## Male–Female Differences in Foraging on Crops by Asian Elephants

Males and females may differ in morphology or behaviour because of contrasting factors affecting their reproductive success. In polygynous mammals with a marked sexual dimorphism, males are more likely to exhibit risky behaviour promoting reproductive success (Trivers 1985). In this study we present evidence that pubertal and adult male Asian elephants, *Elephas maximus* (above 15 years) incur greater risks than female-led family herds by foraging on cultivated crops which have more nutritive value than wild food plants.

The population structure, seasonal movement patterns and foraging behaviour of about 500 elephants, of which about 35 were adult males, were studied within a forested area of 1130 km$^2$ (12°0′N–11°30′N and 76°50′E–77°15′E) in the Chamarajanagar and Satyamangalam Forest Divisions of southern India (Sukumar 1985, in press a, b). Damage to crops by elephants in 10 enclaves of cultivation (46 km$^2$) was monitored between April 1981 and March 1982. Records were kept by local contact persons on the composition of the raiding elephant groups for every instance of raiding in the study villages. For 77 raids by bull groups and 33 raids by family herds, the quantities of crops consumed were estimated by quadrat sampling of plant densities and weights in undamaged and damaged portions of the field. Whenever clear imprints were available in the fields, the circumferences of the forefeet of the elephants were measured. Wild elephants were photographed to identify them individually and to estimate their shoulder heights (Douglas-Hamilton 1972). These measurements were used to assign age and weight classes to the animals based on relationships established for captive elephants (Kurt 1974; Sukumar 1985). Seasonal population numbers of elephants in the study area were estimated by ground transects using a vehicle and on foot. The mean quantity of crops consumed per elephant per raid was computed from these samples, separately for the adult bull and family herd segments of the population. Assuming daily dry weight food requirements of 60 kg for an adult bull and 23·6 kg for a member of a family herd, which are 1·5% of their respective average body weights (Laws et al. 1975), the total quantities of crops consumed each season in all the study villages were expressed as average proportions of the bull population's and herd population's total requirements. Commonly consumed wild and cultivated plants were analysed for crude protein by the standard Kjeldahl method and for minerals by an atomic absorption spectrometer.

The peak raiding season was October–December when finger millet, *Eleusine coracana*, was in its flowering and grain stages (Table I). Adult bulls raided crops more frequently than did the family herds throughout the year. This was most obvious during October–December when an adult bull raided crops on 38 nights on average while a member of a family herd did so on only 6 nights, deriving 26·7% and 4·5% of their total food requirement, respectively. For the entire year, adult bulls derived 9·3% and female herds 1·7% of their diet from cultivation.

To protect their crops, farmers scare and shoot at the elephants, which may be injured or killed in the process. Injuries received during raiding may also render them more susceptible to mortality

**Table I.** Seasonal patterns in crop raiding by elephants

| | April–June 1981 | July–September | October–December | January–March 1982 |
|---|---|---|---|---|
| Rainfall (cm) at 900 m | 17·9 | 41·2 | 30·9 | 3·1 |
| Percentage of arable land under cultivation* | 6% | 37% | 60% | 7% |
| Number of days of crop raiding during 3 months by | | | | |
| An adult male | 2·3 | 4·7 | 38·1 | 3·5 |
| Member of family herd | 0·8 | 1·0 | 5·9 | 0·5 |
| Proportion of crops in the diet of | | | | |
| An adult male | 1·5% | 3·0% | 26·7% | 2·5% |
| Member of family herd | 0·7% | 1·0% | 4·5% | 0·2% |
| Mean group size of adult males | | | | |
| While raiding | 1·0 ($N=29$) | 1·3 ($N=29$) | 1·9‡ ($N=201$) | 1·3 ($N=46$) |
| In forest† | 1·1 ($N=40$) | 1·1 ($N=17$) | 1·0‡ ($N=14$) | 1·1 ($N=42$) |
| Mean group size of female herds | | | | |
| While raiding | 10·1 ($N=9$) | 7·9 ($N=16$) | 8·6 ($N=83$) | 5·9 ($N=12$) |
| In forest† | 7·6 ($N=47$) | 6·2 ($N=15$) | 8·8 ($N=25$) | 7·7 ($N=40$) |

* This refers only to cultivated plants consumed by elephants.

† Mean group sizes in forest refer to data collected over corresponding seasons during 2 years (April 1981–March 1983).

‡ Group size frequency distributions of male groups while raiding and in forest were tested for each season for statistical significance by the $G$-test. Only during one season (October–December) were the two distributions significantly different ($G=22·3$, $df=3$, $P<0·005$). In all other cases there was no significant difference ($P>0·05$).

from other causes; such deaths have not been categorized as due to crop defence in our records. Records of 396 elephant deaths during 1977–1983 over a larger area in southern India show that 13 adult bulls and 29 elephants in family herds (a ratio of 1:2·2) were killed directly during crop raiding. The focal study villages witnessed a total of 948 adult bull and 1965 family herd nights of raiding (a ratio of 1:2·1) during the year. Assuming that elephants in the larger population exhibited a similar raiding behaviour as those in the main study area, an adult bull runs the same risk of being killed as a member of a family herd per night of raiding. Since a bull enters fields far more frequently it incurs much higher risks in the process.

Male elephants appear to respond to the risks during raiding by forming larger groups (Table I). While solitary bulls constituted 93% of total bull group sightings in the forest ($N=113$) during the day, only 58% of crop raiding bull groups ($N=305$) were solitary bulls. Associations of two, three or four bulls were far more frequent in cultivation than in the forest ($G=24·4$, $df=3$, $P<0·005$). However, the tendency to form larger groups was significant only during October–December, when crops were plentiful and cooperation, rather than competition, for obtaining this resource could be expected. Although mother–calf units rarely entered cultivation, the family herds did not show any clear tendency to aggregate while raiding crops.

The additional risks accepted by elephants in raiding could be related to the higher nutrient value of crops compared to the analogous wild plants. For instance, the crude protein content of cultivated grasses (range 5·3–10·0% dry weight) during October–December is much higher than that of the basal portion of the wild grasses (2·0–3·8%) consumed by elephants at this time. Finger millet has much more calcium during the flowering stage (10·8 mg/g) and grain stage (7·4 mg/g) than any of the wild grasses (0·8–2·3 mg/g). Similarly, the sodium content of finger millet inflorescence (0·94 mg/g) and paddy (0·36 mg/g) is higher than that of any wild plant, including dicot browse, analysed (all below 0·28 mg/g).

Increased nutrition from crops may contribute towards better survival, growth, maintenance of

good physical condition and, for bulls, an increased success in male–male competition. Laws et al. (1975) and Sukumar (1985) presented some evidence for a secondary growth spurt in male elephants during the post-pubertal period of 15–25 years, though Hanks (1972) and Lee & Moss (1986) found no pubertal rate change. In any case, male elephants continue to gain weight even after 50 years (Hanks 1972; Laws et al. 1975). Any increased nutrition obtained can thus be translated into a larger adult size which should enhance the fighting abilities of a bull during male–male competition (Clutton-Brock et al. 1982). Better nutrition and body condition would also enable bulls to express musth successfully when they become dominant over other non-musth bulls and have an improved access to oestrous cows for mating (Kurt 1974; Poole & Moss 1981; Poole 1987). Ultimately a larger body size and a successful expression of musth should enhance the reproductive success of a bull.

That adult male elephants take a much higher risk than females may well be related to the much greater variance in male reproductive success. A high variance in reproductive success is positively correlated with a high degree of sexual dimorphism in polygynous mammals with low male parental investment (Ralls 1977). Elephants are amongst the most dimorphic of mammals. The ratio of asymptotic body length of males to females of 1:1·14 for the Asian elephant (Sukumar 1985) is comparable to the extreme values reported for ungulates (Ralls 1977). The elephant is also polygynous and adult bulls do not normally participate in the protection of the calves (Douglas-Hamilton 1972). In addition, the risk of reduced reproductive success may not be worthwhile for female elephants since not only themselves but also their closely related kin would be exposed to injury and mortality during raiding.

Of course, crop raiding itself is a behaviour pattern acquired by elephants over the last few thousand years at best. The risks experienced during raiding may have also been changing rapidly with human technological and social changes. We, therefore, do not argue that the particular levels of additional risk taken by bulls in crop raiding today are necessarily offset by any higher reproductive success derived thereby. Nevertheless, we infer that the high level of crop raiding by male elephants is a consequence of its 'high-risk, high-gain' strategy, moulded by natural selection, to enhance reproductive success.

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