Table 1. Fission track ages of Rio Hondo obsidians from Columbia (Thermal neutron fluence $F = 3.512 \times 10^{15}$ n/cm^2)

| Sample | Track density (per cm$^2 \times 10^4$) | | Fission track age (Ma) $\pm 1\sigma$ |
	ρ_s (n_s)	ρ_i (n_i)	
RH-1	0.573 (85)	31.25 (821)	3.87 ± 0.42
RH-2	0.559 (79)	30.87 (736)	3.82 ± 0.42
RH-3	0.587 (90)	32.69 (756)	3.79 ± 0.40

Mean fission track age $= 3.83 \pm 0.42$ Ma (Figures in parentheses show the number of tracks counted).

microscope. The track density in the standard glass dosimeter was used to estimate the neutron fluence.

Fission track ages are calculated using the simplified version of age equation[13]

$$T = \frac{\rho_s \sigma \, IF}{\rho_i \lambda_f},$$ (1)

which reduces, on substitution of values of σ (582×10^{-24} cm^2), $I(7.26 \times 10^{-3})$ and λ_f $(7.03 \times 10^{-17}$ yr$^{-1})^{14}$, to

$$T = 6.01 \times 10^{-8} \frac{\rho_s}{\rho_i} F,$$ (2)

where ρ_s and ρ_i denote recorded fossil and induced track densities respectively and F, thermal neutron fluence during irradiation.

Fission track ages of obsidian artefacts from Rio Hondo archaeological site near Popayan in Columbia are listed in Table 1. The statistical counting error, 1σ, calculated on the basis of fossil track counts is also given. The mean fission track age value of 3.83 Ma agrees well with the source age 3.70 Ma determined for this site[11]. It is obvious that the fission track technique combined with PIXE can prove useful for source identification and provenance studies of obsidian artefacts.

1. Fleischer, R. L. and Price, P. B., Geochim. Cosmochim. Acta, 1964, 28, 755–760.
2. Fleischer, R. L., Price, P. B. and Walker, R. M., Nuclear Tracks in Solids: Principles and Applications, University of California Press, Berkeley, 1975.
3. Durrani, S. A., Khan, H. A., Taj, M. and Renfrew, C., Nature, 1971, 233, 242–245.
4. Bigazzi, G. and Bonadonna, F., Nature, 1973, 242, 322–323.
5. Storzer, D. and Poupeau, G., C. R. Acad. Sci. Paris, 1973, 276, 137–139.
6. Miller, D. S. and Wagner, G. A., Nucl. Tracks, 1981, 5, 147–155.
7. Yegingil, Z. and Goksu, Y., Nucl. Tracks, 1982, 6, 43–48.
8. Virk, H. S., Mineral. J. (Japan), 1986, 13, 34–38.
9. Virk, H. S., Singh, G. and Kaur, S., Nucl. Tracks Radiat. Meas., 1988, 15, 719–722.
10. Virk, H. S., Curr. Sci., 1977, 46, 583–585.
11. Bellot-Gurlet, L., Calligaro, T., Dorighel, O., Dran, J-C., Poupeau,
G. and Salomon, J., Int. Assoc. Obsidian Studies Bull., 1996, 16, 3–7.
12. Suzuki, M. and Tomura, K., St. Paul's Rev. (Japan), 1983, 4, 99–110.
13. Virk, H. S. and Koul, S. L., J. Phys. Earth, 1977, 25, 177–186.
14. Roberts, J. H., Gold, R. and Armani, R. J., Phys. Rev., 1968, 174, 1482–1484.

Asian elephants with longer tusks have lower parasite loads

Milind G. Watve and R. Sukumar

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

The Hamilton and Zuk hypothesis[1] that the intensity of male ornamentation allows females to assess a male's ability to resist parasites has been much debated recently[2–12]. Much of the empirical work to test this hypothesis has been with insect[2], fish[3,4], reptilian[5] or avian[6–9] hosts. In a southern Indian population, we show that the length of tusks of male Asian elephants (Elephas maximus), corrected for differences due to age, is significantly negatively correlated with intestinal parasite loads. The less aggregated distribution of parasites in this elephant population, as compared to other mammalian species, indicates that ivory poaching may have already selectively removed a significant proportion of parasite-resistant individuals. Ivory poaching which targets larger-tusked elephants may thus affect the health status of the population.

FREELAND[13] suggested that mate choice by females may be related to parasites and pathogens carried by males. Hamilton and Zuk[1] further developed the hypothesis that host-parasite coevolutionary cycles might drive the evolution of female preferences for extreme male displays. Males carrying genes for resistance to parasites will be healthier and in a better condition to develop expensive secondary sexual characters. By preferring such males, a female ensures 'good genes' for her offspring. Unlike other 'good gene' hypotheses, however, the resistance genes will be constantly changing since the parasites are also evolving, and thus the system remains dynamic maintaining the importance of female choice.

Negative correlations between parasite loads and secondary sexual characters have been shown in invertebrate, fish, reptilian and avian systems[2-9]. In a mammalian system, Folstad et al.[14] found that experimental removal of parasites, through antihelminthic treatment, in female reindeer (Rangifer tarandus) did not increase antler length but increased antler symmetry. We have examined the length of tusks in male Asian elephants in relation to their intestinal parasite loads.

We have been studying the ecology of elephants in southern India since 1980[15]. Our study on mammalian parasites[16,17] was carried out in the Mudumalai Wildlife Sanctuary, a 321 km[2] reserve which is part of a much larger elephant range in southern India. The vegetation in Mudumalai changes from tropical moist deciduous forest in the west through dry deciduous forest to dry thorn forest in the east, corresponding to a gradient in rainfall from 1800 mm to about 700 mm per annum. The density of elephants in the reserve is about 3 individuals/km[2] (ref. 18). As with most other reserves in southern India, the elephants of Mudumalai have also suffered from poaching of males for ivory[15]. Consequently the ratio of adult (> 15 years) male to female has changed from about 1 : 5 in 1981 to about 1 : 15 in 1996 (unpublished data).

Wild elephants at Mudumalai were sampled by collecting fresh defecations during 1990–92 and 1994–95. Elephants were identified, whenever possible, based on the characteristics of their tusks, ears, tails and other prominent marks, and photographs of side profiles were taken for measuring tusk length. These elephants were followed until fresh dung could be collected. The approximate age of the animal was determined by its estimated height, ear foldings, and thickness of the tusk at its base[19]. The photographs were enlarged for better resolution, and the actual tusk length along the curves determined by comparison to the height of the animals.

Densities of helminth propagules in the faecal samples were determined by a quantitative modification of the sedimentation flotation method. Parasite ova from weighed quantities of dung samples were concentrated by zinc sulphate density gradient centrifugation and all the ova floating to the top counted[16,17]. Elephants in the study area showed a high prevalence of parasites as compared to other herbivorous mammals of the study area, although the species richness was low[17]. The parasite fauna was dominated by nematodes of the genera Quilonia, Murshidia and Decrusia. The estimated faecal output of nematode eggs per day varied from zero to twenty million. There was a significant difference in parasite loads in the elephant population between seasons, with the dry season loads being significantly higher than the wet season loads (median loads of 25 and 9 respectively; $n1 = 39$, $n2 = 60$, $T = 1547$, $p < 0.01$). Since the faecal samples from bull elephants were also collected in different seasons, the seasonal differences were controlled by subtracting the seasonal and overall population median difference from each of the samples.

Tusks grow throughout the life of a male Asian elephant, although the rate of growth slows down after 30 years[19]. We constructed a standard growth curve of tusks (Figure 1) by the following procedure. For a given population, the girth of tusks of an individual is known to be a reliable indicator of age[19,20]. The tusk length, on the other hand, is much more variable. The relationship between circumference of tusks at the lip line (TC) and age (t in years) is given by: $TC_t = 43.4 \{1 - \exp[-0.064t]\}$ cm for Asian elephants in southern India[18]. We took measurements of tusk length (TL) and tusk circumference (TC) of 158 pairs of tusks from museum specimens and post mortem examinations of wild elephants. After determining age from circumference, we plotted tusk length versus its estimated age (Figure 1). The following equation offered the best fit to the data, $TL (cm) = -57 + 130 \log (t)$

The deviation in tusk length of individual wild bulls from the standard curve was plotted against the parasite propagule densities (Figure 2). Faecal samples from 38 tuskers (> 10 years of age) representing at least 26 distinctly identified bulls were analysed. Two of these identified bulls were sampled more than once. Some of the unidentified bulls may have been different individuals,
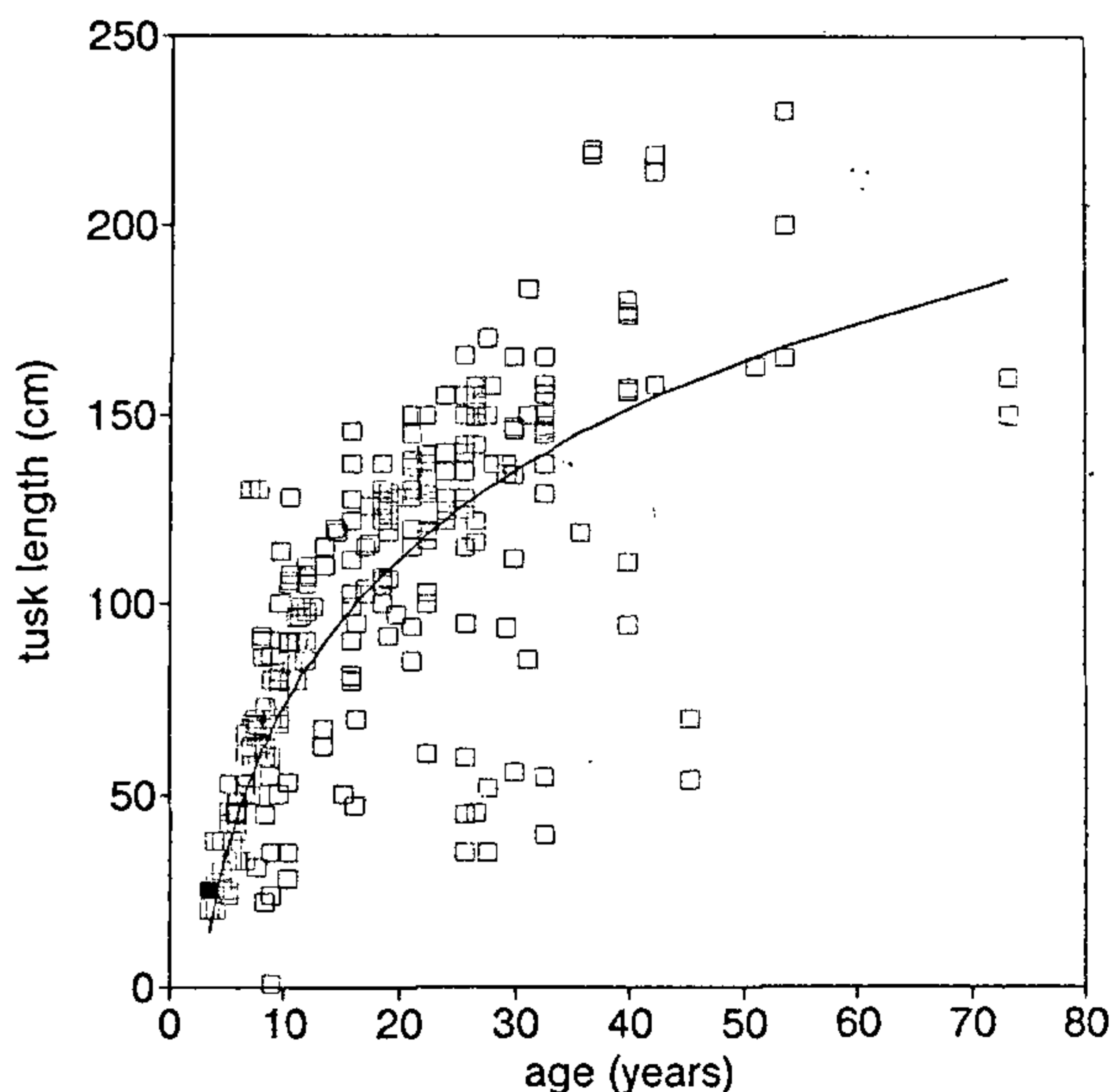

Figure 1. Tusk length in male Asian elephants as a function of age. An equation for the best fit line was obtained by fitting a linear regression of tusk length on a log transform of age ($r = 0.78$). The equation gives a curve on a linear axis. This curve was used as the expected tusk length for a given age class. The modal tusk length for each age class is above this curve. A number of individuals having substantially smaller tusks tend to pull down the best fit line.

while others may have been sampled repeatedly. A significant negative correlation between tusk length deviation and parasite density was obtained using Kendall's Tau (Tau $= -0.255$, $p < 0.01$). Statistical significance is not lost by omitting data from repeated sampling of identified bulls. Our analysis did not include tuskless bulls.

The correlation is compatible with, although not necessarily a substantial proof of, the Hamilton and Zuk hypothesis[1]. Tusk growth may be affected by genetic as well as environmental variables and our data suggest that parasite loads may be one of the important factors. One of the limitations of our data is that they represent a one time sampling for parasite loads, which may not reflect the real parasite burden experienced by the bull
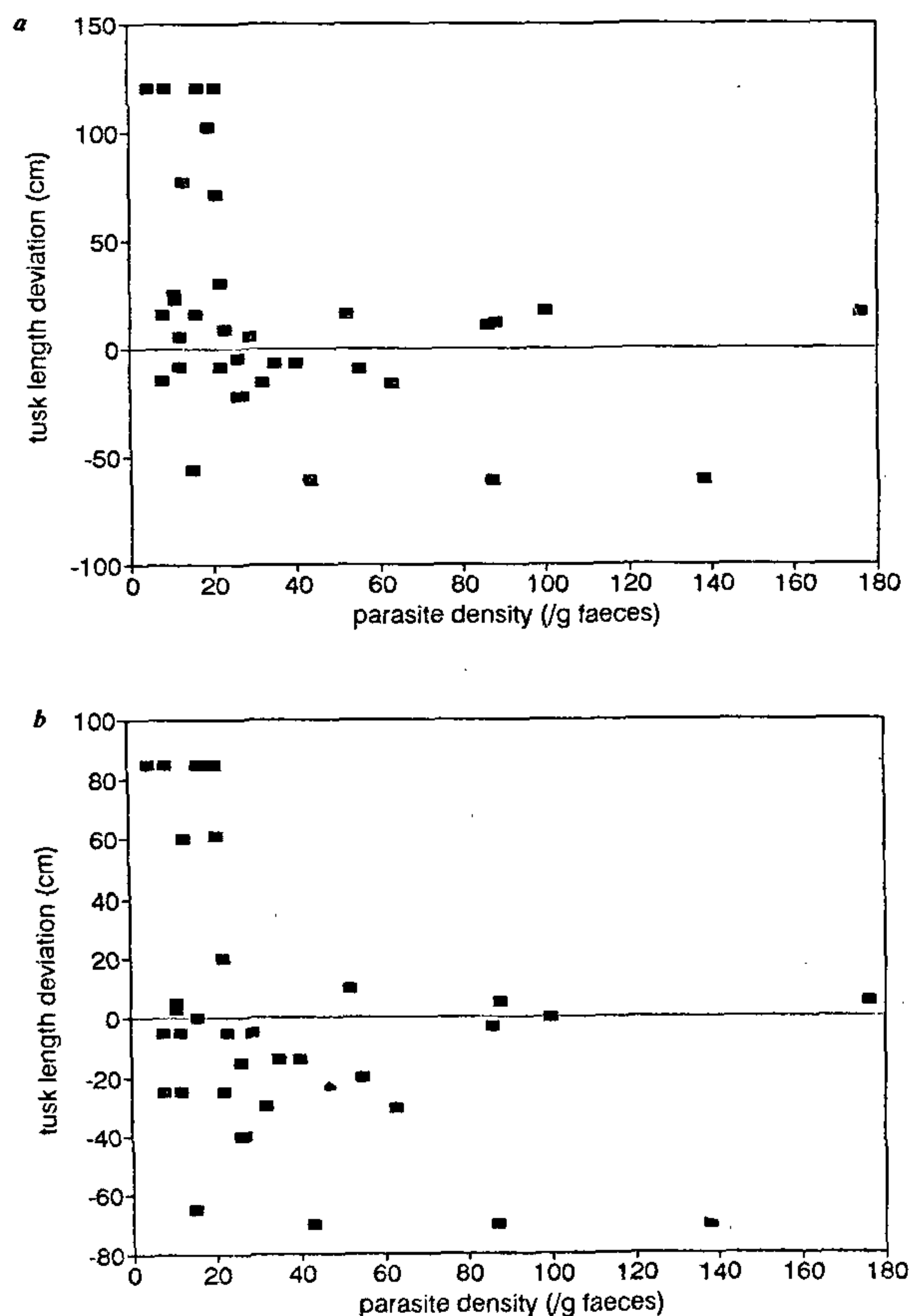

Figure 2. Correlation between tusk length deviation (from the expected) and parasite loads in male elephants. *a*, Deviation from the best fit line. *b*, Deviation from the modal tusk length.

The extreme outlier on the right was a bull in *musth* condition for at least three weeks before sampling. The food intake reduces considerably during *musth* resulting in an apparent increase in density of parasite ova. The negative correlation is significant including this individual. A possible correction for *musth* condition will shift the point to the left, strengthening the correlation further.

during the entire period of tusk growth. It is also likely that parasite loads during a certain age is more important for tusk growth. We observed, however, that two of the identified animals that were sampled repeatedly over a period of five years showed much lower variation (SD $= 11.0$) in parasite propagule densities than the population variation (SD $= 33.3$). One time sampling of other animals therefore can be considered fairly representative.

Earlier works on parasite loads in relation to sexual selection, have considered different types of parasites including blood parasites[1,21], coccidians[22], ciliates[4] and gregarines[2]. These parasites multiply for several generations within the host body. Only certain types of parasites can be involved in coevolutionary cycles, leading to sexual showiness. Parasites ideally suited are of the medium virulence, chronic type which are likely to produce coevolutionary cycles long enough to create average positive parent–offspring fitness correlations[1]. Too short a cycle may produce negative correlations, while parasites that can multiply within a host individual will probably evolve too fast and may not be suitable for this model. The external life-cycle parasites such as the visceral helminths, on the other hand, must have life cycle stages outside the host that would invade any host individual again. For such parasites, selective pressures will operate to overcome not the genotype of an individual host but the most prevalent genotype in the host population. These are the parasites expected to lead to coevolutionary cycles of appropriate duration and therefore should be the parasite group of choice.

Thomas et al.[23] point to the possibility of a negative correlation between parasite loads and male showiness being a fallacy. Parasitism can be negatively correlated with host age while male showiness and female choice covary positively with age. This bias is unlikely in our data because we considered the deviation from expected tusk length for a given age, and also because elephants parasite loads in the study area did not vary significantly with age. For a sample of 184 elephants of all ages and both sexes tested during 1990–92 in the study area, no relationship was observed between dung bolus diameter (a simple measure of age class) and parasite loads[16].

The ecological and evolutionary role of tusks in elephants is debatable. Tusks may play a role in obtaining nutrition (debarking of trees, for instance), in defense against predators, in male–male competition, and may also act as a secondary sexual character influencing female choice of mates. Even when both the sexes possess tusks, as in the African elephant (*Loxodonta africana*) or the extinct mastodon (*Mammut americanum*), there is sexual dimorphism for tusk size with the males having larger tusks than do females of corresponding age[20,24]. Beyond a certain size, the tusks may also become

a handicap (heavy, long tusks may slow the mobility of the individual, while tusks which cross at their tips may actually hamper the use of the trunk in feeding). The tusks can thus be potential candidates for Zahavi's 'handicap principle'[25], according to which females may actually prefer males exhibiting a 'handicap', because an exaggerated secondary sexual character which reduces a male's chances of survival also acts as a signal of genetic quality. In elephants the question as to whether females choose males with longer tusks still remains unanswered. Female African elephants are known to choose larger and older bulls[26,27] and older bulls generally have longer tusks[20,28]. A similar choice may exist for longer tusked bulls in a given age class. Our data show that, while short-tusked males may have either low or high parasite loads, the long-tusked males almost invariably have low parasite loads. Females choosing long-tusked males would thus ensure a parasite-resistant mate.

A negative correlation between tusk length and parasite loads also has implications for conservation. The high incidence of poaching of African elephants[29,30] and Asian elephants[15] in recent decades may thus have made impacts more serious than just lowering total population sizes[29] or genetically effective population sizes[15,31], causing demographic changes, or randomly eroding the genetic variation in a population. Ivory poachers tend to preferentially target elephants with longer tusks and in the process may be selectively eliminating genes for resistance to parasites or diseases from the population. Such a process can be expected to affect the distribution of parasite abundance among the host population.

Parasite distributions in a population are known to be highly skewed with a large number of individuals carrying few or no parasites and a few individuals carrying large loads[32-35]. In the study area, other herbivorous mammals such as chital (*Axis axis*) and sambar (*Cervus unicolor*) showed typically skewed distributions[16]. Parasite-free individuals constituted the modal class in these species. There were very few elephants in the parasite-free class (Figure 3). Elephant droppings had a mean parasite propagule density of 19 as compared to 7 of chital and 2.8 of sambar. The shift in the modal class for elephants may not be just an effect of the higher mean value. Two other mammalian hosts in our study area, the omnivorous sloth bear (*Melursus ursinus*) and the carnivorous dhole (*Cuon alpinus*), had parasite-free individuals in spite of having much higher mean parasite densities (130 and 45 respectively).

The positive shift in the modal class of parasite frequency distribution in the elephant population may well be the consequence of selective poaching of tusked males (presumably larger tusked) in this class (parasite resistant). When a negative binomial is fitted to the parasite frequency distributions, the parameter k is rela-
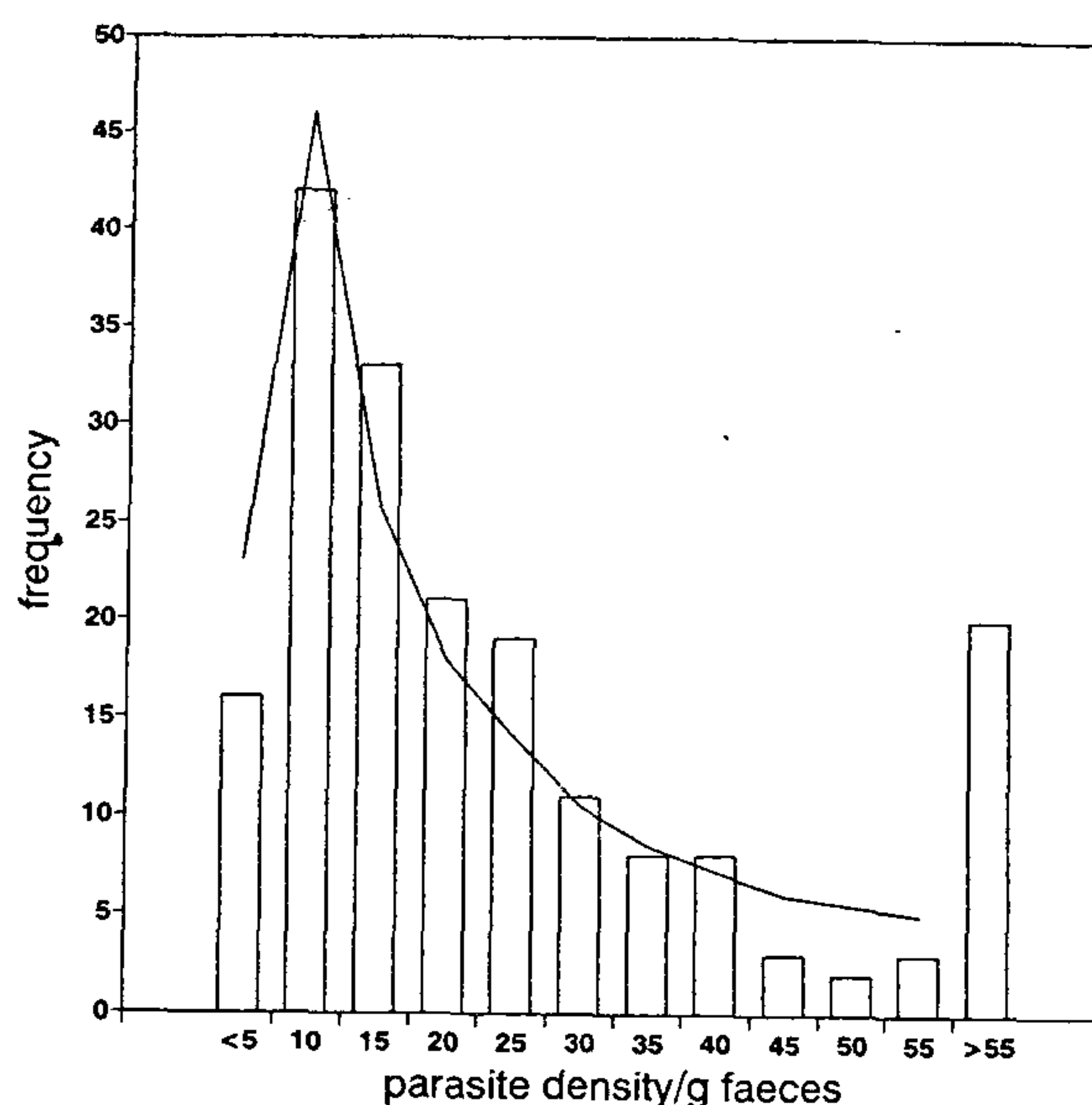

Figure 3. Frequency distribution of faecal parasite propagule densities in the elephant population. The line represents the fitted negative binomial distribution. Parasite distributions are known to be generally positively skewed, with parasite-free individuals forming the modal class. In the case of our study population there is a distinct depression in the parasite-free class. Selective removal of parasite-resistant genes from the population, for several generations may result in such a distribution.

tively low for chital (0.3–0.9 annual range), sambar (0.4), sloth bear (0.4) and dhole (0.28). For elephants the parameter k ranged from 0.5 to 1.83 in different seasons. Higher values of k indicate less aggregated distribution of parasites. Selective poaching for several generations may be one of the reasons for the peculiar distribution of parasites in elephants. A high degree of aggregation is known to stabilize the host–parasite dynamics[34,35]. Populations with less aggregated distributions may become more vulnerable to population depressions from parasitic diseases. Moreover, with the loss of resistance genes from the population, species of parasites which have existed in an endemic state of low virulence for several generations may become a serious health problem. The spate of ivory poaching that swept through Africa and Asia in recent years has to be viewed in this light.

1. Hamilton, W. D. and Zuk, M., *Science*, 1982, **218**, 384–387.
2. Zuk, M., *Behav. Ecol. Sociobiol.*, 1987, **21**, 65–72.
3. Kennedy, C. E. J., Endler, J. A., Poynton, S. L. and McMinn, H., *Behav. Ecol. Sociobiol.*, 1987, **21**, 291–295.
4. Milinski, M. and Baker, T. C. M., *Nature*, 1990, **344**, 330–333.
5. Ressel, S. and Schall, J. J., *Oecologia*, 1989, **78**, 158–164.
6. Moller, A. P., *Ecology*, 1990, **71**, 2345–2357.
7. Moller, A. P., *Evolution*, 1990, **44**, 771–784.
8. Moller, A. P., *Anim. Behav.*, 1991, **41**, 723–730.

9. Hoglund, J., Alatalo. R. V. and Lundberg, A., *Behav. Ecol. Sociobiol.*, 1992, **30**, 71–76.
10. Howard, R. D. and Minchella, D. J., *Oikos*, 1990, **58**, 120–122.
11. Borgia, G. and Collis, K., *Behav. Ecol. Sociobiol.*, 1989, **25**, 445–454.
12. Ligon, D. L. and Zwartjes, P. W., *Anim. Behav.*, 1995, **49**, 117–125.
13. Freeland, W. J., *Biotropica*, 1976, **8**, 12–24.
14. Folstad, I., Arneberg, P. and Karter, A. J., *Oecologia*, 1996, **105**, 556–558.
15. Sukumar, R., *The Asian Elephant: Ecology and Management*, Cambridge University Press, New York, 2nd edn, 1992.
16. Watve, M. G., Ph D. thesis, Indian Institute of Science, Bangalore, 1992.
17. Watve, M. G. and Sukumar, R., *Proc. Natl. Acad. Sci. (USA)*, 1995, **92**, 8945–8949.
18. Varman, K. S. and Sukumar, R., *J. Biosci.*, 1995, **20**, 273–287.
19. Sukumar, R., Joshi, N. V. and Krishnamurthi, V., *Proc. Indian Acad. Sci. (Anim. Sci.)*, 1988, **97**, 561–571.
20. Pilgram, T. and Western, D., *Biol. Cons.*, 1986, **36** 39–52.
21. Boyce, M. S., *Am. Zool.*, 1990, **30**, 263–270.
22. Buchholz, R., *Anim. Behav.*, 1995, **50**, 929–943.
23. Thomas, F., Renaud, F., De Meeus, T. and Cezilly, F., *Oikos*, 1995, **74**, 305–309.
24. Fisher, D. C., in *The Proboscidea: Evolution and Palaeoecology of Elephants and their Relatives* (eds. Shoshani, J. and Tassy, P.), Oxford Univ. Press, Oxford, 1996, pp. 296–315.
25. Zahavi, A., *J. Theor. Biol.*, 1975, **53**, 205–214.
26. Moss, C., *Behaviour*, 1983, **86**, 167–185.
27. Poole, J. H., *Anim. Behav.*, 1989, **37**, 842–849.
28. Laws, R. M., *East Afr. Wild. J.*, 1966, **4**, 1–37.
29. Poole, J. and Thomsen, J. B., *Oryx*, 1989, **23**, 188–189.
30. Western, D., *Tree*, 1987, **2**, 343–346.
31. Sukumar, R. in *A Week With Elephants* (eds Daniel, J. C. and Datye, H.), Bombay Natural History Society, Bombay and Oxford Univ. Press, New Delhi, 1995, pp. 279–288.
32. Crofton, H. D., *Parasitology*, 1971, **62**, 179–193.
33. Keith, I. M. and Keith, L. B., *J. Wild. Dis.*, 1986, **22**, 349–363.
34. Anderson, R. M. and Gordon, D. M. *Parasitology*, 1982, **85**, 373–398.
35. Anderson, R. M., *J. Anim. Ecol.*, 1991, **60**, 1–50.

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