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Tuskless bulls in Asian elephant *Elephas maximus*. History and population genetics of a man-made phenomenon[1]

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In Asian elephant *Elephas maximus* Linnaeus, 1758 tuskless bulls or maknas are generally rare. Only in Sri Lanka 93% of subadult and adult bulls have been reported to be maknas. Using historical records and computer simulations we demonstrate that this situation is man-made. The following mechanisms were identified to be associated with a loss of tuskers: (1) When using elephants, man has always preferred tuskers. (2) Selective hunting and capturing frequently led to a decrease of tuskers in wild-living populations. (3) The impact of selective hunting and capturing was highest in isolated populations, such as Sri Lanka. (4) Selective removal of tuskers for protecting a maximum wild-living male population resulted in an increase of maknas. The rate of increase in the frequencies of maknas in particular populations with known history could be best explained by a dominant mode of inheritance of tusks in combination with a slight advantage of tuskers in reproduction. For the mainland populations it can be predicted that even in those where tuskers are already largely lacking the allele responsible for the expression of tusks should often be sufficiently abundant to allow the recovery of tusk bearing males.

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Introduction

In Asian elephant *Elephas maximus* Linnaeus, 1758 tuskless bulls or maknas are generally rare and their frequency hardly exceeded 10% of subadult and adult bulls in the last century. Only in Sri Lanka 93% of subadult and adult bulls have been reported to be maknas (Tennent 1861, Sanderson 1907, Jayewardene 1994), and three hypotheses have been put forward to explain this phenomenon (Phillips 1980): (1) Tuskers and maknas belong to two different races present in Sri Lanka (Lydekker 1916). (2) Elephants from Sri Lanka and those on the Indian subcontinent belong to different races or subspecies. According to this hypothesis all tuskers in Sri Lanka should be the descendents of escaped or liberated tame

[1] This paper is dedicated to Prof Dr Hans Kummer, Zürich, on occasion of his 65th birthday.

tuskers imported from the Asian mainland. (3) The high frequency of maknas in Sri Lanka is a result of massive culling or capturing of tusk bearing bulls.

Modern studies proved the invalidity of the first hypothesis. In Sri Lanka there exists, if at all, only one separate subspecies, namely *Elephas maximus maximus* (Eisenberg and McKay 1970, Phillips 1980). Also the hypothesis of an introduction of tuskers by man into a population originally characterized by a natural lack of tuskers is highly questionable. Tuskers from Myanmar and the Indian subcontinent have been donated to Sri Lankan kings and temples at least since the third century BC (eg Geiger 1960, Digby 1971). They were extremely rare and well cared for, practically permanently chained when not used, and led under strict commands when brought forward as royal mounts. Bulls kept that intensively hardly breed (Schmidt *et al*. 1992, Kurt 1995) and cannot be expected to have had an appreciable genetic impact on the local elephant population. The third hypothesis, considering the predominance of maknas in Sri Lanka a consequence of selective persecution by man and first put forward by Tavernier (1984), has not been convincingly refuted so far. If a high frequency of maknas on Sri Lanka is the result of predominate culling and capturing of tuskers, maknas should generally be more abundant in populations subjected to those management practices than in other populations. It should also be expected that once selective removing of tuskers from a population has been abandoned, apart from minor fluctuations due to genetic drift there should be no further increase in the frequency of maknas. In both these considerations it is implicitely assumed that tuskers and maknas do not differ as to their reproductive success, a question that also needs to be addressed in this context.

In the present paper the development of tusker-makna-ratios in several wild-living and captive elephant populations of South Asia is described and examined as to a relationship with the respective management practices applied. Various modes of inheritance of tusks and their consequences for the impact of selective hunting and capturing are investigated by a stochastic mathematical model (Tiedemann and Kurt 1995), and conclusions regarding the future management of Asian elephant are provided.

Definitions and methods of data collection

In Asian elephant only males possess tusks, which are elongated second upper incisors of different length and form (eg Evans 1910). In Sri Lanka only 17% of maknas are bare of second upper incisors (Ratnasooriya and Fernando 1992). The remaining bulls (as many females) possess tushes, which are incisors much smaller and thinner than the poorest tusks. These tushes may be either circular or oval in cross-section and sometimes protrude to 20 cm or more beyond the lips. The oval type, which is generally 15 to 30 cm long and decurved (as opposed to the recurved tusk) seems to occur only in males. The circular type, which is often broken at the gumline, is found in both sexes (McKay 1973).

Most data presented in this study have been collected for practical reasons without particular interest in the form of tusks, type of tushes or complete absence of tushes. Therefore we distinguish only between two types of bulls: tuskers and maknas. The frequencies of tuskers and maknas given in the paper are their respective percentage in the total population of adult and subadult males. Sex ratio is given as the number of adult and subadult males per 100 adult and subadult females. Subadults are animals between 8 and 20 years of age and able to reproduce (Kurt 1974). In captivity subadult bulls copulate only with young females (Kurt 1995). In wild-living populations their reproductive performance must be even lower, since female choice favours adult bulls in musth (Kurt 1992, Ishwaran 1993).

Data presented in this paper stem from records on hunting and capturing operations, from estimates of poaching, from stud books, and from investigations on wild-living populations. Demography of wild-living elephants is well known only from studies on relatively small populations of elephants individually recognized by investigators. Population censuses carried out in large populations within a short time tend to underestimate the actual population size, the result is skewed towards adults and subadults, and amongst them towards bulls. Unskilled observers are not always able to distinguish maknas from females.

In the management of captive elephants two systems are distinguished (Kurt 1993, 1994): (1) Working elephants in forest camps, used for transport and timber hauling, are kept extensively. When unemployed they spend their time with hobbled forelegs in the nearby forests where they find natural food and meet with tame and wild-living conspecifics. If wanted by the owners, breeding occurs regularly and babies born are fathered mainly by wild-living bulls. (2) Temple elephants, mainly used for processions, are kept intensively. When not working they are chained and fed by man, as war and state elephants in former times. Intraspecific social contacts are minimal or absent, and breeding occurs very rarely.

The annual mortality rate for the total captive population is estimated to be about 7.5%. This estimate is based on annual mortality rates of 11% in British elephant establishments in Bengal (Sanderson 1907) and Sri Lanka (Tennent 1861) as well as on recent reports from Thailand (Santiapillai and Jackson 1990). The Dehli Sultanate seems to have lost between 5% and 10% of its tame elephants per year (Digby 1971).

Since some techniques of capturing are highly selective, captive born animals are distinguished from captured ones throughout the paper. Furthermore, different techniques of capturing and taming lead to different mortality rates (see Kurt 1992, 1993, for reviews). Especially the use of pitfalls caused mortality rates of up to 90% (Sanderson 1907), while 86% to 97% of hand noosed elephants survived the capturing operations (Jayewardene 1994). In kheddas, ie large enclosures, mortality rates could be as high as 70% by the end of the 19th century. Later they were reduced to 5% to 30% (Stracey 1963). Mela-shikar, ie noosing selected animals from the back of tame elephants, produced mortality rates of some 14% (Toke Gale 1974). The various methods of capturing are well described in the Arthasastra (300 BC – 300 AD), a manual of Buddhist statecraft, and were well known in all antique and medieval south Asian reigns (Meyer 1929). The Arthasastra and other old sources of elephant lore provide a qualification of single methods according to their effectiveness in selective capture and to the survival rate of the captives.

Are tusker-makna-ratios in captive populations different from those in wild ones?

The least skewed sex ratio in undisturbed populations of wild-living elephants at reproductive age is 65 $males_{a+sa}$: 100 $females_{a+sa}$ (Table 1). In captive elephant populations at reproductive age a much higher proportion of bulls is observed (Table 2). In Kerala only tuskers are used for temple festivals. In Sri Lanka bulls have been preferred as long as selective capturing operations were permitted, ie before 1965. In Myanmar, where some 90% of working elephants are captive bred, the proportion of bulls is similar to that in the undisturbed wild populations mentioned above. For the time before 1980 the maximum proportion of maknas in the wild-living south Indian population is estimated to be 10%. By contrast, the frequency of maknas among privately owned elephants of Kerala is as low as 2.1%. Since capturing operations were prohibited, tuskers for temple festivals in Kerala are purchased at the elephant fair in Sonpur (Bihar), and originate from captive populations or poaching operations in northeastern India (Roy 1993).

Do selective hunting and capturing result in increased frequencies of maknas?

In the 19th century maknas had been rare in northeastern India (Sanderson 1907), but their frequency increased significantly from about 8% to 48.7% in the period between 1937 and 1950 ($\chi^2_{n=1} = 16.33$, $p << 0.001$; Table 1). Unselective kraling as practiced in the late 19th and the early 20th century certainly only had an influence on population size, but not on the proportion of maknas present. However, in recent years tuskers have been heavily poached by tribal people for ivory and meat (Chowdhury 1992, Roy 1993), which obviously resulted in a considerable increase of the proportion of maknas. In Myanmar and Thailand ivory poaching has increased in the last years to such an extent that even the tusks of captive bulls are stolen (Frädrich 1993). In Myanmar maknas had been rare in the last century (Evans 1910). However, by 1950 a total of 10% of tame bulls were maknas (Deraniyagala 1955), and by 1993 their frequency was as high as 43.5% ($\chi^2_{n=1} = 20.87$, $p << 0.001$; Table 1). In Tamil Nadu 217 bulls including four (1.8%) maknas were caught between 1926 and 1980. From 1981 to 1983 selective poaching reduced the frequency of males to 20%, and also a decline the proportion of tuskers was observed. In Kerala heavy poaching for ivory has taken its toll in recent years.

Table 1. Proportion of maknas among subadult and adult males (Pma), and sex ratio (number of adult and subadult males per 100 adult and subadult females, Sm) in wild-living populations of Asian elephant as found in extensive field studies (I), extensive censuses (E) and non-selective capturing operations (C). Sample sizes (*n*) are given as the number of adult and subadult males.

Sources of data: 1, 17 – Sanderson (1907); 2 to 6, 21 – Sukumar (1992); 7 to 12 – Surendran (1992); 13 to 15 – Karoor (1992); 16 – Chandran (1990); 18, 19, 31 – Deraniyagala (1955); 20 – Chowdhury (1992); 22, 26, 28, 32, 36 – F. Kurt (unpubl.); 23 – Kurt (1974); 24 – Dissanayake (1992); 25, 35 – Santiapillai (1993); 27, 29 – McKay (1973); 33 – Jayewardene (1994); 34 – Ishwaran (1993); 30, 37 – Hendavitharana *et al.* 1994.

Region	Period	Method	*n*	Pma	Sm
Southern India					
1. Karnataka	1875	C	16	18.8	–
2. Tamil Nadu	1926–1980	C	217	1.8	–
3. Travancore-Cochin	1939–1943	C	34	0.0	–
4. Travancore-Cochin	1946–1951	C	31	0.0	–
5. Karnataka	1968–1974	C	55	5.5	–
6. Satyamangalam-Chamaraj.	1981–1983	I	24	8.3	22.0
7. Kerala (Ke)	1983	E	641	32.3	37.8
8. Ke: Southern Forest Circle	1983	E	174	30.5	54.4
9. Ke: High Range Circle	1983	E	55	30.9	20.1
10. Ke: Central Circle	1983	E	54	37.0	36.2
11. Ke: Northern Circle	1983	E	176	9.1	51.6
12. Ke: Periyar (a)	1983	E	119	67.2	21.8
13. Ke: Periyar (b)	1983	E	92	57.6	16.9
14. Ke: Thekkady	1983	E	55	61.8	18.1
15. Ke: Vallakaduwa	1983	E	37	51.4	15.4
16. Ke: Periyar	1987–1990	E	54	57.6	16.9
Northeastern India					
17. Chittagong	1874	C	25	8.0	–
18. Assam	1937–1946	C	606	46.2	–
19. Assam	1947–1950	C	707	50.8	–
20. Anurachal Pradesh	1961–1977	C	1117	59.4	–
21. Assam	1981	C	67	46.3	–
Sri Lanka					
22. Yala	1967	E	31	77.4	59.5
23. Yala	1967–1968	I	13	84.6	65.0
24. Yala	1990	E	–	83.8	67.0
25. Yala	1993	E	12	89.8	26.3
26. Gal Oya	1967	E	13	84.6	34.0
27. Gal Oya	1967–1968	I	31	97.2	37.8
28. Lahugala	1967	E	49	89.8	41.0
29. Lahugala	1968	E	25	92.0	40.0
30. Gal Oya and Lahugala	1993	E	51	91.0	–
31. Mahaweli	1945	E	–	100.0	–
32. Mahaweli	1968	E	27	100.0	–
33. Mahaweli	1970–1985	E	–	100.0	–
34. Mahaweli	1977–1986	I	229	100.0	56.1
35. Mahaweli	1993	E	147	98.7	–
36. Sri Lanka	1967–1968	E	190	92.1	–
37. Sri Lanka	1993	E	–	92.7	71.6

Table 2. Proportion of maknas among subadult and adult males (Pma), and sex ratio (number of adult and subadult males per 100 adult and subadult females, Sm) in intensively (IC) or extensively (EC) kept captive population of Asian elephant. Sample sizes (*n*) are given as the number of adult and subadult males. In χ^2-tests the respective findings were compared to the maximum sex ratio in wild-living populations of 65 $males_{a+sa}$: 100 $females_{a+sa}$ (Ps), to a maximum natural makna-tusker ratio of 10% for the Asian mainland (Pm), and an average tusker ratio of 7% for Sri Lanka (Pm).

Sources of data: 1 – Panicker (1990); 2, 4, 7, 10 – F. Kurt (unpubl.); 3 – Chandran (1990); 5, 8, 9 – Deraniyagala (1955); 6 – Khyne U Mar (1992); 11 – Ilangakoon (1993); 12 – Ratnasooriya and Fernando (1992).

Region	Period	System	*n*	Pma	Sm	Ps	Pm
Kerala							
1. Private owners	1979–1989	IC	140	2.1	–	–	< 0.01
2. Private owners	1993	IC	25	0.0	625.0	< 0.001	< 0.2
3. Forest Dept.	1988	EC	25	0.0	208.3	< 0.001	< 0.2
Tamil Nadu							
4. Forest Dept.	1978–1979	EC	48	2.1	129.7	< 0.02	≥ 0.05
Myanmar							
5. Forest Dept.	1950	EC	200	10.0	–	–	1.00
6. Forest Dept.	1981–1991	EC	582	–	60.2	≤ 0.1	–
7. Forest Dept.	1993	EC	23	43.5	–	–	< 0.001
Sri Lanka							
8. Processions	1940–1945	IC	32	69.0	229.0	< 0.001	< 0.001
9. Total population	1940–1945	IC	364	89.0	119.0	< 0.001	< 0.002
10. Processions	1967	IC	33	81.8	80.5	< 0.5	< 0.02
11. Processions	1991	IC	68	–	73.9	< 0.5	–
12. Processions	1992	IC	43	81.4	57.2	> 0.5	> 0.5

Censuses between 1983 and 1989 revealed a strong decline in the number of tuskers, and the sex ratio in subadults and adults was found to be skewed towards females (Table 1). The reduction of the subadult and adult male population was significantly related to an increase in the frequency of maknas ($\chi^2_{n=1}$ = 120.65, $p << 0.001$).

Why did man affect tusker-makna-ratios in Sri Lanka but not on the Asian mainland?

With the exception of the remote regions in the hinterlands of northeastern India, Myanmar, Thailand, Laos, and Vietnam, where elephants are still hunted, captured and tamed by tribal people, hunting and capturing was always a strictly enforced monopoly of rulers and later of colonial forces. Under the Buddhist and Hindu kings of southern Asia, management of wild elephants was carried out according to Kautiliya's Arthasastra. It advised people to eliminate elephants from settled and cultivated valleys but to preserve them in guarded elephant sanctuaries at the periphery of the respective kingdoms. Furthermore, the Arthasastra instructed people to capture only subadult and adult tuskers and to disregard sick, young, and female elephants as well as maknas and bulls with small tusks (Meyer 1929). These recommendations could not be strictly followed. In each elephant riding culture females were kept either as especially docile mounts and as indispensable decoys for capturing operations, or just because too few males were available.

Numbers of elephants kept by rulers in antiquity and the Middle Ages have often been extremely exaggerated by contemporary writers. During its largest extension, the Dehli Sultanate (1192–1398) controlled practically the whole Indian peninsula and, thus, at least some 1.5 million km^2 of elephant land. If a low density of one elephant per 4 km^2 is assumed, the wild-living population consisted of at least 375 000

Table 3. Number of captive elephants (Nc), estimated size of wild-living populations (Nw), and relative sizes of captive populations (Nc:Nw) in different regions of Asia during different periods. Captive breeding (CB) can be absent (–), rare (+/–), or regular (+). Unselective capturing operations (CU) are keddha (ke) and pitfalls (pe). Selective capturing operations are hand noosing (hn), mela-shikar (ms), selective drives (dr), and decoy (de).

Sources of data: 1 – Trautmann (1982); 2 – Digby (1971); 3 – Lahiri-Choudhury (1991); 4 – Tavernier (1984); 5 to 9 – Santiapillai and Jackson (1990); 10 – Khyne U Mar (1992); 11 – Baldaeus (1960), Pieris (1920), McKay (1973); 12 – Deraniyagala (1955); 13 – Jayasinghe and Jainudeen (1970), McKay (1973); 14 – Ratnasooriya and Fernando (1992); Santiapillai (1993).

Region/reign	Period	Nc	Nw	Nc:Nw	CB	CU		CS			
						ke	pe	hn	ms	dr	de
Indian peninsula											
1. Mauriya	330 BC	9 000	375 000	0.024	–	+/–	–	–	+	+	+
2. Delhi Sultanate	1340	3 000	375 000	0.008	–	+	–	–	–	–	–
3. Vijanagar	1565	1 000	125 000	0.008	–	–	+	–	–	–	–
4. Moghul	1650	30 000	375 000	0.080	+/–	+	–	–	+/–	–	–
5. Southern India	1990	300	7 150	0.042	+/–	+	+	–	–	–	–
Northeastern India and southeastern Asia											
6. Northeastern India	1990	1 600	12 135	0.132	+	+/–	–	–	+	–	–
7. Vietnam	1990	600	2 000	0.333	?	–	–	–	+	–	–
8. Laos	1990	1 332	3 000	0.444	+	–	–	–	+	–	–
9. Thailand	1990	5 300	2 000	2.650	+	+/–	–	–	+	+	–
10. Myanmar	1993	4 500	6 500	0.692	+	+/–	–	–	–	–	–
Sri Lanka											
11. United Kingdoms	1680–1696	2 500	12 000	0.208	–	–	–	+	–	+	+
12. Private owners	1945–1950	670	2 000	0.335	–	+/–	–	+	–	–	–
13. Private owners	1967–1979	532	2 500	0.021	–	–	–	–	–	–	–
	(recruitment from abandoned wild babies)										
14. Private owners	1992	480	2 000	0.240	–	–	–	–	–	–	–
	(recruitment from abandoned wild babies)										

individuals. Most of the captive elephants were tributes from subordinate rulers or taken as plunder from southern India, some had been imported from Bengal, Myanmar, and Sri Lanka. At the peak of its power the Sultanate possessed 3 000 elephants (Digby 1971). However, even if a captive population with a sex ratio of 2 $males_{a+sa}$: 1 $female_{a+sa}$, an annual mortality of 7.5%, and a high mortality rate of 75% during capturing and taming operations are assumed, the annual demand for animals to maintain the captive population must have been negligible for the demography of the wild population. The same applies for the south Indian kingdom of Vijanagar (Table 3). During the peak of the Mogul empire in the 17th century the population of captive elephants was estimated to be 30 000 (Tavernier 1984). Even the maintenance of such a large population would hardly have had an impact on the wild-living resources. However, this holds if the Moguls had caught their elephants in all parts of their immense reign. But they satisfied their demand primarily through unselective large-scale kheddas in the vicinity of their capitals. On the Indian peninsula the captive population has been not larger than 8% of the wild population. Northeastern India and southeastern Asia harbour relatively large populations of tame elephants (13% to 200% of the size of the respective wild populations). In all these regions elephants are regularly bred in captivity. The economics of the Khmer (802–1431) depended on a tremendous system of irrigation and therefore on a large-scale use of elephant power. Nevertheless, the frequency of maknas in Cambodia is as low as in other regions of the Asian mainland (Bazé 1955). The Khmer drew tributes from as far away as present-day Laos, Myanmar, and Malaysia as well as from what were later to become Thai kingdoms to the west (Chandler 1993). The large demand for working elephants could easily be satisfied from practically unlimited resources, which is in a sharp contrast to the situation in Sri Lanka.

Sri Lanka always possessed a considerable tame population (20% to 33% of the wild population). Since Sri Lankan kingdoms only exceptionally controlled territories on the Asian mainland, these populations must always have been restocked from the resources of the island itself. Import as well as captive breeding of elephants were practically absent. During the Portugese (1505–1658) and the Dutch (1602–1670) periods high frequencies of maknas were well documented (eg Pieris 1920, 1929). Contrary to this, paleontological records and rockpaintings indicate the presence of an elephant population with tusk bearing males in the Neolithic and even in later periods (Deraniyagala 1955). Assuming that the high rate of maknas is man made, it is likely that the Sri Lankan kingdoms have had a profound impact on the demography of wild-living elephant populations.

How could Sri Lanka harbour large captive populations without captive propagation?

Contrary to the contemporary Indian or Myanmar armies, the elephant units of antique and medieval Sri Lankan forces were very small (Geiger 1973). For example, by the end of the 16th century amongst 2067 tame elephants only 122 (5.9%) were war elephants (Baldaeus 1960) while the contemporary Turko-Afghan or Mogul rulers kept 25% to 33% of their elephants fit for war (Digby 1971). The bulk of tame elephants must have been indispensible for the construction of monumental religious and public buildings. First of all, however, they must have played a major role in the creation of a multiplicity of irrigation works, mainly in the dry zone, for nowhere in the pre-modern world was there such a dense concentration of irrigation facilities observed. Elephants were used to draw earth plugs, to haul heavy weights, and to work on levers (Murphy 1957, Brohier 1965, Boner and Sarma 1972, De Silva 1991).

Generally, male elephants were preferred to females since, on the one hand, they are substantially stronger, and, on the other hand, the wild-living herds had to be kept as large and productive as possible. A relatively large captive population had been maintained on the long run only through the creation of sanctuaries, as evidently done since 38 AD, and through strictly controlled selective capturing at low mortality (Geiger 1960, Knox 1966). Until the middle of the 17th century elephants were practically omnipresent on the island; bulls threatened people and caused crop damages (eg Schweitzer 1953, Brohier 1975). As 75% of all crop raids and 80% of all man slaughter were done by the highly demanded bulls, it was obvious to combine the protection of men and crops with selective noosing (Jayewardene 1993).

What is the price for achieving large captive stock without exhausting the wild-living population?

Elephants are polygamous, and their genetic variation is low as compared to other large ungulates (Nozawa and Shotake 1990, Hartl *et al.* 1995). There is no or no pronounced seasonality in reproduction (Toke Gale 1974, Kurt 1992), and birth intervals are 4.5 years or more (Kurt 1970, Sukumar 1992). Bulls have the largest testes amongst ungulates (Ginsberg and Rubenstein 1990). Testis size is directly related to daily sperm production, sperm density, and absolute numbers of sperms per ejaculate (Møller 1989). Thus, with respect to social, genetic or physiological capacities of bulls there does not seem to be any limiting biological factor for the maintenance of a skewed sex ratio in the reproducing age classes of a population. This assumption is wrong. Heavy poaching of adult bulls has been found to reduce the fecundity of females (Poole 1987, 1989, Chandran 1990). The proportions of infants and juveniles in the population drop sharply already at a sex ratio of one fullgrown bull per six to ten reproducing females (F. Kurt, in prep.). Hence, in Asian elephant the availability of adult bulls is a limiting factor for female fecundity as it is the case in other gregarious ungulates (Ginsberg and Milner-Gulland 1994).

As a consequence of the former, the rulers of Sri Lanka had to take into account not only the negative effects of capturing too many females but also those of capturing too many bulls. This could be accomplished by the very selective, but highly protective techniques of hand noosing. One may ask the question: Was it actually possible to maintain on the long run 2 500 captive elephants (Pieris 1920, Baldaeus 1960) by permanent restocking from a wild-living population of only 12 000 (McKay 1973)? We have addressed this problem by using a computer simulation program developed by Sukumar (1992) with the following basic assumptions: In the captive population sex ratio was 2 males : 1 female, and annual mortality was 7.5%. In the wild-living population there were 5.9% of juvenile males (5–10 years old), 8.3% of adult and subadult males, and 42% of adult and subadult females (cf Sukumar 1992). Mortality during capturing operations was 10%. Based on this data, annual losses in the wild-living populations would have been 125 bulls and 62 females, corresponding to 8.1% and 1.5%, respectively. Such losses can be considered medium for bulls and low for females. After 50 years with constant medium off-take of males and low off-take of females the population had a sex ratio in reproducing age classes of 1 male : 8 females, and still grew at a rate of 1.5%. High off-takes of bulls (15%) would have skewed the sex ratio to 1 male : 28 females, ultimately resulting in a reduced fecundity of females. Thus, it was paramount for Sri Lankan kings to omit overexploitation. However, the permanent and highly selective off-take of tusk bearing males must have resulted in an increasing proportion of maknas in the wild-living population, as demonstrated in the following comparison.

Why did sacred places save the tuskers?

In the southeast of Sri Lanka tuskers are more abundant than in all other parts of the country. This area, today represented by the Yala or Ruhunu National Park and its surroundings, was part of the kingdom of Rohana, and until 1250 AD it was subjected to intensive wet rice cultivation. Abandoned fields and silting water tanks later changed into secondary habitat with high carrying capacity for elephants. Kataragama, the heart of this area, has been considered one of the most sacred places both by Hindus and Buddhists since ancient times (Wirz 1966). Therefore it is not surprising that the first traceable elephant sanctuary had been established in its vicinity already in 34 AD (Geiger 1960). Ptolomy's map (100 AD) quotes the area of the present Yala National Park as "Pasqua elephantorum". Later maps indicated the southeast of Sri Lanka as a promising capturing ground for elephants (Baldaeus 1960). By the end of the 17th century colonial powers introduced unselective kraling, which resulted in a massive reduction of the wild-living population but did not affect tusker-makna-ratios. This is reflected by temporary accounts of their bags: Between 1690 and 1697 (De Vos 1872, Van Goens 1932, Schreuder 1946) and in 1805 (Cordiner 1983) some 15% of all captive bulls were tuskers. In the Yala National Park the frequency of wild-living tuskers was 15.4% in 1967–68 (Kurt 1969), 16.1% in 1991–1992 (Dissanayake 1992), and 15.3% in 1993 (Santiapillai 1993).

A completely different situation prevails in the Mahaweli basin in the east of Sri Lanka. Here antique and medieval wet rice culture was most intensive and lasted for at least 1800 years (Brohier 1975, De Silva 1991), and it can be assumed that the rulers of Polonnaruwa removed considerable numbers of tuskers from the wild-living population. To a certain extent selective noosing continued to be practiced here until the 20th century (eg Spittel 1951), not without an enduring effect on the proportion of tuskers present in the wild. In fact, almost all contemporary reports agree that today tuskers are completely absent in the Mahaweli population (cf Deraniyagala 1955, Jayewardene 1994).

A historical approach to the inheritance of tusks

The rate of increase of the proportion of maknas in a population can be expected to depend to a certain extent on the mode of inheritance of tusks, which is as yet unknown. To provide some predictions as to the further development of tusker--makna-ratios in extant wild-living elephant populations Tiedemann and Kurt (1995) developed a stochastic simulation model. This model puts strong emphasis on the inheritance of tusks, which are assumed to be controlled by a single autosomal gene or a major gene in a polygene system. From applications to a fictive population they concluded that the tusk allele is most likely dominant under the assumption of a slightly higher (40–50%) reproductive success of tuskers. Based on real data, in the present paper we simulated frequencies of the tusk allele for three distinct populations, differing as to human impact on their development over time.

Table 4. Initial population size and mortality schedules used in the simulation of elephant populations. Data are derived from Table 1.

	Initial population size	Mortality rates (in %)							
		300BC –600	600 –1250	1250 –1600	1600 –1800	1800 –1900	1900 –1950	1950 –2000	time period
Mahaweli									
Females	360	5.5	5.5	5.5	5.5	5.5	5.0	5.0	
Tuskers	130	10.0	10.0	10.0	15.0	15.0	8.5	8.0	
Maknas	10	7.5	7.5	7.5	12.0	15.0	7.0	7.0	
Yala									
Females	600	5.5	5.5	5.5	5.0	5.0	5.0	5.0	
Tuskers	280	9.0	10.0	10.0	15.0	15.0	8.5	7.0	
Maknas	20	7.0	7.5	7.5	15.0	15.0	7.0	7.0	
Southern India									
Females	4000	5.5	5.5	5.5	5.5	5.5	5.5	5.5	
Tuskers	1920	8.0	8.0	8.0	8.0	8.0	8.0	8.0	
Maknas	80	7.0	7.0	7.0	7.0	7.0	7.0	7.0	

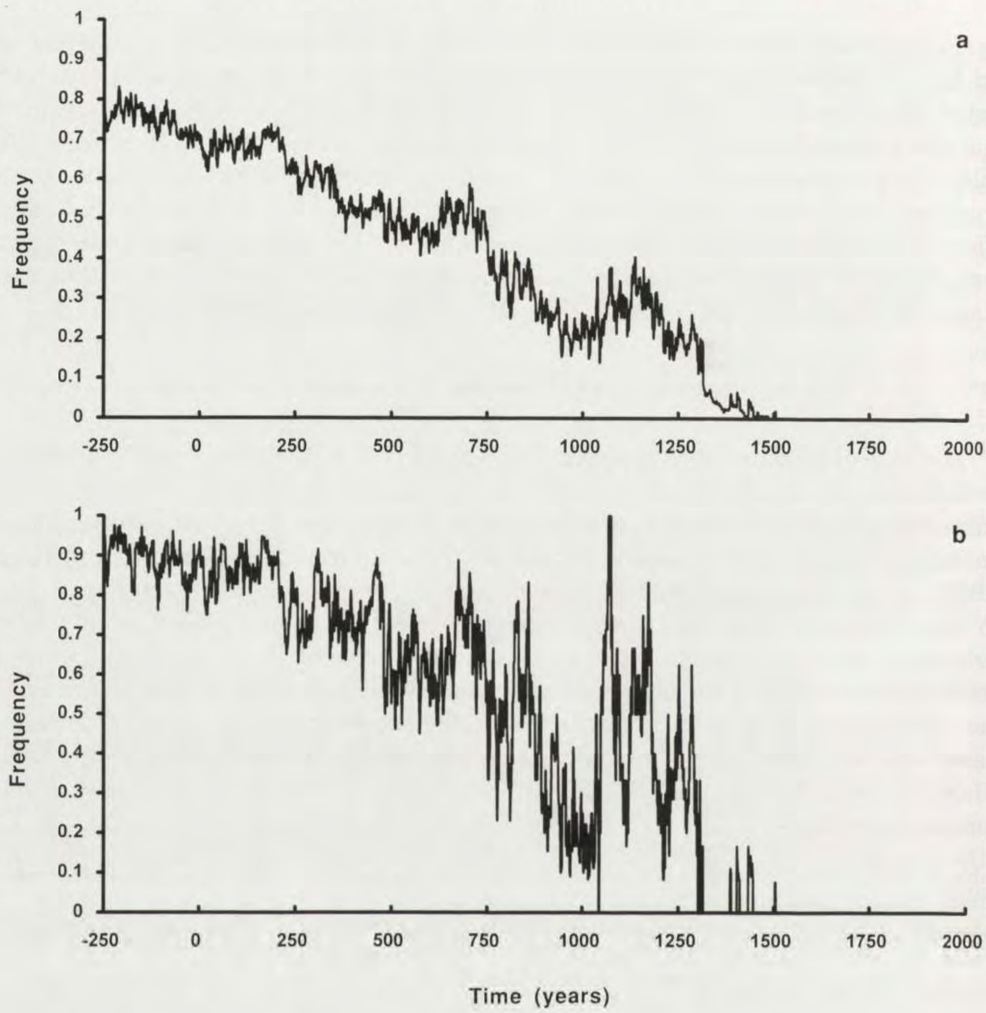

Fig. 1. Frequency of the tusk allele (a) and frequency of tuskers (b) among reproductive males as predicted by the simulation for the Mahaweli basin (see Table 4 for simulation parameters). Note the random drift effects prior to the extinction of the tusk allele, which are due to a small absolute number of remaining reproductive males.

The most drastic impact on tuskers has been reported from Mahaweli basin on Sri Lanka. We simulated the mortality scheme presented in Table 4, with an initial population size of 500. Under the assumption of an extremely high mortality of tuskers due to selective hunting, the model predicts that at about 1500 AD the proportion of tuskers should have declined from about 95% to zero (Fig. 1). This result is in agreement with the historical record for Mahaweli. However, for this case the prediction of the model is similar, when a recessive inheritance of the tusk allele is assumed.

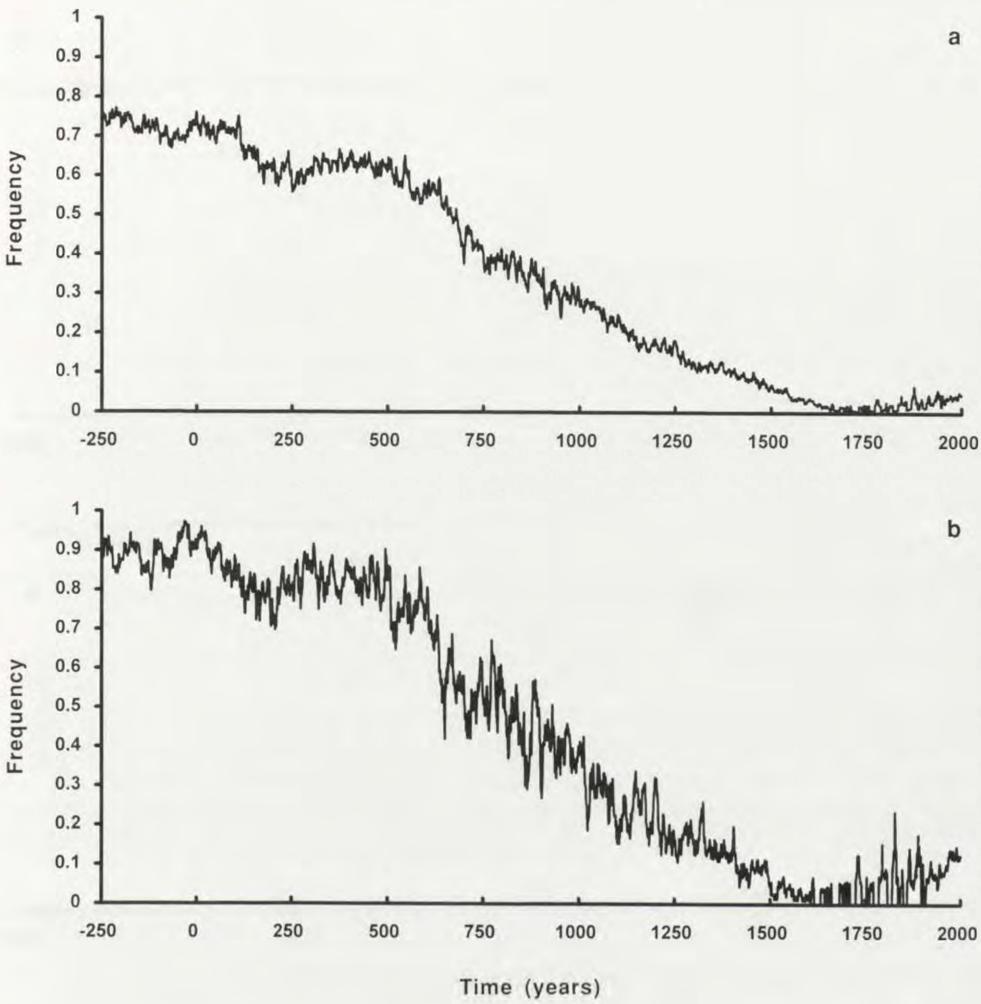

Fig. 2. Frequency of the tusk allele (a) and frequency of tuskers (b) among reproductive males as predicted by the simulation for the Yala area (see Table 4 for simulation parameters).

A more moderate mortality scheme is reported for the Yala area in the southeast of Sri Lanka where the initial population size had been about twice as high as in Mahaweli (Table 4). There a period of slightly higher mortality for tuskers (9–10%) than for maknas (7–7.5%) had lasted from about 300 BC until 1600 AD. The available census data suggest a reduction of tuskers from an initial proportion of 95% to a mere 10% within this period. However, the highest human impact on males, causing a mortality of about 15% between 1600 and 1900, had been unselective with respect to tusks. The simulation is again in agreement with these data, if a dominant inheritance of tusks and a selective advantage of tuskers

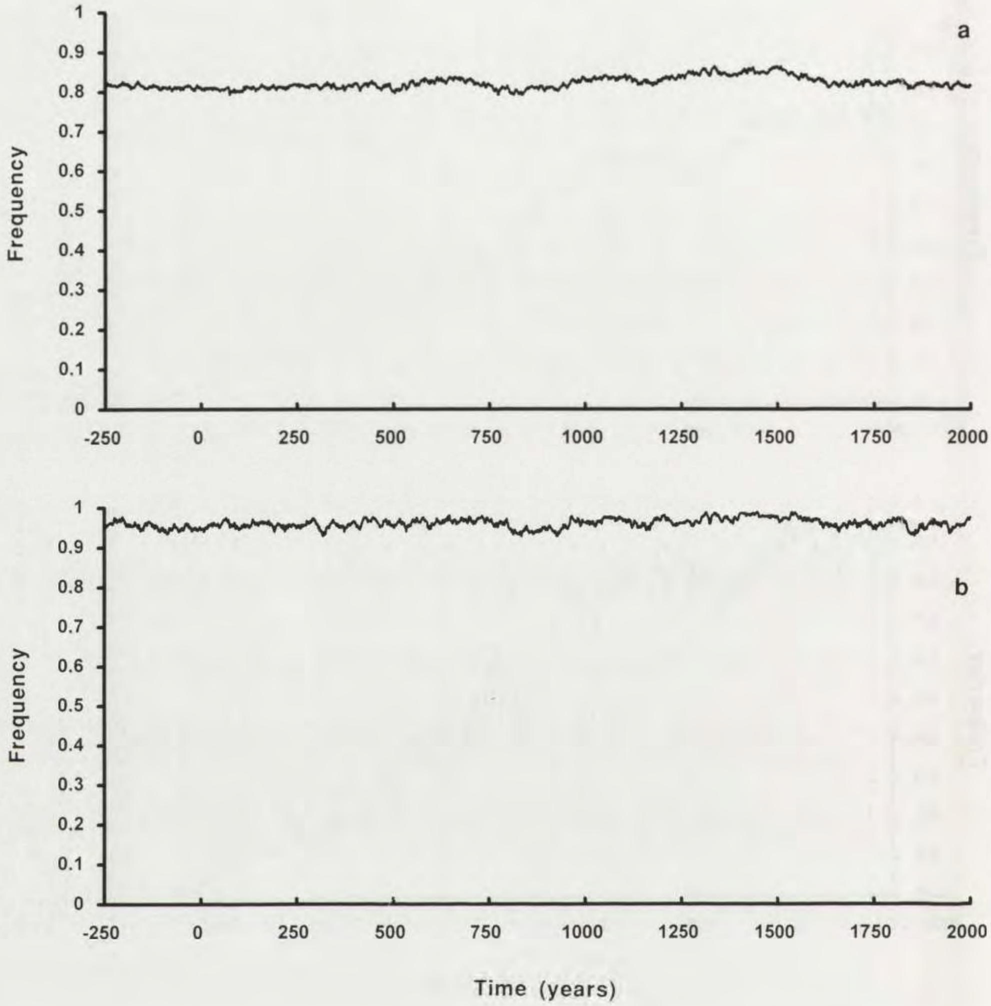

Fig. 3. Frequency of the tusk allele (a) and frequency of tuskers (b) among reproductive males as predicted by the simulation for southern India (see Table 4 for simulation parameters).

in mating of about 40% to 50% are assumed (Fig. 2). On the contrary, if we exclude sexual selection, the model predicts the extinction of the tusk allele after about 500 years, which does not fit to the census data concerning tuskers. Given a recessive inheritance of the tusk allele without sexual selection, the model predicts a survival of the tusk allele at frequencies that low that tuskers are predicted to be absent or very rare, which is again in contrast to the historical data.

In a third test of the supposed dominant inheritance with sexual selection, we simulated the elephant population in southern India (see Table 4). There the minimum population size is estimated to be about 6 000 individuals, and human

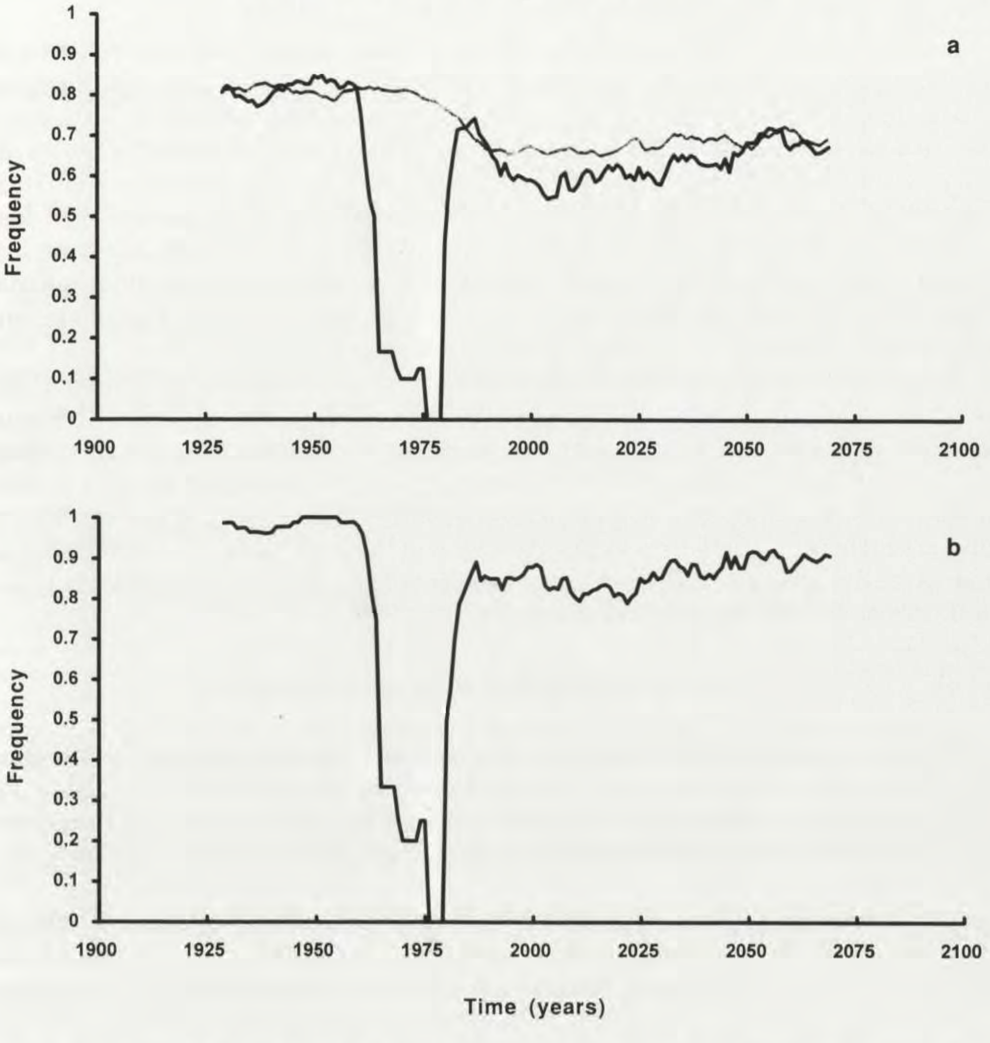

Fig. 4. Frequency of the tusk allele (a) and frequency of tuskers (b) among reproductive males as predicted by a short-term simulation (1930–2070) for the Periyar Tiger Reserve. Female mortality was assumed to be 5%, makna mortality to be 7%, and tusker mortality to be 7% as well (except for time period from 1970 to 1980, where it was assumed to be 50%). In (a) allele frequencies are given for both sexes (dark for males, shaded for females).

impact on frequencies of tuskers has been rather small. Until the end of the 19th century the mortality of tuskers was about 8% as compared to some 7% in maknas. The dominant inheritance model with sexual selection predicts a stable proportion of tuskers in the population (Fig. 3), once again in accordance with historical data. Hence, a selective advantage of about 40–50% counteracts the slightly higher mortality of tuskers. Assuming dominance without sexual selection, 1% additional mortality is sufficient to drive the tusk allele to extinction within a period of 2 000 years. If the tusk allele is simulated to be recessive it survives, but contrary to historical data for southern India the frequency of tuskers declines significantly.

But how can we exclude the remaining possibility of recessive inheritance of the tusk allele in combination with sexual selection towards tuskers ? To evaluate this, we simulated the population from southern India, before man started to hunt selectively. The model predicts that the selective advantage of tuskers will lead to the extinction of the makna allele, if the latter is dominant. On the contrary, when the tusk allele is dominant and abundant, sexual selection against maknas is overriden by drift processes due to the low frequency of the makna allele, and the makna allele may survive for thousands of years.

In summary, the results of all applications of the simulation model support the assumption of a dominant inheritance of the tusk allele in conjunction with sexual selection in favour of tuskers. However, this only holds for a selective advantage of about 40–50%. A higher selective advantage would no longer cause a decline of tuskers in the simulated population from southern Sri Lanka. A lower selective advantage, however, will lead to the extinction of the tusk allele in that population, and cause a decline of tuskers in the simulated population of southern India. Both cases are contrary to the census data.

Are tuskers doomed to extinction?

In the foregoing sections we have shown that (1) when using elephants, man has always preferred tuskers, (2) selective hunting and capturing frequently led to a decrease of tuskers in wild-living populations, (3) the impact of selective hunting and capturing was highest in isolated populations (eg Sri Lanka), (4) a loss of tuskers is not necessarily associated with a decline of population size, (5) selective removal of tuskers for protecting a maximum wild-living male population resulted in an increase of maknas, (6) unselective capturing of large numbers of elephants did not change the tusker-makna-ratio, (7) the assumption of a dominant inheritance of tusks in combination with slight sexual selection is corroborated by historical data. Reasons for a decline of tuskers in wild-living elephant populations can thus be well documented. Based on this information, it should be possible to provide some predictions as to the future development of tusker-makna-ratios in particular populations.

The example from Mahaweli has shown that continuous reduction of tuskers finally resulted in the complete absence of tuskers. Given this situation the population practically protects itself from further poaching. From a less fatalistic point of view concerning the biological significance of tuskers in present-day populations of Asian elephant, they should be protected by all means.

The mainland population still harbours enough tuskers to regain this character even in populations heavily affected by poaching. As demonstrated in the short-term simulation for the Periyar Tiger Reserve (Fig. 4), even a complete lack of tuskers does not necessarily mean that the relevant allele is also exterminated.

In fact the tusk allele has survived in the females, which are thus also shown to play an important role for the development of a particular phenotype in males.

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