Forest elephants in a rainforest fragment: preliminary findings from a wildlife conservation project in southern Ghana

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Summary

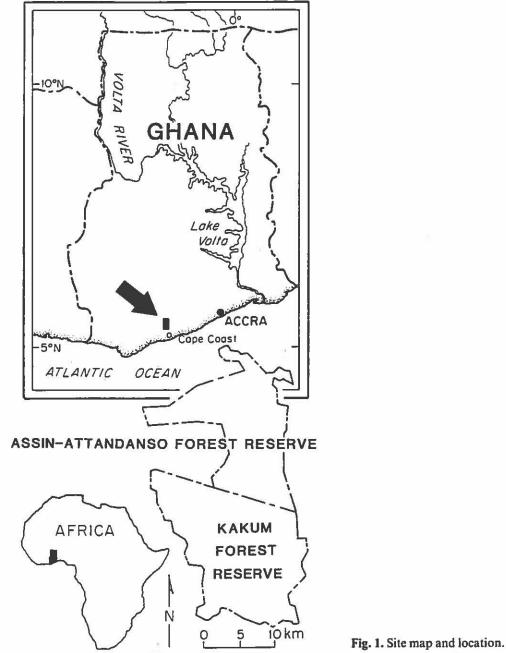
Data on the population status, foraging habits, and crop depredation activities of African forest elephants (*Loxodonta africana cyclotis*) were collected in conjection with a three-month reconnaissance study of wildlife populations in the Kakum and Assin-Attandanso Forest Reserves, Central Region, Ghana. There were no visual sightings of elephants; spoor data were used to derive group size, age class, and population density estimates. The resident elephant population contains an estimated 100–150 individuals, which is equivalent to a crude density of 0.3-0.4 elephants/km². Social group size estimates from fresh spoor data ranged from two to six elephants. Typical group size appears to be three or four although solitary individuals were not uncommon. The Kakum-Assin elephants appear to be completely isolated from contact with other elephant populations. Elephant poaching is not a problem in the area at the present time. Elephants frequently cause major damage to food crops in farms bordering the two reserves, but do not damage orchard crops of oil palm (*Elaeis guineensis*), cocoa (*Theobroma cacao*), and orange (*Citrus sinensis*). Cows with small calves are not known to raid farms.

Key words: browser, forest elephant, frugivore, spoor

Résumé

On a collecté des données sur le statut des populations d'éléphants de forêt africains, sur leurs habitudes alimentaires et les dommages causés aux récoltes lors de trois mois de recherches sur des populations sauvages dans les Réserves de Kakum et Assin-Attandaso Forest, Central Region, au Ghana. Il n'y a pas eu de contact visuel avec les éléphants, les traces qu'ils avaient laissées ont servi à estimer la taille du groupe. les classes d'âge et les densités de population. La population locale d'éléphants doit s'élever à quelque 100–150 individus, ce qui correspond à peu près à une densité de 0,3–0,4 éléphant/km². D'après les traces fraîches, la taille du groupe social est estimée de 2 à 6 éléphants. La taille type d'un groupe semble être de 3 ou 4 mais les solitaires ne sont pas rares. Ces éléphants semblent être complètement coupés des autres populations. Le braconnage des éléphants n'est, pour le moment, pas un problème dans la région. Les éléphants causent souvent de sérieux dommages aux récoltes dans les fermes voisines des deux réserves mais pas

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Kakum Reserve by the Ghana Department of Game and Wildlife between 1984 and 1986.

A helicopter survey was made to evaluate the character of the landscape mosaic and determine the overall integrity of forest cover within the reserves. The use of aerial surveys for locating elephants or other large ungulates was precluded by the dense forest and secondary growth canopies which blanket nearly all of the two reserves. Vehicle surveys were limited to some twenty kilometres of motorable logging tracks located within the Kakum Forest Reserve. Foot surveys predominated, usually following existing paths (boundary line paths, newly cut hiking trails, hunters' paths, former logging roads or hauling traces and game trails) due to the difficulty of moving quietly or efficiently in the thick forest undergrowth. Reports of crop raiding by elephants were followed up immediately whenever possible;

elephant spoor and crop damage data were collected at the site and the elephants tracked to determine the routes taken when leaving and entering the reserve.

Spoor data collection

Logistical and time constraints obviated use of a dung transect method for estimating elephant population densities in this study (Barnes & Jensen, 1987). We focused instead on the use of spoor data collected during foot surveys as a means for identifying and differentiating between individual elephants and herd groups recorded within a series of focal survey areas. Results reported here are from spoor data collected by the authors. Game Protection Guards and Game Scouts are being trained in these techniques in order to more readily monitor elephant activities within the Kakum and Assin-Attandanso Reserves. The techniques employed appear to be readily understood and learned by Game and Wildlife staff with limited educational backgrounds.

Footprints and dung measurements were used to establish the probable age/ size-class distributions of elephants within herd groups. Although the footpads of elephants are elastic and footprint dimensions vary slightly according to the character of the substrate, footprint measurements and peculiarities can be used to identify individual elephants or differentiate between elephants within a group (Carter, 1970). Forefoot prints not overlapped by hindfoot prints were preferred. Clear well-defined fresh tracks were measured for diameter in two perpendicular dimensions, sketched and photographed if possible. Observed peculiarities in foot or toenail shape and footpad corrugations were noted.

The faeces of elephants display consistent and identifiable individual characteristics with regard to the size, shape, texture and consistency of dung boli. Dung characters can be used to estimate elephant age and size class (Jackmann & Bell, 1984), to differentiate between elephants within a herd for estimates of group size and, under certain circumstances. to recognize individuals (Carter, 1970; Williams, 1950). Fresh and intact dung boli were measured for length and diameter, and the general texture, consistency, content and configuration of the dung bolus noted when possible.

Although a minimal number of individual estimates were made occasionally from old and deteriorated spoor, the group size data reported here were calculated from fresh spoor data which were discrete enough to be reliably judged as representing single-event occurrences. Group size, composition or age class estimates were not made from old, deteriorated and scattered spoor although occurrences were noted. The estimate of the total population size was extrapolated from these data. Although the methodology employed obviously contains significant potential for subjective error, we believe that it was the most practical method available for use under the existing circumstances.

Multiple dung piles at a single site exhibiting boli of similar size and consistency characteristics were assumed to be from a single individual if secondary evidence indicated that elephant(s) were active or present on the site for half an hour or more. Secondary evidence could include extensive browsing damage to vegetation, vegetation well-flattened by an elephant in a laterally recumbent posture or a heavily disturbed substratum. It should be noted that highly aroused elephants will defaecate repeatedly. and under such circumstances the stool becomes increasingly looser and more watery with each defaecation. Observations on captive *L. africana africana* indicate that in situations of prolonged stress during dominance confrontations this process can lead ultimately to the evacuation of the entire caecum contents as well (J.P. Dudley, pers. obs.).

Results

Landscape characteristics

The forest of the Kakum and Assin-Attandanso Reserves is largely secondary in character with few areas possessing an intact overstory of canopy emergents. Timber harvests by private contractors in some recently logged areas reached virtual clearcut proportions with only scattered undersize, uneconomic or malformed canopy trees left standing on several 5–10 ha sites. Nonetheless, the forest cover remains largely intact.

The Pra Suhien Forest Reserve adjoins the southwestern corner of Kakum Reserve, but the reserves are contiguous only along a 300 m front and a 15 m wide all-weather road divides the two reserves. Elephants no longer inhabit the Pra Suhien Reserve. All forest reserves in this region are surrounded by farmlands (cultivated plots and bushfallow), which extend right to the boundaries of the reserves. Forest cover outside the forest reserves is limited for the most part to a few outlying groves or small (1-5 ha) forest patches on rocky outcrops.

Large tracts of recently logged forest and the margins and tracks of hauling roads in these reserves have been invaded by *Commolina odorata*, a weedy herbaceous shrub which has become a major pest in Ghana during the past 15 years. *C. odorata* is an aggressive exotic, recently introduced from central Africa, which grows to 1-3 m in height and forms extensive and very dense monospecific stands on disturbed sites. The plant does not appear to be browsed by elephants or other ungulates within the reserves, although bongo and other animals appear to make occasional use of *C. odorata* stands as cover.

Elephant population and distribution

There are many established elephant trails in the dense understory vegetation of the Kakum and Assin-Attandanso Reserves. Elephants tend to use paths when travelling but not while actively foraging (Barnes & Jensen, 1987; Short, 1983), and elephants will often move in queues on established trails even in open grassland with minimal ground cover. The Kakum-Assin elephant trails often follow old skid traces and logging tracks and elephants frequently use the cleared boundary lines of the reserves as paths when raiding farms. Elephants have apparently begun to adopt portions of several newly-cleared hiking trails as travel routes. For this reason we believe that permanent transects will not provide an accurate means for estimating elephant population densities within these forests (Barnes & Jensen, 1987).

Paijmans & Jack (1959) reported that some 100 elephants were believed to be present in the Kakum and Assin-Attandanso Reserves. Elephant spoor data collected during the three month study period (July-September 1990) yield an estimated minimum of 25-30 different individuals encountered. Focal survey areas comprised approximately 15% of the surface area in the two reserves. The ecological density of the Kakum/Assin elephants may be $\leq 66\%$ of crude density, as reconnaissance surveys by Game and Wildlife staff and interviews with local residents indicate that elephants do not frequent the western panhandle or the western half of the Assin–Attandanso Reserve and some areas of higher ground within Kakum Reserve. Avoidance of the panhandle area is probably caused by factors related to human disturbance; avoidance of other areas may be due to patchiness in the distribution of forage.

From these figures a conservative population estimate of 100 elephants can be computed, while a more liberal estimate could be as many as 200 elephants. Our working estimate for the current elephant population is 100–150 individuals. Given the limitations of the existing data (non-random sampling and single season data), the population density figures for the Kakum/Assin–Atandanso populations are presented for heuristic purposes only.

The estimate of 100–150 elephants translates to a crude density estimate of approximately $0.3-0.4/\text{km}^2$ for the 347 km² combined area of the two reserves (N.B. this density estimate for the Kakum/Assin population was calculated by working *backward* from the total population estimate to the density estimate rather than *vice-versa*). Average population density estimates reported for forest elephant populations in other West African rainforests are: $0.33/\text{km}^2$ for the Bia National Park of western Ghana (1977–1978) (Short, 1983) and $0.23/\text{km}^2$ for the Tai National Park, Ivory Coast (1978–1980) (Merz, 1986).

Group size estimates

Group size estimates for elephant social units recorded from fresh spoor data during the study period (July-September 1990) tended to be small (2–6 individuals). Typical group size was three or four (n=9) elephants and pairs recorded consisted of adult animals only. Spoor of solitary elephants was frequently encountered. The estimated group sizes from this study are similar to those recorded for forest elephants in Tai National Park (Merz, 1986b). Spoor from herds with small calves (<8–10 years) was encountered only well within the interior (0.5 km) of these reserves. Spoor data from crop depredation sites recovered to date indicate that matriarchal groups with young calves rarely if ever leave the reserves to forage in adjacent farmlands.

Poaching

Local sources have indicated that there was sporadic shooting of elephants for ivory taking place within the reserves until about 1970. Elephants from the Kakum Reserve had been killed on a few occasions by Game and Wildlife officers during crop depredation control operations in the past but a moratorium on the practice is now in effect. No elephants are known to have been killed by poachers in the area within the recent past, and elephant poaching does not appear at present to be a present problem in the reserves. Poaching by local hunters still occurs within the Kakum and Assin–Attandanso Forest Reserves on a limited scale but appears restricted to the monkeys, rodents and the smaller antelopes. Commercial bushmeat hunting has been eliminated from the reserves only recently (Mensah-Ntiamoah, 1989). Incidental poaching of elephants still occurs in other parts of Ghana, and could conceivably become a threat in the Kakum/Assin–Attandanso region in the future.

Foraging behaviour

Obvious indications of elephant browsing activity were typically lacking even in areas of demonstrably high elephant activity. No evidence of significant damage to mature trees from bark stripping or stem damage by elephants was found and mature canopy trees and emergents in these forests may not be subject to significant mortality as the result of elephant browsing (Short, 1981). Elephant browsing damage was recorded most frequently on the umbrella tree (*Musanga cercopoides*) and the raffia palm (*Raphia hookeri*).

Musanga cercopoides is a light-demanding. gap-colonizing canopy species also found along forest margins and former logging tracks within the reserves. *M.* cercopoides in the 10–30 cm DBH size classes were found which had been pushed over and completely stripped of foliage by elephants; this species is also eaten by forest elephants in Ivory Coast (Merz, 1981). Raffia palms (*Raphia hookeri*) dominate on low-lying swampy or boggy areas of the two forest reserves, often as monospecific stands. Large raffia palms frequently exhibit evidence of browsing by elephant. Raffia bogs are utilized as drinking and/or mudbathing sites by elephants.

Fragments of endocarp from *Tieghemella heckelii* fruits were commonly observed in elephant dung throughout the period of this study. The fruit is a large $(9 \text{ cm} \times 5 \text{ cm})$ dense spheroid possessing a soft outer skin covering a thick hard shell. *T. heckelii* fruits are also eaten by forest elephants in the Tai National Park of Ivory Coast and the Bia region of western Ghana; *T. heckelii* appears to be an important seasonal forage for elephants in West African moist forest habitats (Merz, 1981; Short, 1981; Leiberman, Leiberman & Martin, 1987).

Crop depredations

Farms located adjacent to the forest boundary frequently suffer from depredations by wildlife inhabiting these reserves. Elephants, various rodents, river hog (*Potamochoerus porcus*), monkeys (principally *Cercopithecus* spp.), duikers (*Cephalophus* spp.). bushbuck (*Tragelaphus scriptus* (Pallas)), and bongo are known to cause significant damage in farm plots near the reserves. Elephant and river hog depredations tend to be localized, severe, and readily apparent; crop damage by other wildlife is typically more diffuse and cryptic. Total crop losses around the reserves caused by birds and other mammals probably exceeds that caused by elephants. Where it occurs, however, elephant damage causes the greatest losses to individual farmers.

It was found that crop raiding elephants often use the cleared boundary lines as travel routes, walking along the 1–2 m wide boundary strip until cultivated plots adjacent to the boundary are encountered. Elephant depredations in farms were largely confined to food crops growing in plots adjacent to the reserve boundary. Elephants seldom travelled more than 100–200 m beyond the forest edge during crop raiding forays. Trampling damage by elephant often equalled or surpassed the amount of feeding damage *per se*. Crops subject to severe damage by elephants in this region include maize (*Zea mays*), cassava (*Manihot esculenta*), banana/plantain (*Musa acuminata*/M. × *paradisiaca*), cocoyam (*Xanthosoma sagittifolium*). and papaya (*Carica papaya*).

Important crops in this area not subject to elephant depredations include oil palm (*Elaeis guineensis*). orange (*Citrus sinensis*). and cocoa (*Theobroma cacao*).

An extensive commercial oil palm plantation bordering the southwestern border of the Kakum Reserve is heavily utilized by primates, squirrels and birds but avoided by the elephants, which often raid adjacent farm plots. Elephants in this region are not known to eat browse or fruits from orange trees although these are present in farm plots immediately adjacent to the reserve boundary.

Smallholder cocoa plantations are distributed along many portions of the reserve boundaries. Elephants will occasionally travel short distances through cocoa groves bordering these reserves, but do not browse cocoa trees or fruits. Elephants may be seeking other forage in cocoa plantations, as cocoa is often interplanted within a shelterwood of native forest-canopy trees. The fact that cocoa farms aloang the perimeter of the Kakum and Assin–Attandanso Forest Reserves are not disturbed by elephants is somewhat anomalous. In other parts of Ghana elephants feed on cocoa fruits (Short, 1981) and may cause significant damage to local cocoa crops (Mensah-Ntiamoah, 1989). The Kakum–Assin elephants appear reluctant to move more than 100–200 metres beyond the reserve boundaries even within cover of mature cocoa 'woodlands' or dense bush fallow.

Reports of elephant depredations dropped off sharply during the final month of this study (mid-August to mid-September). This period coincides with the second major peak of fruiting for *Tieghemella heckelii* within these reserves. The reduced frequency of crop depredations at this season may be attributable to the relative distribution and abundance of fruiting *T. heckelii* trees within the reserves (see Discussion).

Discussion

Logging, forest gaps, and forage availability for elephants

Changes in selective logging regimes during the past few decades from the expanding international market for tropical hardwoods may have profoundly altered forage availability for elephants inhabiting commercial forest reserves in West Africa. Whereas fifty years ago only a single tree species (*Kaya ivorensis*) was logged in Ghana for the export market (Paijmans & Jack, 1959), some fifty species are now heavily exploited (E.O.A. Asibey, pers. comm.). *T. heckelii* is currently a valuable hardwood in both domestic and export timber markets; other major timber species in the Kakum and Assin–Attandanso Forest Reserves are important mast and fruiting trees. Conversely, the loss of elephants as seed dispersal agents within commercial forest reserves may be affecting the regeneration of *T. heckelli* and other economically important tree species (Lieberman et al., 1987).

Patchiness in the distribution of fruiting *T. heckelii* may have a significant influence on the seasonal movements of elephants in rainforest habitats in Ghana. Short (1983) found that forest elephant densities in Bia National Park reach their lowest levels during late August and September, when the resident elephants move southward from the park into the adjoining primary forest areas of the Bia Game Production Reserve (G.P.R.). Elephants may be shifting foraging ranges at this season to feed on fruits of *Teighemella heckelii*, which occur at higher densities in the Bia G.P.R. than in Bia National Park (Short, 1983).

The seasonal fruiting peak for *T. heckelii* in Ghana comes during late August and September; the apparent reduction in the frequency of elephant depredations around the southern perimeter of the Kakum Reserve recorded during this season may have been caused by a shift in elephant foraging areas into interior areas of the reserve where fruiting *T. heckelii* are more common. Although data to test this hypothesis are lacking. the latest cycle of commercial logging within the reserves (1980–1987) may have reduced densities of *T. heckelii* within the southern and western portions of the Kakum Forest Reserve and influenced seasonal distribution of elephants within the reserves. Alternatively, there may be a natural cline in the density of *T. heckelii* within Kakum and Assin–Attandanso Forest Reserves sufficient to produce a shift in foraging ranges of elephants into the reserve interior and away from farmlands around the southern periphery.

Merz (1981) has suggested that forest elephants preferentially utilize gapcolonizing plants. Population densities of African forest elephants have been found to be significantly higher in secondary forest than in primary forest habitats (Merz, 1986; Barnes *et al.*, 1991). The preferential utilization of gap vegetation by elephants is attributable to the interaction of two principal factors:

(1) Accessibility: Plant biomass in gaps is concentrated near ground level within reach of elephants rather than in the canopy above as is typical of primary forest habitats (Eisenberg, 1980; Bodmer, 1990).

(2) Palatability: Gap-colonizing plants contain much lower levels of structural and chemical antiherbivory compounds than forest-interior plants (Coley, 1983; Bryant et al., 1989). Studies have shown that herbivores consume mature leaves of gap-colonizing plants six times more rapidly than leaves of shade-tolerant species in the tropical rainforests of Panama (Coley, 1983).

Comments on the autecology of West African forest elephants

Studies of West African forest elephants to date have shown that fruits are a major source of forage while grasses constitute a negligible portion of the diet (Merz, 1981; Short, 1981). West African rainforest elephants thus properly occupy a browser/frugivore feeding niche, whereas Central African forest elephant (L. a. cyclotis) bush elephant (L. a. africana) and Asian elephants (Elephas maximus L.) occupy a grazer/browser/frugivore niche with a marked dependence on grazing resources during at least one season of the year (Wing & Buss, 1979; Laws, Parker & Johnstone, 1975; Eisenberg, 1981; Bodmer, 1990; R. Carroll, pers. comm). This distinction is believed to be quite important.

The browser/frugivore diet of West African forest elephants imposes very different physiological and ecological constraints with regard to the seasonality, availability, relative distribution, and toxicity of forage resources when compared to those of elephants utilizing grazing resources in savanna and forest-grassland mosaics (Janis, 1976; Bodmer, 1989). Forest elephants in West African rainforests are predicted to exhibit significant differences in foraging strategies, social behaviour (modal group size), population densities, carrying capacities, and seasonal movement patterns from those of populations inhabiting forest-grassland and forest-savanna habitat mosaics of Central and East Africa (McNab, 1980). Most importantly, the dynamics of grazing systems permits and encourages large aggregations of elephants and other grazers (McNaughton, 1979), whereas the diffuse distribution of forage resources in West African rainforests should prohibit even the temporary formation of large elephant herds (arbitrarily defined here as n > 25). The existing data appear to support this hypothesis (Short, 1983; Merz, 1986; this study).

The seasonal movements of elephants inhabiting savanna and forest-grassland mosaics are primarily tied to patchiness in the seasonal distribution of water and/or

grazing resources within habitats (Wing & Buss, 1970; Laws *et al.*, 1975; Leuthold, 1977; Eltringham, 1980; Buss, 1989). In the Upper Guinea rainforest habitats of West Africa where grasses for the most part are simply not available (Merz, 1986; Short, 1983; this study) and water resources are not limiting, seasonal movements of rainforest elephants are most likely to be keyed to patchiness in availability of fruit resources (Short, 1983).

Management considerations

Forest elephant populations in Ghana are small (100–200 individuals), isolated and restricted to a few parks and reserves still possessing substantial areas of relatively intact high forest habitat (Stuart, Adams & Jenkins, 1990). The management of national parks and adjoining forest reserves as large integrated conservation units will be necessary to permit the survival of elephant populations in Ghana's highly fragmented rainforest landscapes (Asibey & Owusu, 1982; Dudley, 1990). Multiple-use management plans for forest reserves need to recognize the importance of timber species in providing critical food and habitat resources for local wildlife populations, particularly those characteristic of old-growth forest habitats (Harris, 1984).

Increased knowledge of the foraging ecology of forest elephants and their dependence on seasonal fruitfall resources is of critical importance for the long-term conservation of West African forest elephant populations and the native biodiversity of plant communities within their rainforest habitats (Alexandre, 1978; Hall & Swain, 1982; Leiberman *et al.*, 1987). Canopy gaps produced under low-intensity selective timber harvest regimes need not necessarily limit the overall availability of forage for elephants in West African rainforest habitats but removal of mature trees can significantly alter the distribution and abundance of critical fruitfall resources for elephants. Logging of important fruiting species such as *T. heckelii* may seriously deplete the availability of seasonal forage resources necessary to the survival of forest elephant populations within West African rainforest habitats.

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References

ALEXANDRE, D.Y. (1978) Le role disseminatuer des elephants en foret de Tai, Cote-d'Ivoire. Terre et Vie 32, 37-72.

ASIBEY, E.O.A. & OWUSU, J.G.K. (1982) The case for high-forest national parks in Ghana. Env. Conserv. 9, 293-304.

BARNES, R.F.W., BARNES, K.L., ALERS, M.P.T. & BLOM, A. (1991) Man determines the distributions of elephants in the rainforests of North-eastern Gabon. Afr. J. Ecol. 29, 54-63.

BARNES, R.F.W. & JENSEN, K.L. (1987) How to count elephants in forests. Tech. Bull. Afr. Elephant and Rhino Spec. Grp. 1, 1-6.

BODMER, R.E. (1990) Ungulate frugivores and the browser-grazer continuum. Oikos 57, 319-325.

- BODMER, R.E. (1989) Ungulate biomass in relation to feeding strategy within Amazonian Forests. *Oecologia* 81, 547–550.
- BRYANT, J.P., KUROPAT, P.J., COOPER, S.M., OWEN-SMITH, N. & FRISBY, K. (1989) Resource availability hypothesis of plant antiherbivore defense tested in a South African savanna. *Nature*, Lond. 340, 227–229.
- BUSS, I.O. (1990) Elephant Life: Fifteen Years of High Population Density. Iowa State University Press, Ames, Iowa.
- CARTER, B. (1970) Knysna Elephant Survey: February 1969-January 1970. Wildlife Protection and Conservation Society of South Africa, Eastern Province Branch. Knysna, South Africa.
- COLEY, P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol.* Monogr. 53, 209-233.
- DUDLEY, J.P. (1990) Kakum and Assin-Attandanso Wildlife Reserves Project: Wildlife Consultant Report October 1990. Central Region Development Project UNDP/CEDECOM. International Science and Technology Institute, Washington D.C.
- EISENBERG, J. F. (1980) The density and biomass of tropical mammals. In: Conservation Biology, an Evolutionary-Ecological Perspective (Eds M. Soule & B.A. Wilcox). Sinauer, Sunderland, Massachusettes.
- EISENBERG, J.F. (1981) The Mammalian Radiations: an Analysis of Trends in Evolution, Adaptation, and Behavior. University of Chicago Press, Chicago.
- ELTRINGHAM, S.K. (1980) A quantitative assessment of range usage by large mammals with particular reference to the effects of elephants on trees. Afr. J. Ecol. 18, 53-71.
- HARRIS, L.D. (1984) The Fragmented Forest. University of Chicago Press, Chicago.
- HALL, J.B. & SWAIN, M.D. (1981) Distribution and Ecology of Vascular Plants in a Tropical Rainforest: Forest Vegetation in Ghana. Junk, The Hague.
- IUCN (International Union for the Conservation of Nature and Natural Resources) (1988) Ghana: Conservation of Biological Diversity. Conservation Monitoring Centre, Cambridge, UK.
- JACHMANN, H. & BELL, R.H.V. (1984) The use of elephant droppings in assessing numbers, occupance, and age structure: a refinement of the method. Afr. J. Ecol. 22, 127–141.
- JANIS, C.M. (1976) The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. Evolution 30, 757–774.
- LAWS, R.M., PARKER, I.S.C. & JOHNSTONE, R.C.B. (1975) Elephants and their Habitats: the Ecology of Elephants in North Bunyoro, Uganda. Clarendon Press, Oxford.

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- LEIBERMAN, D., LEIBERMAN, M. & MARTIN, C. (1987) Notes on seeds in elephant dung from Bia National Park, Ghana. *Biotropica* 19, 365–369.
- LEUTHOLD, W. (1977) Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya. Z. Saugetierk. 42, 358–379.
- MCNAB, B.K. (1980) Food habits, energetics, and the population biology of mammals. Am. Nat. 116, 106-124.
- MENSAH-NTIAMOAH, A.Y. (1989) Pre-feasibility Study on Wildlife Potentials in the Kakum and Assin-Atlandanso Forest Reserves, Central Region, Ghana. Ghana Department of Game and Wildlife, Accra.
- MERZ, G. (1981) Recherches sur la biologie de nutrition et les habitats preferes de l'elephant de foret, Loxodonta africana cyclotis Matschie, 1900. Mammalia 45, 299-305.
- MERZ, G. (1986) Counting elephants (Loxodonta africana cyclotis) in tropical rain forests with particular reference to the Tai National Park, Ivory Coast. Afr. J. Ecol. 24, 61-68.
- MERZ, G. (1986b) Movement patterns and group size of the African forest elephant Loxodonta africana cyclotis in the Tai National Park, Ivory Coast. Afr. J. Ecol. 24, 133-136.
- PALIMANS, K. & JACK. W.H. (1959) Greater Kakum Forest Reserves Working Plan, Vol. I: Parts I, II, and III. Ghana Department of Forestry, Accra.
- SEIDENSTICKER, J. (1984) Managing Elephant Depredation in Agricultural and Forestry Projects. World Bank Technical Paper. World Bank, Washington D.C.
- SHORT, J. (1983) Density and seasonal movements of forest elephant (Loxodonta africana cyclotis, Matschie) in Bia National Park, Ghana. Afr. J. Ecol. 21, 175–184.
- SHORT, J. (1981) Diet and feeding behaviour of the forest elephant. Mammalia 45, 177-186.
- SIMPSON, G.G., ROE. A. & LEWONTIN, R.C. (1960) *Quantitative Zoology*. Harcourt, Brace and World, New York.
- STUART, S.N., ADAMS, R.J. & JENKINS, M.D. (1990) Biodiversity in Sub-Saharan Africa and its Islands: Conservation. Management, and Sustainable-Use. IUCN SSC Occasional Paper No. 6. Gland, Switzerland.

WING, L.D. & BUSS, I.O. (1970) Elephants and forests. Wildl. Monogr. 19, 1-92.

WILLIAMS, J.H. (1950) Elephant Bill. Doubleday, New York.