The Influence of Leaf-monkeys on their Feeding Trees in a Cyclone-Disturbed Environment[1]

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ABSTRACT

A cyclone in November 1978 caused extensive damage to a site of natural dry evergreen forest in Sri Lanka. The cyclone destroyed more than 50 percent of the woody vegetation that had produced most of the food for two species of leaf-eating monkeys or langurs. Apparently, this caused an imbalance between these langur populations and their natural food supply and resulted in overbrowsing on those feeding trees which were not destroyed by the cyclone. Preferentially browsed tree species that were relatively rare and/or small in size died at significantly greater rates due to overbrowsing than those which were buffered against overbrowsing by virtue of being large in tree size and/or relatively abundant in the forest. The virtual disappearance of three overbrowsed tree species from the forest suggests that langurs may contribute to the change in floristic diversity in cyclone-disturbed areas. However, such an effect of langur folivory is thought to be short-lived and specific to this kind of rare disastrous environmental situation.

On November 23, 1978, a cyclone swept across the island of Sri Lanka in the Indian Ocean causing extensive damage. Studies concerning the forest and its primate inhabitants were conducted before and after the cyclone at a site, Polonnaruwa, which lay directly in its path. This provided a unique opportunity to examine the effects of such a natural disaster on the relationship between the primates and their natural forest habitat.

Earlier (Dittus 1985) I described the cyclone damage to the forest at Polonnaruwa and considered the influence of recurrent cyclones on the dry evergreen forest of Sri Lanka in general. At Polonnaruwa one immediate effect of the cyclone was the destruction of much of the food supply for two folivorous monkeys, the grey langur *Presbytis entellus* and the purple faced langur *Presbytis senex* (Figs. 1 and 2). My aim in this paper is to examine the effect that browsing by these langurs had on the survivorship of several of their feeding trees within 42 months after the cyclone. The focus is on the trees rather than on the langurs during what probably represents a transient phase of imbalance between the langur populations and their feeding trees. The examination is of interest on two counts. First, it clarifies the nature of the relationship between the langur populations and their feeding trees at a time of sudden drastic environmental change. Second, as overbrowsing by langurs contributed to the cyclone damage and consequent death of several of their feeding trees, it defines langur browsing as an additional agent influencing the floristic diversity of dry evergreen forest of Sri Lanka in areas that have recently undergone cyclone damage.

The meteorological details of the cyclone, its path, and the kind and degree of damage it inflicted on the forest at Polonnaruwa were described earlier (Dittus 1985). Cyclone damage involved the uprooting of trees (tree falls), breakage of trunks and large branches (crown damage), and extreme defoliation and loss of twigs particularly in the upper layers of the forest. In addition, many trees that survived the immediate effects of the cyclone died within 42 months thereafter. Some of this post-cyclone tree mortality could be attributed to extensive crown damage; thus trees which lost 40 percent or more of their branches and trunks died at significantly greater rates after the cyclone than trees with lesser crown damage. But, not all post-cyclone tree mortality could be thus explained.

METHODS

Study area.—The site of dry evergreen forest considered herein is located within the Polonnaruwa Sanctuary and Archaeological Reserve in the northeast dry zone at 07°56′N and 81°00′E. The site encompasses about 3 km^2. The forest and climate at Polonnaruwa have been quantitatively described and compared to other dry evergreen forest areas in Sri Lanka (Dittus 1977, 1985). Plant nomenclature follows Abeywickrama (1959).

Pre-cyclone sample.—The trees that were used to measure cyclone damage had been selected and individually marked 6 months before the cyclone for the purpose of phenological studies. This sample included 400 trees from the 44 most common tree species (as measured by relative density) at Polonnaruwa. A sample of 10 trees or shrubs had been chosen for most species, and trees had been selected at random without special regard for their sizes. The sample of trees was taken over an area of approximately 3 km in length in a north-south direction, and less than 1 km wide in the east-west direction.

[1] Received August 1983, revision accepted 26 June 1984.

Post-cyclone sample.—For many species the number of trees in the pre-cyclone sample was reduced through tree falls and deaths. In order to obtain a finer measure of post-cyclone tree mortality a second sample was established. This consisted of all trees from the pre-cyclone sample that survived the cyclone, plus newly selected trees to replace those that fell during the cyclone or that died soon thereafter. Replacement trees were selected randomly with regard to size or location within the study area; trees that were moribund or obviously badly damaged were omitted whenever possible. The sample consisted of apparently healthy trees that survived the immediate effects of the cyclone.

Estimating crown damage.—To estimate crown damage each tree in the pre-cyclone sample was visually examined within one month after the cyclone to assess the proportion of large branches (greater than 10 cm in diameter) that had been broken from the crown of the tree (Fig. 1). For very large branches and trunks this often involved estimating the proportion of empty space in the crown that was left by a missing limb. Estimates of "proportion of crown missing" were made on a scale of 0 to 10 for each tree. The means of these scores were calculated for each species.

RESULTS

Post-cyclone tree mortality.—Tree species which were subject to tree mortality of 20 percent or more based on the post-cyclone sample are listed in Table 1. Also listed are the numbers of trees that died from the pre-cyclone sample and the distributions of the degrees of crown damage among these dying trees. Crown damage among replacement trees in the post-cyclone sample was not estimated; generally, trees with minimal damage were selected to replace dead ones in the sample. Known crown damage was negligible or low for at least two species, *Cassia fistula* and *Chloroxylon swietenia.* Furthermore, one might expect crown damage to cause mortality fairly soon after its occurrence. An examination of the temporal distribution of tree deaths on the post-cyclone sample (Table 2) indicated that for three species (*Cassia fistula, Chloroxylon swietenia,* and *Walsura piscidia*) 11 trees (42%) died within 18 months after the cyclone, whereas 15 trees (58%) died 19 to 42 months after the cyclone. This distribution differed significantly ($\chi^2 = 4.27$, $P < .05$) from that for the remainder of species where most, or 20 trees (74%), died within the first 18 months after the cyclone. These data suggest that crown damage was not a cause, or not the only cause for post-cyclone tree mortality for some trees.

Post-cyclone mortality in relation to primate folivory.—The two langur species, *Presbytis entellus* and *P. senex,* were fairly common at the Polonnaruwa study site. Mature and young leaves constitute 60 percent of the diet by fresh weight of *P. senex* and 48 percent of that of *P. entellus* (Hladik and Hladik 1972). In examining the relationship between langur folivory and tree mortality, two considerations were important: the diet of the langurs, and the relative availability of food species (Table 3).

No quantitative observations of feeding by these langurs were taken after the cyclone. However, Ripley (1970) and Hladik and Hladik (1972) had studied their diets at Polonnaruwa before the cyclone. Hladik (1977) ranked the foods for each langur species in order of importance of food intake by wet weight. In Table 3 a food was considered as "important" if it was one of the five top ranking foods (18% of 28 food species) of *P. senex,* or one of the eight top ranking foods (19% of 43 food species) of *P. entellus* that contributed approximately 70 percent of the total wet weight diet of each species, respectively. In addition casual notes taken after the cyclone suggested that both langurs fed on the young and mature leaves of *Chloroxylon swietenia,* which, even before the cyclone, was the second most important food tree in the langur diets at some sites (Hladik and Hladik 1972). It was therefore included in Table 3. Important species where only the fruits were eaten (*e.g., Ficus benghalensis*), or which were herbaceous, were omitted.

The availability of different foods can be estimated from the Importance Values (IV) (Curtis and McIntosh 1951). The IV takes into account the relative density of trees, their distribution (relative frequency), and relative dominance (basal area). The IV data are from a pre-cyclone survey of the forest at Polonnaruwa and are based on an enumeration of 3015 trees from 55 species (Dittus 1977). Since basal area is proportional to biomass, and the relative density and relative frequency reflect the distribution of this biomass in the habitat, the IV is a fair measure of a tree species' relative availability at the site.

Considering the food species in Table 3, the low IVs of *Walsura piscidia, Chloroxylon swietenia,* or *Alangium salviifolium* reflected small tree size and/or their scarcity in the forest. The high IVs, on the other hand, signified either a moderate tree size but very common occurrence (*Drypetes sepiaria*), or a moderate occurrence but a very large tree size (*Schleichera oleosa* and *Adina cordifolia*).

Post-cyclone tree mortalities (based on the post-cyclone sample) were compared to the IV for the nine tree species that were important foods for either one or both langurs (Table 3). A Spearman rank correlation test (Siegel 1956) indicated a significant correlation between the ranks of the percentages of tree mortality and the ranks of the inverse values of the IVs ($r_s = 0.610$, $P < .05$). That is, preferentially browsed tree species that were rare and/or small in tree size (low IV) were more vulnerable to browsing and hence died at significantly greater rates

FIGURE 2. Detail of a damaged *Adina cordifolia* canopy, showing *Presbytis senex* feeding on leaves.

than those with high IVs. Food trees with high IVs were buffered against browsing (and consequent mortality) by virtue of their large tree sizes and/or their common occurrence in the forest.

DISCUSSION

The major mammalian consumers of the arboreal vegetation at Polonnaruwa are the two langurs, *Presbytis senex* and *P. entellus,* and the toque macaque, *Macaca sinica.* The densities of these primates prior to the cyclone were approximately 150–200 monkeys/km^2 (1000–1350 kg/km^2) for *P. senex,* 90–120 monkeys/km^2 (600–800 kg/km^2) for *P. entellus* (modified after Eisenberg *et al.* 1972), and approximately 100 monkeys/km^2 (300 kg/km^2) for *M. sinica* (Dittus 1975). Before the cyclone the average yearly diet of *P. senex* included 60 percent leaves and 40 percent fruits and flowers, that of *P. entellus* included about 48 percent leaves and 52 percent fruits and flowers. Young leaves made up about 33 percent of the leaf intake of *P. senex* and more than 50 percent of that of *P. entellus* (Hladik and Hladik 1972). The macaque is primarily frugivorous and leafy material from trees makes up less than 2 percent of its total diet (Dittus 1974). So of these

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FIGURE 1. Cyclone-damaged *Adina cordifolia* trees showing an extreme loss of twigs and small branches and some loss of large branches. These trees, which are bearing new leaves, were photographed about six weeks after the cyclone.

TABLE 1. *The number of trees from the pre-cyclone sample that died after the cyclone and their respective crown damages, and mortality among trees from the post-cyclone sample.*

Tree species	Post-cyclone sample			Pre-cyclone sample	
	Number of live trees	Tree mortality Number	Tree mortality Percent	Number of trees dying after the cyclone	Distribution of crown damage among moribund trees (%)
Alangium salviifolium	6	3	50	1	90
Cassia fistula	13	3	23	2	10, 20
Chloroxylon swietenia	12	12	100	4	0, 0, 0, 0
Diospyros montana	10	3	30	1	90
Stereospermum personatum	14	4	29	4	20, 40, 40, 70
Walsura piscidia	20	11	55	5	40, 50, 50, 70, 80

three primates, the two langurs have the major impact on the leafy arboreal vegetation. Given that a single langur consumes approximately 400 kg (fresh weight) per annum (Hladik 1977), the amount of fresh vegetal material that the two langur species consume per annum is approximately 1000 to 1300 kg/ha.

Hladik and Hladik (1972) studied the relationship between the diet of the primates at Polonnaruwa and the productivity of the forest. They found that the total food production in the forest areas occupied by groups of ***P. entellus*** and ***P. senex*** exceeded the dietary intake of these langurs. But since a large proportion of the langur diets consists of young leaves, Hladik (1977) postulated that the dietary intake is the maximum permissible without endangering the food plant population. Or, the biomass of langurs at Polonnaruwa was the maximum in relation to the available food production before the cyclone (*ibid.*).

The cyclone had two effects on the food supply of the primates at Polonnaruwa, as indicated by measures of cyclone damage (Dittus 1985). First, total tree loss was 40 percent and shrub loss was 21 percent. In addition, surviving trees suffered an average crown loss of about 33 percent and small branches and twigs were stripped especially from trees in the upper layers (Figs. 1 and 2). These losses represent a greater than 50 percent reduction in the leaf producing vegetation of the forest. Second, there was a statistically significant loss of both flowers and fruits among trees, and of flowers among shrubs, shortly after the cyclone (*ibid.*). Furthermore, phenological samples taken from before and after the cyclone indicate that for about two years following the cyclone the production of flowers and fruits was greatly reduced from pre-cyclone levels (Dittus, unpublished data). Quantitative records of the diets of the two langur species after the cyclone are lacking. However, in light of the phenological changes it is likely that the langur diets shifted towards a greater proportion of leaves following the cyclone. Also, the langur populations decreased by no more than 5 percent for ***P. entellus*** and perhaps 5 to 10 percent for ***P. senex*** within one month after the cyclone (Dittus 1979, Rudran, personal communication). Overall, these changes point to a considerable increase in langur folivory among the trees that were left standing after the cyclone.

The results related to Table 3 imply that concentrated browsing on preferred food plants in the post-cyclone diets of the langurs heightened the tree mortality among some of these food species. There is a significant inverse correlation between the IVs of preferentially browsed food species and their post-cyclone tree mortality. Tree species with large IVs were either relatively rare but large in size, or of moderate size but abundant. The lesser mortality of

TABLE 2. *The temporal distribution of the numbers of post-cyclone tree deaths among seventeen "early dying" species and among three "early and late dying" species.*

	Number of tree deaths						
	Dec '78 to May '79	June '79 to Nov '79	Dec '79 to May '80	June '80 to Nov '80	Dec '80 to May '81	June '81 to Nov '81	Dec '81 to May '82
Seventeen early dying species	10	3	7	1	0	0	6
Three late and early dying species							
Cassia fistula	1	0	0	0	0	0	2
Chloroxylon swietenia	3	0	0	3	2	3	1
Walsura piscidia	1	5	1	1	1	2	0
Subtotal	5	5	1	4	3	5	3

TABLE 3. *Relationship between tree mortality, degree of browsing by langur monkeys, and measures of relative "availability" of tree species.*

Tree species	Degree of importance in the diet of		Relative density (%)	Importance value index	Tree mortality (%)
	P. entellus	*P. senex*			
Drypetes sepiaria	important	important	21.3	55.5	0
Schleichera oleosa	important	important	4.2	21.1	6
Cassia fistula	important	minor	6.3	13.2	23
Adina cordifolia	important	important	2.8	12.8	9
Cassia roxburghii	important	minor	5.2	11.0	0
Strychnos potatorum	important	minor	4.7	10.0	0
Walsura psicidia	important	minor	2.6	8.5	55
Chloroxylon swietenia	important	important	0.6	2.4	100
Alangium salviifolium	minor	important	0.1	0.3	50
Stereospermum personatum	non-food	non-food	0.8	3.0	29
Diospyros montana	non-food	non-food	1.5	0.7	30

preferentially browsed food trees with high IVs suggests that the proportional extent of browsing on any individual tree was diminished if that tree was large in size and/or there were many other trees of the same species available for browsing.

Overbrowsing seemingly aggravated the stress on trees that already had been incurred by the direct forms of cyclone damage and probably contributed to the high mortality (>50%) of *Walsura piscidia, Chloroxylon swietenia,* and *Alangium salviifolium.* Even before the cyclone, Hladik (1977) mentions the death of several *Alangium salviifolium* trees in the home range of one group of ***P. senex*** which plucked the young leaves of these trees too frequently. The reduced food supply for langurs following the cyclone apparently had the effect of exacerbating the problem of overbrowsing over a larger area of forest and among additional tree species. After the cyclone, one group of ***P. entellus*** abandoned its traditional home range after all the *Walsura piscidia* trees had been overbrowsed and had died. The group shifted to an adjacent area to feed on a few remaining live *Walsura piscidia* trees. The foliage of *Adina cordifolia* trees is the most preferred food item of ***P. senex*** at Polonnaruwa, and several damaged *Adina cordifolia* trees (outside the study sample) that had been heavily browsed by ***P. senex*** also died, apparently as a result of a combination of cyclone damage and browsing.

Hladik and Hladik (1977) proposed a relative equilibrium between the population of food trees and its dependent folivores at Polonnaruwa. With a reduction in the langur food supply owing first to the destruction of trees directly from cyclone damage, and indirectly from overbrowsing, I predict that the langur populations themselves will decline (Dittus 1979).

In New Zealand, introduced populations of the bush-tailed opposum *Trichosurus vulpecula* have also been noted to overbrowse and thereby to kill several of their food trees (Fitzgerald 1978). This imbalance, however, is an example of the classical danger of introducing new species. It is not strictly comparable to the situation at Polonnaruwa where, conceivably, a long-term balance between plant consumer and the vegetation had already been established. The cyclone caused a perturbation in this balance. I speculate that the imbalance may be short-lived and the dying and overbrowsed food plants might eventually become reestablished with a predicted decrease in the langur population.

Where plant and animal populations have had a "normal" or historically long-term association, the influence of animal activity on plant populations is sometimes evident as well. For example, browsing by Asian elephants in southeastern Sri Lanka results in extensive crown distortion among trees less than 5 m in height (Mueller-Dombois 1972). Similarly, *Gustavia superba* trees show a higher incidence of branching where they have been browsed by *Cebus capucinus* monkeys of South America (Oppenheimer and Lang 1969). In the extreme case, African elephants have been identified as a major factor in the conversion of woodland to grassland (Laws 1970). Such effects of habitat change due to overuse have usually been produced by ground dwelling herbivores (*e.g.,* see Wynne-Edwards 1962). These examples again differ in kind from the cyclone-induced changes at Polonnaruwa.

Five tree species at Polonnaruwa were lost from the forest or greatly reduced in their relative densities as a result of cyclone damage. These changes represented a 22 percent loss or great reduction of tree species in the upper forest layers or 12 percent from the forest (Dittus 1985). Three of the lost tree species, *Walsura piscidia, Chloroxylon swietenia,* and *Alangium salviifolium,* were preferentially browsed by the langurs. Hence, it is possible that overbrowsing by langurs contributed to the change in floristic composition of the forest. However, the data also indicate that the role of overbrowsing by langurs in effecting such changes is restricted to the rare and specific conditions prevailing for a brief period immediately after severe cyclone damage. Furthermore, such an effect of langur folivory conceivably would be confined to areas where langur populations are limited principally by their feeding trees rather than by predators or by the availability of water. In the arid regions of dry evergreen forest, for example, the density of langurs is one hundredth of that at Polonnaruwa (Eisenberg *et al.* 1972). In addition, natural predators such as leopards, which are known to prey on langurs in certain areas (Muckenhirn and Eisenberg 1973), were absent at Polonnaruwa (although feral dogs preyed on langurs there). Thus, fairly extensive ecological data are required in order to determine the influence of langur browsing on tree survivorship at any one site in a cyclone-disturbed area.

ACKNOWLEDGMENTS

I thank the Office of the President of the Democratic Socialist Republic of Sri Lanka for permission to do basic research in Sri Lanka, and especially Professor Hilary Crusz for his heroic efforts in securing this permission. The successive Directors of the Institute of Fundamental Studies, Sri Lanka, Professors N. C. Wickramasinghe and Cyril Ponnamperuma, sponsored the research under the aegis of the Institute. Neville Selastian assisted with field work, and Shirani Nathanael helped with data summarization. I am grateful to the following persons for helpful comments on the manuscript: Peter S. Ashton, S. Balasubramaniam, Anne Baker-Dittus, Martin Kellman, and Peter L. Marks.

The research was supported by National Science Foundation grants, BNS-7619740, BNS-7924057 and BNS-8300092. I thank Devra Kleiman for assistance in obtaining supplementary funding from the Friends of the National Zoo and from the Smithsonian Institution Bacon Fund.

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