.1% of the spotted deer (pers. obs.). Only 53.8% of the animals were found in groups of three or higher. Although the largest group observed in the current study was 14 in the Block I of the Ruhuna National Park (RNP), Santiapillai, et al., (1981) in the same area observed groups of 16 and 21 individuals. Although the average group size in the entire YPC was 2.2, the average group size observed in the Block I of the RNP was 3.1, which agrees well with the average group size of 3.4 observed by Santiapillai, et al. (1981) for the same area. The highest average group size observed in the present study was 3.4 in the Block II of the RNP. Eisenberg & Lockhart (1972) found that in Wilpattu National Park 60.7% of the groupings (38.3% of the individuals classified) were solitary, the average group size being only 1.72. In Mudumalai Wildlife Sanctuary in southern India, Varman & Sukumar (1993) found the average group size of sambar to be 4.23. They observed groups containing up to about 50 individuals. They also observed that the group size varied between seasons, being smaller during the dry season when the groups tend to break up. This agrees with the observations of the present study that the average group size is higher during the wet seasons and lower during the dry season. The group size and social organisation of ungulates may be influenced by availability of food sources (Clutton-Brock, et al., 1982), and, dur-

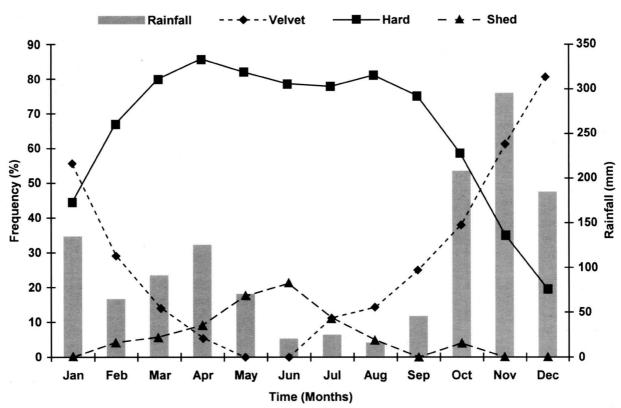


Figure 7. The frequency of different categories of adult males (those with hard antlers, velvet antlers and antlers shed) observed during the study period. (April and October data from 1996 surveys, others from 1995 surveys.) (The pattern of rainfall is also shown.)

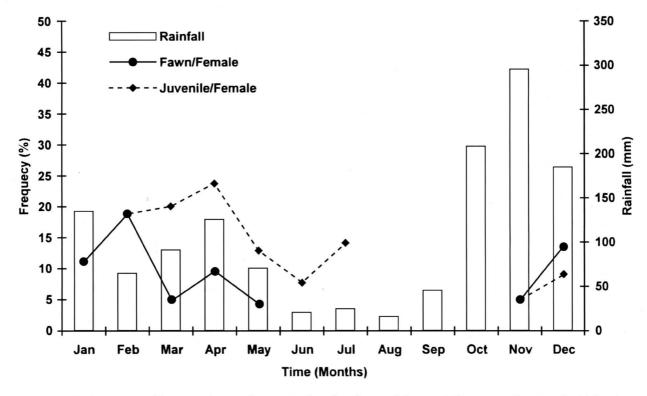


Figure 8. The frequency of fawns and juveniles per 100 females observed during different months. (April and October data from 1996 surveys, others from 1995 surveys.) (The pattern of rainfall is also shown.)

Vol. 4, No. 1.

ing the dry season, scrub and grass dry up and become more fibrous and less nutritious. Shaller (1967) also states that, although the sambar is both a browser and a grazer, it tends to form groups when fresh grass is available.

It has been shown that the mean group size of elephant also could be related to the availability of food (Leuthold, 1976; Dublin, 1996) and that smaller groups could perhaps better exploit available patchy resources (White et al., 1993). Similarly, it could be argued that when the availability of food resources dwindle during the dry season, smaller groups would be advantageous to sambar as well.

The smaller group size of sambar is probably also associated with its forest habitat. The ungulates that live in more open areas such as the spotted deer (Axis axis) tend to form larger groups as an anti-predator behaviour (Varman & Sukumar, 1993). In open areas when fleeing away from the predator the large groups confuse the latter. But there is not much advantage of large groups in the forest, concealment or camouflage being of primary importance, and smaller the group better the concealment. The sambar prefer forest and scrub to grassland, and in the former habitats the solitary existence may confer advantage for remaining concealed. The observed lower group size of 1.2 in the forest habitat and the higher group size of 2.9 in the grassland habitat agree with this. The Blocks I and II of the RNP, in which higher group sizes of 3.1 and 3.4 respectively were observed, contain more scrub and grassland than forest in comparison to other components of the YPC.

Although the sambar is generally considered to be a browser rather than a grazer in comparison to the spotted deer, Ngampongsai (1987) observed that in Khao-Yai National Park in Thailand sambar prefer grassland species. He states that the ideal habitat of sambar in Khao-Yai NP is a mixture of grassland and forest. The observations of the present author are also that sambar densities are higher in forest-grassland mosaic habitats both in YPC and Horton Plains NP. Therefore, drying up of grasslands (also scrub) during the peak of the drought (August and September) in YPC may cause stress in sambar and may contribute to population regulation mechanism of the species.

The sambar are shy and elusive animals (Phillips, 1984) and usually seen at night. Feeding in grasslands of YPC was observed to commence only around 2000 hours. However, the sambar in Horton Plains National park (elevation over 2,000 m a.s.l.) (Fig. 1) were observed to move into the open grasslands in large numbers by about 1700 hours and remain there feeding till about 0800 hours next day (pers. obs.). This was not so about a decade back. The density of

sambar has increased during this decade in the Horton Plains NP and the early and extended feeding time in grasslands may be a response to its higher densities.

The monthly adult sex ratio observed during the present study does not deviate significantly from the expected ratio of 1:1. However, skewed sex ratios of sambar favouring females were found to be common by other workers. In southern India the sex ratio of sambar populations varied from 2.4:1 to 3:1 favouring females (2.4:1 in Bandipur Wildlife Sanctuary (Johnsingh, 1983) and Nagarhole Wildlife Sanctuary (Karanth & Sunquist, 1992), 2.7:1 in Mudumalai wildlife Sanctuary (Varman & Sukumar, 1993) and 3:1 in Kanha National Park (Schaller, 1967)). Santiapillai et al. (1981) in their earlier study of sambar in RNP-Block I found the female:male sex ratio to be 2.1:1 However, they did not distinguish between adult and yearling females and therefore the estimated sex ratio involves both age groups. According to the data presented by Eisenberg & Lockhart (1972) in their study of sambar in Wilpattu national Park (WNP), the adult sex ratio was 1.1:1 in favour of the males, although the sex ratio fluctuated in some samples favouring males and in others favouring females. Barring unequal numbers of males and females at birth, which are unlikely, the skewed sex ratio must be due to differential mortality, either natural or by predator, although skewed foetal sex ratios are known from other deer (e.g. white-tailed deer (Odocoileus virginianus)) (Degayner & Jordan, 1987). In captive white-tailed deer, it was found that nutritional status of the mothers influences the foetal sex ratios (Verme, 1969). Unlike in Sri Lanka, in India, the tiger (Panthera tigris) is an important predator of adult deer including sambar (Shaller, 1967), and it may be that the adult males of sambar are more prone to predation by the tiger than the adult females. Also, adult males and adult females (and their progeny) may have different habitat preferences as in red deer (Clutton-Brock, 1982) which could lead to differential predation and even sampling bias.

Ashby & Santiapillai (1986) in their life expectancy studies of sambar in RNP found no evidence to suggest the mortality rates of adult males and adult females of RNP to be different. The lower proportion of yearling males observed in the present study may be spurious. Until the spike antlers are visible yearling male is difficult to identify as such and probably would have been classified as yearling female.

The sambar male attains a larger size than the female (Phillips, 1984) and probably has a faster growth rate. The sambar in the YPC probably breed during most months except the height of the dry season (June, July, August). But, there is an enhanced

birth period during the main rainy season of October to January. Eisenberg & Lockhart (1972) observed that in Wilpattu National Park the birth season commences in November and continues into March or April. In Mudumalai sanctuary, southern India, Varman & Sukumar (1993) found that fawn:female ratio is more or less constant in all seasons and therefore probably there is no seasonality in reproduction. However, they are of the opinion that there is a peak in the rut during the dry season (see later). In Chitwan National Park, Nepal, although fawns were observed throughout the year except in October, there is a main breeding season from June to August (Mishra & Wemmer, 1987), which is the main rainy season (Dinerstein, 1987). The data of Mishra & Wemmer (1987) show that over 50% of the births occur in June and July and over 10% in August. According to the data of Dinerstein (1987), over 84% of the annual rains are received during these three months. These observations agree with the observations of the present work that the breeding of sambar in YPC is mainly non-seasonal but with a major birth period from November to January during the rainy season. Although the fawns were first observed during November they would probably have been born in October. Eisenberg & Lockhart (1972) observed that probably the fawns are first seen with the mother about a month after its birth.

Photoperiod, which is very important in inducing the production of hormones the levels of which regulate the breeding cycle of the temperate deer, is relatively constant in the tropics. Therefore, a complex of other locally variable phenomena including the rainfall becomes important as the proximate regulating factors of the breeding cycle (Branan & Marchinton, 1987). In this respect, Bubenik, et al., (1991) point out that one of the most important factors affecting the timing of reproduction is the availability of food, which is often determined by local climatic factors such as the timing of the rainy period. Therefore, the fawning period of tropical cervids is usually at the beginning of the wet season.

Eisenberg & Lockhart (1972) are of the opinion that females become pregnant only once in two years. They also state that the pregnant females give birth in isolation and the new born fawn does not consistently follow the mother during the first three weeks but rests alone and the mother attends it at set intervals. Thus, the very young fawns are not commonly seen. However, the juvenile consistently follows the mother and the two are not completely separated at least for two years (until yearling stage) (Eisenberg & Lockhart, 1972). The juvenile stage lasts probably from 6 to 12 months.

The gestation period of sambar is given as eight months (Phillips, 1984). Therefore, if the major birth season is from November to January, then there must be a major rutting period from March to May. During this period the frequency of hard-antlered males reaches its peak and the frequency of velvet antlered males reaches its minimum (Fig. 7). The frequency of the velvet antlered males are high from October to January and reaches its maximum in December. Santiapillai et al. (1981) observed velvet antlered males in RNP-Block I only during November and December. In WNP, Eisenberg & Lockhart (1972) observed velvet-antlered males mainly during the period of December to April. In RNP, by April, the frequency of males that have shed their antlers starts increasing indicating that some males have completed the rut by April.

The antler cycle of the sambar in Sri Lanka is poorly synchronised and hard antlered males could be seen in all months while males with antlers in velvet and those with shed antlers could be seen during most months. However, the hard antlered males are in a high percentage from March to August (Fig. 7). If the rut continues at a high frequency throughout these months, then a high frequency of births should occur from November to April and a high frequency of fawns should be observed from December to May. However, a high frequency of fawns was observed from December to March, although fawns were observed also in November, April and March. Thus, although the hard antlered males occur at a high frequency from March to August, rut may take place mainly from March to May. It may be that most of the females get pregnant during the early part of the rut or hard antlers persist several months after the rut. The latter hypothesis is more likely. According to Mishra & Wemmer (1982) although the major birth season of sambar in Nepal is from June to August, the males with hard antlers are at a high frequency from December to April. If rutting takes place at a high frequency during the latter period, then parturition should continue at a high rate from August to December. Thus, in Nepal, rutting seems to take place mainly during the months in which the frequency of the hard antlered males reaches its peak. This agrees with the observations of the present study. In a captive group of spotted deer (Axis axis) in southern Texas, the antler cycle was relatively well synchronised and rutting occurred in June and July whereas the old antlers were cast from December to March (Bubenik, et al., 1991). Thus, hard antlers persisted well after the rutting

Phillips (1984) states that antlers are shed soon after the rutting season, but "later in life" they may

be shed more irregularly and that after the stag has passed its prime the antlers tend to diminish in size. However, Varman & Sukumar (1983) found no evidence to support the observation that antlers persist for more than one season.

The life expectancy of sambar in RNP is probably relatively long. Ashby & Santiapillai (1986) found that the average life expectancy of sambar in RNP is 10 years with a maximum life expectancy of 24 years. Phillips (1984) states that the average life expectancy of sambar in captivity is about 10.5 years and that there is a record of a sambar living for 19 years in captivity.

Acknowledgements

I am very grateful to the former Directors of the Department of Wildlife Conservation of Sri Lanka W.A. Jayasinghe and P. Attanayake for granting me permission to carry out this work, B.A. Muthubanda (former Park Warden of the Ruhuna National Park), B.V.R. Jayaratne (former Deputy Park Warden of Ruhuna National Park) and W. A. Sarath, (former Wildlife Ranger, Moneragala) for their help during the study. Thanks are also due to S.P.U. Premachandra and A.A. Weerakoon who helped in the study, and to various Wildlife Guards, especially Wimal Kodituwakku who accompanied us to different areas of YPC and helped in many ways during the study. I am very grateful to John F. Eisenberg of Florida Museum of Natural History, University of Florida, and Hans Kruuk of the Institute of Terrestrial Ecology, Banchory, Scotland, for reading the manuscript carefully and suggesting valuable improvements. Thanks are also due to T.S.B. Alagoda of Dept. of Zoology, University of Peradeniya, for drawing the figures.

Literature cited

- Ashby, K.R. & C. Santiapillai. 1986. The life expectancy of wild artiodactyl herbivores, water buffalo (*Bubalus bubalis*), sambar (*Cervus unicolor*), spotted deer (*Axis axis*) and wild pig (*Sus scrofa*) in Ruhuna National park, Sri Lanka, and the consequences for management. Tigerpaper, 13(2): 1-7.
- Branan, W.V. & R.L. Marchinton, R.L. 1987. Reproductive ecology of white-tailed deer and red brocket deer in Surinam. *in* Wemmer, C.M. (ed.), Biology and Management of the Cervidae. Smithsonian Institution Press, Washington, D.C. pp. 344-351.
- Bubenik, G.A., Brown, R.D. & Schams, D. 1991. Antler cycle and endocrine parameters in male axis deer (*Axis axis*): Seasonal levels of LH, FSH, testosterone, and prolactin and results of GnRH and ACTH challenge tests. Comp. Biochem. Physiol. 99A: 645-650.
- Clutton-Brock, T.H., Guinness, F.E. & S.D. Albon. 1982.Red Deer: Behaviour and Ecology of Two Sexes. The University of Chicago Press, Chicago. 378 pp.

- Degayner, E.J. & P.A. Jordan. 1987. Skewed fetal sex ratios in white-tailed deer: evidence and evolutionary speculations. *in* Wemmer, C.M. (ed.), Biology and Management of the Cervidae. Smithsonian Institution Press, Washington, D.C. pp. 178-188.
- Dinerstein, E. 1987. Deer, plant phenology, and succession in the lowland forests of Nepal, *in* Wemmer, C.M. (ed.), Biology and Management of the Cervidae. Smithsonian Institution Press, Washington, D.C. pp. 272-288.
- Dublin, H.T. 1996. Elephants of the Masai Mara Kenya: seasonal habitat selection and group size patterns. Pachyderm. 22: 25-35.
- Eisenberg, J.F. & M. Lockhart. 1972. An ecological reconnaissance of the Wilpattu National Park, Ceylon. Smithsonian Contrib. Zool., Smithsonian Institution Press, Washington DC. 101. 118 pp.
- Johnsingh, A.J.T. 1983. Large mammalian prey-predators in Bandipur, J. Bombay Nat. Hist. Soc., 80: 1-49.
- Karanth, K.U. & M.E. Sunquist, 1992. Population structure, density and biomass of large herbivores in the tropical forest of Nagarhole, India. J. Tropical Ecol., 8: 21-35.
- Leuthold, W. 1976. Group sizes of elephants in Tsavo National park and possible factors influencing it. J. anim. Ecol., 45(2): 426-436.
- Mishra, H.R. & C. Wemmer. 1987. The comparative breeding ecology of four cervids in Royal Chitwan National Park, Nepal, *in* Wemmer, C.M. (ed.), Biology and Management of the Cervidae. Smithsonian Institution Press, Washington, D.C. pp. 259-271.
- Müeller-Dombois, D. 1968. Vegetation cover types. Ruhuna National Park, Ceylon. Report No. 12. Smithsonian Ceylon Ecology project. Mimeo. 8 pp.
- Ngampongsai, C. 1987. Habitat use by the sambar (*Cervus unicolor*) in Thailand: A case study for Khao-Yai National Park, *in* Wemmer, C.M. (ed.), Biology and Management of the Cervidae. Smithsonian Institution Press, Washington, D.C. pp. 289-298.
- Phillips, W.W.A. 1984. Manual of the Mammals of Sri Lanka. (2nd revised ed.) Wildlife & Nature Protection Society of Sri Lanka, Colombo. 389+xxxv pp.
- Santiapillai, C., Chambers, M.R. & C. Jayawardena. 1981. Observations on the sambar (*Cervus unicolor* Kerr, 1792) in the Ruhuna National Park, Sri Lanka, and observations relevant to its conservation. Ceylon J. Sci. (Biol. Sci.) 14: 193-205.
- Shaller, G.B. 1967. The deer and the tiger a study of wildlife in India. University of Chicago Press, Chicago. 370 pp.
- Varman, K.S. & R. Sukumar. 1993. Ecology of sambar in Mudumalai Sanctuary, Southern India, *in* Ohtaishi, N. & H.-I. Sheng. (eds.), Deer of China: Biology and Management. Elsivier, Amsterdam. pp 273-284.
- Verme, L.J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. J. Wildlife Management, 33: 881-887.
- White, L.J., Tutin, C.E.G. & M. Fernandez. 1993. Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lope Reserve, Gabon. Afr. J. Ecol., 31: 181-199.