HEALTH AND SEXUAL SIGNALS OF MALE ASIAN ELEPHANTS (*Elephas maximus*) IN NAGARAHOLE NATIONAL PARK, SOUTHERN INDIA

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BY
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CERTIFICATE

This is to certify that Cheryl Nath of the Wildlife Institute of India has carried out an original piece of research work titled "Health and sexual signals of male Asian elephants (Elephas maximus) in Nagarahole National Park, Southern India" in partial fulfilment of the M.Sc (Wildlife Science) degree of Saurashtra University. These investigations were carried out under my supervision at the Wildlife Institute of India from November 1998 to June 1999. I also certify that this work has not been submitted for any other degree of any university.

Date: 18'06'99

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SUMMARY

Male Asian elephants (Elephas maximus) were studied at Nagarahole National Park, southern India from November 1998 to May 1999. Information was collected on at least 30 identified individuals for investigation of the possible use of musth and tusk length by males as signals of health and genetic fitness to female elephants.

This study followed an earlier study by Watve and Sukumar (1997) which showed a significant negative correlation between tusk lengths and parasite loads in male elephants of the Mudumalai Wildlife Sanctuary, southern India. In this project, musth was studied in addition to tusk length as a possible indicator of good health. It was hypothesised that musth and tusk length in male elephants would be related to better health and body condition and hence could potentially be considered as signals of better genetic quality, within the framework of Zahavi's theory of honest signaling (1975, 1977) and Hamilton and Zuk's theory of heritable true fitness (1982), respectively. The indicators of better health and body condition used were a subjectively scored body condition index (BCI) and a quantitative assessment of intestinal helminth parasite density (parasite load).

Individuals were identified by a combination of several physical features, photographic records were obtained for height and tusk length measurement and information was collected on body condition, parasite loads, musth intensity and social interactions.

The following interesting results were obtained:

1. Individuals exhibiting signs of early musth had significantly better body conditions and lower parasite loads than individuals exhibiting no signs of musth.
2. Longer tusks were not significantly correlated with better body condition, lower parasite loads or musth in this study.
3. Dominance behaviours recorded in dyadic interactions among male elephants indicated that dominance was associated with musth, height of the animal and tusk length in a high percentage of interactions (100%, 89% and 78%, respectively).

The significant association between early musth and better body condition as well as between early musth and reduced parasite loads indicates that male elephants may require better health in order to attain musth. Hence musth appears to be a potential honest signal of better than average health, in males which are able to attain this condition. This information may be used by female elephants in choosing mates. Social interactions among males corroborated this speculation by showing that musth and height in male elephants may be important determinants of dominance, which in turn may influence female choice and reproductive success. Limited samples of male-female interactions suggested that females discriminate between different males, and that male-male dominance interactions may influence female choice. However, small sample sizes limited the extent to which these findings could be extrapolated in this and other elephant populations.

1. INTRODUCTION

1.1 Sexual selection and signals

Differential investment in sexual reproduction by males and females in most species appear to have caused the evolution of interesting adaptations by each sex with respect to the other. One of the important bodies of theory in evolutionary ecology is that of 'sexual selection' which formally originated in Darwin's (1859) *The descent of man, and selection in relation to sex.* There has been much debate on how to separate the effects of natural selection from those of sexual selection and whether the latter is, in reality, as powerful a selective force as Darwin had thought it to be (Mayr 1972). However, several recent reviews have argued in favour of the power of sexual selection in deciding the fate of several traits, and have elaborated on the possible mechanisms by which it may have evolved (Emlen & Oring 1977, Short 1994, Reynolds & Harvey 1994). Whatever may have been the underlying processes, selection of mates of one sex (usually males) by the opposite sex (usually females) (Mayr 1972) has had profound consequences for both.

Of particular interest is the evolution of certain phenotypic traits to apparently unnecessary, unreasonable, or even maladaptive extremes, from the point of view of the forces of natural selection acting on those traits or on the individuals bearing them. Most commonly, exaggerated development of traits occurs in males only (Kirkpatrick & Ryan 1991), such as the long tail plumes of birds, bright and showy colours of butterflies and the large, elaborate antlers of many deer. Such exaggerated development of traits has been attributed to consistent (heritable) choice of extremes by females (Fisher 1930) and to the use of extreme phenotypic characters as signals of genetic quality by males (Zahavi 1975, Hamilton & Zuk 1982).

The extreme character traits mentioned above are often considered secondary sexual character traits in males. These have good potential to serve as signals to females due to their higher variances in comparison to other traits (Moller 1994). This large range of variance exhibited by secondary sexual character traits (sometimes referred to as male ornamentation) may provide the basis for discriminatory choice by females. The use of male secondary sexual character traits to signal differential genetic quality has enormous significance for sexual reproduction under severely competitive conditions. An important theory regarding the evolution of male secondary sexual characteristics as "honest" signals of advertisements of genetic quality is known as the theory of signal selection (Zahavi 1987). By this theory, females chose mates from among diverse males by comparing some aspect of honest advertisements produced by the latter. The advertisements can be considered honest if they can be produced by only some, and not all the individuals of the population (in this case, the male population) under different conditions. Within such a system, only those males which are capable of producing the advertisement or of producing differentially better advertisements are assured of being chosen by females and hence of enjoying better reproductive fitness.

Selection of mates by females is the complementary aspect of sexual signaling by males. Females who choose mates based on information about some aspect of male "quality", which can be compared objectively across all available males, would tend to benefit from better genes for their offspring. However, honesty in signaling, by all males, is a necessary criterion to ensure that the exercise of signaling and signal-based choice become evolutionarily stable. This system is well suited to explain female choice in animals not exhibiting paternal care of offspring, such as elephants. In this case, inheritance of paternal ability and quality by the resulting offspring become critically dependent on female choice, which may, in turn, rely heavily on signals of quality by males. Improved female discriminatory ability is constantly demanded and would benefit from increasingly finer resolution between competing male signals. Simultaneously, competing males across populations and successive generations would benefit from marginal increases in the magnitude of their signals (within biological limits), given female fidelity to a particular signal across populations and generations. This then, could form a basis for directional selection, runaway selection and evolution of male secondary sexual character traits to apparently maladaptive extremes.

Several mate selection theories have been based on extreme character development as sexual signals by males. I have chosen the following two theories to be examined in the context of Asian elephant (Elephas maximus) mating:

1. Zahavi's (1975, 1977) **theory of honest signaling** by use of exaggerated secondary sexual characters (better known as the Handicap Principle) has been gaining support in recent years as a plausible way of explaining extreme character development in males (Grafen 1990, Maynard Smith 1991). According to this theory, a trait may serve as an honest signal of good genetic quality if it plays no role in the survival of the individual but instead confers a handicap in the survival struggle, and is extremely deleterious or lethal for an individual of poor genetic

quality to produce or maintain. Such a trait could, theoretically, serve as a reliable indicator of good genetic quality to a member of the opposite sex, and hence would tend to be favoured by the process of sexual selection.

2. The Hamilton-Zuk (1982) **theory of heritable true fitness** stated that exaggerated development of a secondary sexual character could occur only if the individual has high genetic ability to resist chronic parasite infections. Thus an exaggerated display trait may serve as a true indicator of this aspect of genetic quality, and may be used by females in choosing males. Such a character tends to confer selective sexual advantage to its bearer if it is heritable. This theory is more specific than the one above, and applies strictly to genetic ability to resist chronic parasite infections.

1.2 Role of signals in Asian elephant mating strategy

During this project, I studied the use of secondary sexual characters by identified male elephants as honest signals of some aspects of their genetic quality. Identification of individual elephants was expected to allow for repeated samplings of the same individuals over the study period for intra and inter-individual comparison.

The use of secondary sexual characters as honest signals of quality by male elephants was first investigated by Watve and Sukumar (1997), in their study of tusked male Asian elephants of Mudumalai Wildlife Sanctuary in southern India. Their study showed that tusk length was significantly negatively correlated with intestinal helminth parasite loads and hence tusk length was suggested to serve as an honest signal of quality. Since very long or crossed tusks may impose a heavy burden or hinder trunk movements when feeding, it was further suggested that longer tusks were also potential candidates in support of Zahavi's Handicap Principle.

Among elephants, we can reasonably expect the evolution of discriminatory choice of males by females, and the requirement of effective sexual signals in males, due to the following life history adaptations of the species. (Several life history parameters are derived from studies on African elephants, Loxodonta africana, due to the paucity of scientific data on Asian elephants. Little difference is expected in the same parameters for Asian elephants):

1. Investment in reproductive effort and post-natal parental care is vastly different between male and female elephants. Whereas the males provide only sperm, the females provide eggs, care and nourishment to the growing embryo for 20-22 months and post-natal care to calves up to the age of two years (Poole 1989b). Hence it would probably benefit females to choose males whose genes tend to maximise the chances of proper embryonic development, calf survivorship and reproductive fitness of the adult offspring.

2. Whereas female elephants tend to vary little in their individual fertilities, male elephants tend to differ widely in theirs (Poole 1989b). The reason for high variance in male reproductive success may be the polygynous nature of elephant societies, which often leads to a high proportion of all matings in a season or year being carried out by a few dominant ('high quality') individuals (Poole 1989a, 1989b, Poole & Moss 1981). This would tend to selectively favour the development of sexual signals that effectively convey the message of good quality genes in dominant males.

3. Lack of synchrony in fertile or rut periods of male and female elephants as well as environmental factors such as resource dispersion may have been responsible for the absence of lekking systems in elephants. Male elephants may experience musth

(heightened sexual activity period) for varying lengths of time during any season in a year (Poole 1987, 1989a), just as females appear to come into oestrus once every 16 weeks (Hess et al 1983, Poole 1989b). As a result, efforts are spent on signaling to and searching for mates (Poole & Moss 1989). Signals which tend to optimise the effort required to bring together potential mates would tend to be selected over time (Poole 1989b).

The following two traits were tested as possible sexual signals of male elephants, functioning to advertise positive attributes of genetic quality, within the framework of the theories of mating strategy described above:

1. *Musth - As a signal of handicap.*
2. *Tusk length - As a signal of resistance to chronic parasite infections.*

Although extremely long tusks may serve as a signal of handicap, below a certain length tusks may actually increase the survival of the animal by functioning as digging implements for minerals, for debarking trees, resting the heavy trunk and as a weapon of offence and defence. There is no objective method, at present, by which we could assess the minimum length at which tusks cease to be an advantage and turn into a handicap. Hence I chose to consider the 'phenomenon of musth' (Poole 1987) as an honest signal of handicap, based on the following known effects of musth on African elephants (Poole1987, 1989a):

- The condition of musth is almost solely concerned with sexual reproduction, and only male elephants in exceptionally good health are capable of attaining the condition of musth during a particular season.

- Testosterone levels in the body are elevated to around five times their usual levels (Poole *et al.* 1984, Rasmussen *et al.* 1996). This would serve to reduce the animal's immunity substantially as elevated testosterone levels have been associated with reduced immunocompetence (Folstad & Karter, 1992).

- Male elephants in musth are known to greatly reduce the proportion of time spent on feeding, which usually leads to loss of body condition during this period; furthermore, the greater the length of time spent in musth the higher are the costs in terms of total body condition loss.

- Considerable loss of water, often a critical resource for elephants, results from the practice of dribbling urine continuously while moving, during the period of musth (Poole & Moss 1989). Urine dribbling is thought to warn other males as well as to alert oestrus females who come across the urine path, of the presence of a musth (and hence more dominant) bull in the area (Poole 1989a, 1989b).

Furthermore, whereas tusks may serve as a signal of long term or cumulative adaptation to environmental resources, musth, being expressed for short terms on a regular basis, may provide a more immediate reference on an individual's ability to cope with environmental fluctuations.

The following assumptions were made in order to take up this study :

Assumption 1: The selected traits (musth and tusk length) are heritable. This appears to be a reasonable assumption as both of these are secondary sexual traits which tend to show at least some degree of exaggeration in development beyond that required for survival. Hence they are likely to have evolved to the currently extravagant proportions under the influence of sexual selection.

Support for the assumption that secondary sexual characters selected by females are heritable comes from studies on antlers of male deer, a secondary sexual character which is believed by many to play an important role in mate selection by female deer. Goss (1983) mentions the importance of inheritance and hormonal regulation in shaping antler morphology, while experiments performed by Harmel (1983) on white-tailed deer showed that although diet and nutrition may influence antler growth, genetics are of overriding importance in determining antler presence, length and quality. Further, another study by Scribner and Smith (1990) suggested that genetic heterozygosity is an important characteristic influencing antler growth and size.

Assumption 2: Female elephants exercise mate choice during every encounter and copulation with a male elephant. This assumption is based on long term studies of female African elephants (Moss 1988, Poole 1989b) and is probably applicable in the case of female Asian elephant as well.

Assumption 3: Mate choice by females is based solely on the genetic quality of males, which is indicated by the degree of exaggeration of the selected sexual signals. Although it is difficult to verify this assumption, it has been used in mathematical models of sexual selection (Kirkpatrick 1982, Grafen 1990) which show that heritable characteristics of males, if selected by females over several generations, will become stabilised in those populations under different circumstances. This lends credibility to the assumption that there may be a genetic basis to female choice.

1.3 Relevance of the study

This scientific exploration of wild elephant behaviour and physiology has the following important applied benefits in addition to a possible widening of our understanding of elephant mating strategy.

1. A better understanding of male and female mating strategy has implications for management of elephants with reference to demographic, spatial and resource requirements for maintaining a successfully breeding population in the long term.
2. If appropriate, the males with traits most favoured by females could be given high priority in management planning for elephant conservation areas, in order to promote long term genetic fitness in the protected populations.
3. Important information may emerge regarding the health status of male elephants of the population studied. This would be of use in monitoring the health of male elephants in the future.
4. Demography of males in the population studied can be better understood if identified males of this study are regularly monitored in the future.
5. Few studies have been carried out to date on reproductive behaviours of identified wild male Asian elephants. With the exception of Watve & Sukumar's (1997) and Sukumar's (1989) work, no detailed scientific work involving identified individuals has been carried out in this context. This has left a vacuum in our scientific understanding of a species which has enjoyed close cultural association with humans for almost 4000 years.

1.4 Objectives

The main objectives of this study were to determine the extent to which musth and tusk length are important sexual signals used in Asian elephant mating strategy. More specifically, the aim was to test the relationship between these two secondary sexual character traits and some chosen indicators of genotypic quality in wild male elephants. The indicators of genotypic quality chosen for this purpose were overall external physical (body) condition and internal helminth parasite burden (parasite load or parasite density). The approach used was to test the following relationships:

1. Both these character traits are correlated with the chosen health status indicators in wild male elephants. Thus heightened or prolonged musth and increased tusk length were expected to be characterised by (or correlated with) better body condition and lower parasite load.
2. Both these character traits are correlated with each other and hence may be used in combination as sexual signals.

A subjective composite score called the "body condition index" (BCI) and the helminth parasite propagule density (referred to as "parasite load") per individual were used as indicators of health. Increasing values of both scores were associated with declining health (i.e. declining external body condition or increasing parasite load) in the animals studied. Hypotheses were hence developed in the following manner for testing in the field:

Musth as a signal of handicap: If musth is a true signal of good quality, we would expect body condition to be very good before (or just before) an individual is able to attain and advertise a state of musth. Hence, assuming that musth intensity across individuals reflects comparable states of health and body condition, individuals exhibiting early stages of musth would be expected to have better health indicator values than other individuals. However, we could also reasonably expect that the body condition of an individual would show a declining trend as musth intensity increases, if musth is truly a handicap to the individual. Using subjective scores for musth intensity (musth composite index or MCI) and external body condition (BCI), and objective assessments of helminth propagule densities per individual, the following hypotheses were tested:

H_A 1: Individuals in early musth will have better health indicator values than individuals which did not attain musth during the study period (non-musth individuals);

H_A 2: Health indicator values for individuals during single episodes of musth, will show positive correlation with increasing intensity and duration of musth (where increasing health indicator values indicate deteriorating health, as musth intensity and duration increase. This relied on repeated samplings of identified individuals during single episodes of musth).

Tusk length as an indicator of heritable true fitness: If longer tusks are a signal of higher parasite resistance, then this should be correlated with lower average parasite loads, and with better body condition. The next hypotheses were:

H_A 3: Tusk length will be negatively correlated with average parasite load and with BCI (where increasing BCI and parasite load indicate lower health)

Correlation between the two signals and relationship to social dominance hierarchies: If both, musth and tusk length are positively associated with higher health indicator values, then we can reasonably expect them to be correlated with each other. Thus they may be used together complementarily as signals of overall health and fitness. Further, if health is an important criterion for signaling genetic quality to females, it may also be reflected in male-male dominance interactions. Behavioural signals to females probably play an equally important role in signaling quality, in highly social and intelligent animals such as elephants. Dominance was examined from the viewpoint of sexual signals because elephants tend not to defend territories or food resources. However, when guarding a female mate, the mate as a resource would be of great value to the dominant male (Poole 1989a). Dominance in this context plays a significant role in female choice. Hence the following hypotheses were tested:

H_A 4: MCI and tusk length are correlated with each other

H_A 5: Dominance in male-male interactions are associated with greater ability to come into musth and with longer tusks.

2. STUDY AREA AND ELEPHANTS

2.1 The Park

The study was carried out in the Nagarahole National Park in Karnataka, southern India. This was one of the first notified National Parks in the country and has enjoyed high levels of protection for at least 25 years since achieving National Park status. As a consequence, the populations of many large mammals such as elephants, tigers (Panthera tigris), gaur (Bos gaurus), spotted deer (Cervus axis) and sambar (Cervus unicolor) are among the largest and most secure in the country. The Park is located between 11° 50' – 12° 15' N and 76° 0' – 76° 15' E, sharing borders with the Bandipur Tiger Reserve to its southeast in Karnataka and the Wyanad Wildlife Sanctuary to its southwest in Kerala. The area of the park is 644 km^2, and according to the total count estimate of wild elephants carried out by the Karnataka Forest Department, an estimated elephant population of 1448 animals uses the entire area (Alva 1994). In some areas of the park, the density was estimated to be as high as 3.3 elephants/km^2 (Karanth & Sunquist, 1992). Assuming a low population of adult tuskers in the park (5% to 7% of the total population), and given that I would spend less than 6 months in the study area, I had expected to see 35 - 40 tuskers between November 1998 and April 1999. The study was carried out in the Antharasanthe and D.B. Kuppe Ranges on the eastern side of the Park. The intensive study area used totaled around 100 km^2.

The vegetation types occurring in the study area were mainly dry and moist deciduous with an east-west gradient from drier to wetter types. The park receives most of its rainfall (900-1500mm, Karanth & Sunquist, 1992) during the first monsoon (June-September), and continues to receive smaller quantities at other times, including the second monsoon (October-December) and sporadic showers in April. The eastern side borders the Kabini reservoir, completed roughly around 25 years ago. The clearance of forests and subsequent submergence of land to accommodate the reservoir has had a hidden benefit for wildlife in the Park. During the dry and hot summer months of March-May recession of the reservoir water level exposes extensive grassy banks for grazing ungulates and elephants. In addition, bamboos occur gregariously all along the banks of the reservoir and serve as an important food source at different times of the year.

The main tree species in the study area are deciduous species such as *Anoegeissus latifolia*, *Tectona grandis*, *Lagerstroemia microcarpa*, *Albizia* spp., *Grewia tileaefolia*, *Bombax ceiba*, *Ficus* spp., *Butea monosperma*, *Careya arborea* and *Emblica officinalis*. Shrubs include *Randia* spp., *Ziziphus* spp., *Lantana camara* and *Helicteres isora* among others. Extensive teak plantations and some eucalyptus plantations occupy areas along the banks of the reservoir. *Bambusa arundinacea* and *Dendrocalamus strictus* grow in thick stands along the banks and in more interior areas of the Park.

Wild mammals other than elephants sighted during the study included tiger (*Panthera tigris*), leopard (*P. pardus*), sloth bear (*Melursus ursinus*), wild dog (*Cuon alpinus*), gaur (*Bos gaurus*), sambar (*Cervus unicolor*), spotted deer (*C. axis*), muntjac (*Muntiacus muntjak*), four-horned antelope (*Tetraceros quadricornis*), wild pig (*Sus scrofa*), mouse deer (*Tragulus memmina*), hanuman langur (*Presbytis* entellus), black naped hare (Lepus nigricollis nigricollis) and Indian giant squirrel (Ratufa indica)

2.2 The elephants

The population of elephants in the park was estimated to be roughly 1448 (Alva 1994). This figure is expected to include migratory as well as resident elephants. Between November and December, maximum elephant movement was detected in the Antharasanthe Range between waterholes and along the borders fringing agricultural settlements. Many males as well as small female groups of 3-7 individuals were expected to be concentrating along the Park-human settlement interface in order to capitalise on the high availability of crops (mainly ragi, Eleusine coracana, coconut, Cocos nucifera, banana, Musa paradisiaca, and other fruits and vegetables) just outside the Park boundary. In January and February, when crops were harvested, elephants movement was higher in slightly interior areas, around the man-made waterholes. Males began to frequent the Kabini reservoir banks, feeding on bamboos and submerged vegetation just inside the waterline. Bark stripping by elephants appeared to be more frequent between December and February. During March-April peak elephant activity occurred along the exposed grassy banks of the Reservoir as the water level continued to recede. Many female groups probably converged and formed temporary coalitions, sometimes totaling 50 animals, to graze communally. This may have been an additional attraction for adult males who may have followed the family groups. Interior areas of the Park, frequented during November-February, were almost devoid of elephants after the waterholes began to dry up in late February to early March.

Although the Reservoir area is famous for very large congregations of several hundreds of elephants during April and May each year, this year congregations did not reach such spectacular proportions. The largest agglomerations of elephants seen during this study, until early May, rarely crossed a total of 100 elephants along the banks. Early and heavy rain showers at intervals of 3-4 days throughout the month of April may have been responsible for the absence of very large groupings of elephants by making water, graze and browse available inside the forest. However, elephants stayed closer to the reservoir banks in higher concentrations during March and most of April. During late April a few family groups were seen moving around in the interior areas away from the Reservoir banks. It is not clear whether these elephants had moved west from the Kabini banks or had moved into the study area from other parts of the Park to the north and west.

Data collection was facilitated greatly by the large congregations and tendency of elephants to remain resident on the banks of the Reservoir. Most of the social behaviour sampling was made easy by the good and continuous visibility of elephant interactions at close proximity for long periods of time along the banks during March and April.

3. METHODS

3.1 Identification, ageing and measurement of individuals

Individuals were identified by photographing them and recording details of their tusks, ears, tails, backbone, "handedness" of trunk (or sidedness, as each individual used only one side of the trunk tip consistently when grazing), pink colouration, warts, wounds and bumps. These methods have been successfully used to uniquely identify large numbers of African elephants in the past (Douglas-Hamilton 1975, Moss 1988). For the duration of this study and the number of elephants identified, a combination of all or most of the above features proved satisfactory for accurate characterisation of different individuals. During the study 37 male elephants were positively identified (4 of these were estimated younger than 15 years old). Of these, 30 elephants were used in the analysis (2 below estimated age of 15 years). Eleven elephants were seen in musth, of which data from 10 elephants were analysed.

Ages were estimated in the field by assessing height, tusk thickness at lip level, ear folding at the top edge, temporal depression and body size. Whenever possible the circumference of forefoot prints were recorded as this value doubled gives a rough field estimation of an animal's height (Sukumar, et al, 1988). Photographic records for measurement of height and tusk length were obtained by photographing elephants broadside on and then photographing my field assistant standing in exactly the same spot as a height reference. This method gave an error of 3-5% in repeated photographic encounters. However, the heights measured in this manner were consistently lower than those corresponding to the standard age-height-weight chart for elephants of southern India, established by Sukumar (1989). This bias is possibly an artefact of photography, measurement or subjective age assignments in the field, and is subject to verification in the future by using tamed elephants of known ages and heights. However, for the purpose of this study, absolute heights of individuals were not as important as consistency in the method of height estimation. Since the bias appeared to be consistent across all individuals, the measured heights could be used comparatively in this study.

3.2 Subjective Indexes

Overall body condition was used as a simple proxy for health status. A simple cumulative score of body condition, called the body condition index (BCI) was obtained on each encounter with an animal by scoring visibility of the backbone, ribs, pelvic girdle, pectoral girdle, buccal depression and temporal depression on a scale of 0-3. The scores for each of the physical features was then added up to give an additive BCI score. Older animals are known to show increased facial depressions. Hence the BCI composite index, (BCIC), was divided into the BCI (Body), (BCIB), and the BCI (Face), (BCIF), for better resolution of differences reflecting health, if any. The possible range of values for BCIC was 0 to 18, for BCIB 0 to 12 and for BCIF 0 to 6.

Musth intensity was rated similarly to develop a cumulative musth composite index (MCI, ranging in value from 0 to 9) from the intensity of 3 externally visible features of musth (Poole 1987):

1. *Temporal gland swelling*: ranged from 0-3, depending on whether there was no swelling, the temporal gland area was flush with the skull, the gland was slightly swollen or prominently swollen.

2. *Temporal gland secretion (TGS)*:. A copious discharge of fluid from the swollen temporal gland in male Asian elephants is a sure sign of the occurrence of musth. Rating of this feature ranged from 0-3 depending on the length and width of TGS flow down the side of the face.

3. *Urine dribbling*: This was rated on a scale of 0-3 depending on the rate of passive flow of urine, which is known to be a common feature of musth males, especially during peak musth. Urine dribbling was seen in only two musth males during this study, once as an irregular wetness on the inside of the hind leg, and on another occasion as a complete wetness on the inside of the hind leg of a male in peak musth in pursuit of a female. The actual dribbling of urine as droplets, a thin stream or steady flow, as described in African elephants (Poole 1987), was not seen during this study.

3.3 Helminth parasite assessment

Samples of freshly dropped faeces were collected for quantitative estimation of helminth parasite propagule (eggs or ova) densities, after the method of Watve (1992). 4-8 gms of fresh faeces from identified male elephants were collected and preserved in 10 ml of 10% formalin in the field. These were later filtered to remove fibres and large plant material, and centrifuged at 2000-3000 rpm for 5 minutes to concentrate ova in the pellet. The pellet was then resuspended in 10 ml of saturated zinc sulphate solution and recentrifuged at 2000-3000 rpm for 5 minutes to concentrate ova in the top layer of supernatent solution. An L-shaped wire loop was used to transfer these eggs onto a microscope slide for counting at a magnification of 100x. Identification of parasite ova was carried out by referring to Soulsby 1973, Sloss & Kemp1978 and Watve 1992. Wherever required, additional assistance was provided by Dr. Renukaprasad (Institute for Animal health and Veterinary Biologicals, Bangalore) and Dr. Milind Watve (Pune University).

The main types of parasites identified in this study were:

1. Strongyles and strongyle-like eggs of Class Nematoda (not distinguishable, but probably including Quilonia spp., Murshidia indica and Coniangium spp.) These formed the bulk of the parasite ova counted and ranged in size from 74-89 µm x 35-50 µm.
2. Spirorid nematode, Parabronema spp. 79 x 35 µm.
3. Tapeworm, Anoplocephala spp., 89 x 55 µm.
4. Other large trematode eggs, fluke egg , 220-300 x 80-100 µm.

Total parasite loads per gram of sample were calculated for each individual. This value, representing internal helminth parasite load, was expected to provide a close approximation of the overall parasite resistance of the individual hosts.

3.4 Behavioural sampling

Behavioural sampling of interactions between identified individuals was carried out using mainly focal group sampling (FGS). In FGS continuous monitoring of interacting elephants was carried out by focusing on each individual of the group in turn and recording its behaviour for 10-15 secs (including all actions initiated and received by that individual and its recipient or initiator), before moving on to the next animal. This method ensured that all individuals of the group were represented approximately equally in terms of time, and also maintained a reasonably continuous record of behaviours of all individuals throughout the sampling interval.

Eleven group interactions were analysed for evidence of dominance, musth behaviours and other sexual behaviours. Typical dominance behaviours observed included approach-retreat sequences, use of trunk, tusk and body to push subordinates, and directed threats such as stamping or rubbing the forefoot in mud and "ritualised" throwing of mud over the head while facing the elephant to be subordinated. Musth and sexual behaviours included higher frequency of testing females for receptiveness in addition to the dominance behaviours listed above. Sexual behaviours also included male approaches to and interactions with females. A complete list of behaviours scored (ethogram) is provided in the Appendix.

3.5 Statistical Analysis

All distributions were assumed to be normal and hence parametric statistics such as Pearson's r for correlation, Student's t-tests for difference of means, single factor ANOVA, and the binomial distribution probability test for parametric distributions were used. Wherever significant correlations were obtained with Pearson's r, residuals were examined for unexplained biases.

In order to normalise the tusk length distribution (Sections 4.2.4 and 4.5.2), best fit curves were fitted to the data using the program CurveExpert (version 1.3). Deviations of measured tusk lengths from the standard curve were then used to assess the relationship between tusk length and other parameters.

4. RESULTS

4.1 Details of parameters

The parameters for which data were collected on each individual were identification, height, tusk length, external body condition (BCI), musth intensity (MCI), parasite load (/gm faeces) and social behaviour. It was not possible to collect all types of data from every encounter with elephants, nor to obtain re-sightings of every identified male. However, 17 identified males were re-sighted at least once during the study period and 11 were re-sighted more than once. Fecal samples were collected more than once from 10 individuals. For re-sighted animals, parameter values were averaged for correlation analyses. Details of parameters are in Table1.

Intraindividual variation in health indicator values was found to be high in the case of parasite loads. For 10 individuals which could be sampled more than once, the range of intraindividual variation was from 0.5 to 33.2 /gm, with an average variation of 13.1 /gm. Intraindividual varitation in the case of BCIC was lower, and for 15 individuals which were sampled more than once, the range of intraindividual variation was from 0.25 to 6.0, with an average variation of 2.7.

4.2 Height, age and age effects

4.2.1 Use of height as a proxy for age

Age affects the development of several character traits and is responsible for some proportion of the observed variance across individuals. Since elephant tusks continue to grow throughout the life of an individual (Sukumar, 1989), age would be partly responsible for longer tusks in older males, regardless of their health. It is not known to what extent and manner age affects the ability of males to attain and sustain musth.

Although captive Asian elephant bulls have been known to exhibit signs of musth in their early to mid teens, wild African elephant bulls were seen exhibiting signs of musth only after 20 (Poole1987, 1989a). However, the intensity of musth may be affected by age, simply due to physiological processes not necessarily related to health. These effects of age, if any, had to be eliminated before comparing the two proposed signals with health indicators.

The age of elephants was estimated in the field by using a combination of the following characters: height, thickness of tusks at lip level, folding over of the top edge of the ears, temporal and buccal depressions and overall body size. Elephants were assigned to 5-year age class intervals ranging from 10 to 50 years (8 classes) in the field. Distribution of heights, tusk lengths and tusk widths are shown in Fig. 1 and Table 2 The measured heights of all individuals, when arranged in ascending order, showed good agreement with the subjective field assessments of age. (Pearson $r = 0.85$, $df = 13$, $p < 0.001$) when compared with those of tusk length ($r = 0.61$, $df = 13$, $p < 0.02$) and tusk circumference at lip level ($r = 0.76$, $df = 13$, $p < 0.001$). Hence for the purpose of analyses, height was used to assess age effects in the data.

4.2.2 Age effect on health indicators

Body condition indexes were checked for age effects by Pearson correlation, and by studying scatter plots of average BCIs against height (using height to reflect age, Fig. 2). Significant correlations were obtained for BCIC (Pearson $r = -0.48$, $df = 23$, $p < 0.05$) and BCIB ($r = -0.53$, $df = 23$, $p < 0.05$), reflecting a possible improvement in external body condition with increasing age (reducing BCI indicates better external body condition). However, upon removing all BCI values which were associated with the occurrence of musth, the correlations (r values) between BCIC and height as well as between BCIB and height was reduced to -0.03 and -0.12 respectively. This indicated that external body condition was not related to age when animals were not in musth. Another interesting finding was that facial depressions, approximated by BCIF, were not correlated with height (or age) in musth and non-musth animals.

There was a minor negative linear trend between heights of individuals and their average parasite loads (Fig. 3). However, this was not statistically significant, and was largely an effect of the outlier.

4.2.3 Age effect on musth:

During the study, only males subjectively aged between 25 and 40 years exhibited symptoms of musth. If we grouped the elephants into 10-year age classes, then the modal class for musth males was the 30-40 year class, containing 67% of all musth males seen, and with only 1 out of the 7 males in this class not exhibiting signs of musth. Among males recorded in musth, the average intensity of musth (average MCI) recorded per male , did not show significant correlation with height (Fig. 4).

4.2.4 Age effect on tusk length

Tusk lengths were significantly correlated with heights (Pearson $r = 0.57$, $df = 23$, $p < 0.01$), indicating the strong influence of age on tusk growth (Fig. 5). This was an expected relationship and was eliminated (see section 4.2.5 below) before investigating relationships between tusk lengths and other parameters.

Table 1. Details of data parameters (averaged per elephant).

Parameter	N	Range	Average	Std. Devn.	C.V.
Height (cm)	25	198.7 – 269.8	234.5	19.0	0.08
Tusk length (cm)	25	45 – 127.8	83.6	20.8	0.25
MCI	10	0.5 - 5.5	3.4	1.60	0.53
BCI(Composite)	28	3.38 - 11	7.6	2.15	0.28
BCI (Body)	28	1 - 7	4.4	1.57	0.36
BCI (Face)	28	1 - 5	3.2	0.98	0.31
Parasite (/gm)	30	0.25 – 74.2	12.0	14.5	1.21

Table 2. Distribution of heights, tusk lengths and tusk circumference at the level of tusk lip (TCLL) across subjective age classes.

Age class	n	Height (cm) Avg (±S.E.)	Tusk len. (cm) Avg (±S.E.)	TCLL (cm) Avg (±S.E.)
10-15	1	198.7	45	22.7
15-20	3	215.5 (±20.0)	65.1 (±26.9)	22.8 (±3.6)
20-25	5	216.8 (±16.7)	69.7 (±32.8)	24.5 (±11.2)
25-30	7	236.9 (±16.0)	92.4 (±37.0)	29.0 (±8.5)
30-35	3	251.1 (±13.0)	90.3 (±33.0)	30.7 (±4.0)
35-40	4	251.1 (±28.6)	95.7 (±28.3)	31.4 (±3.7)
40-45	1	254.3	111.1	36.1
45-50	1	262.4	88.7	38.9

Fig. 1 Variation of height, tusk length and tusk circumference at level of tusk lip (TCLL) across age classes

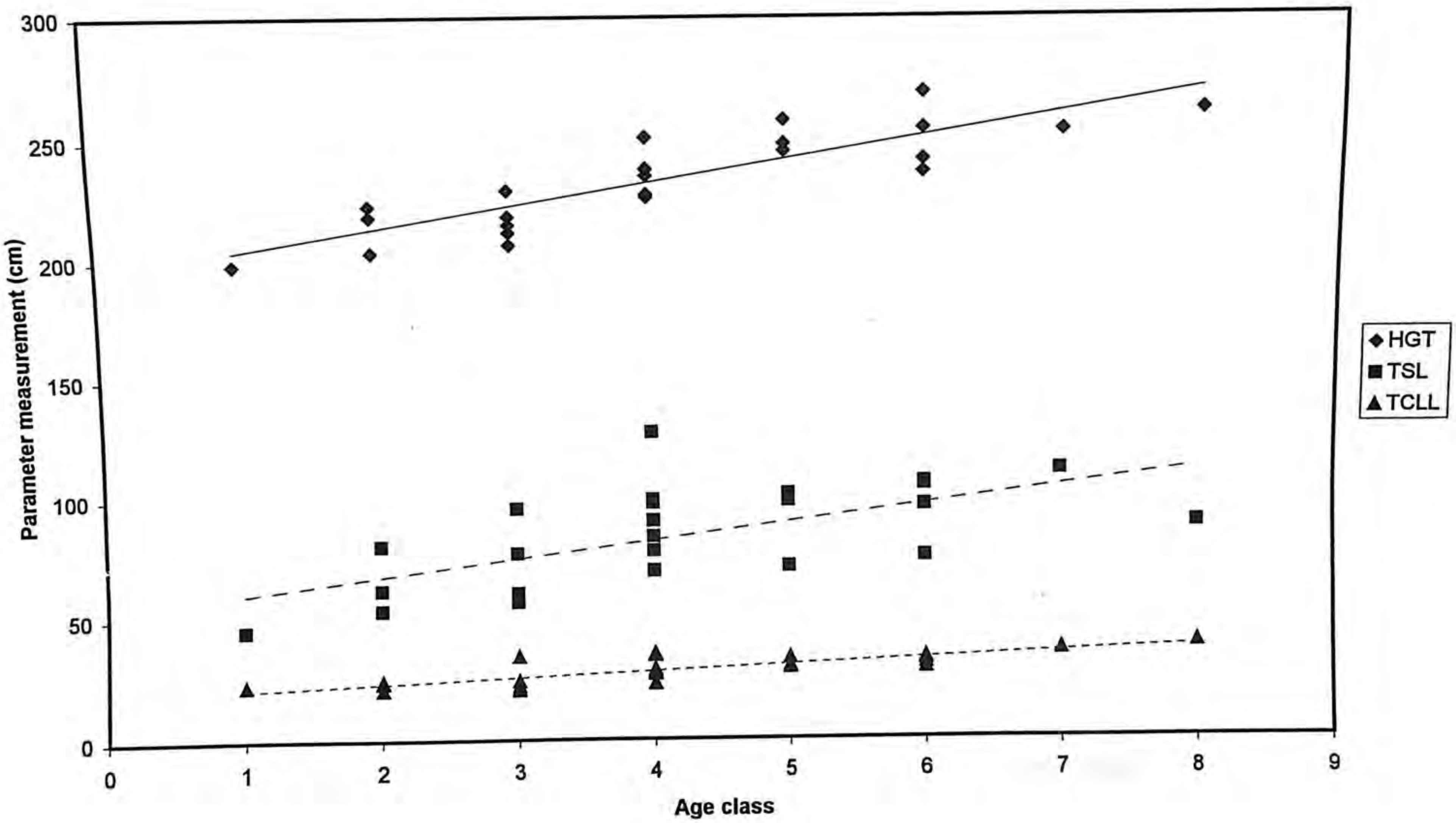
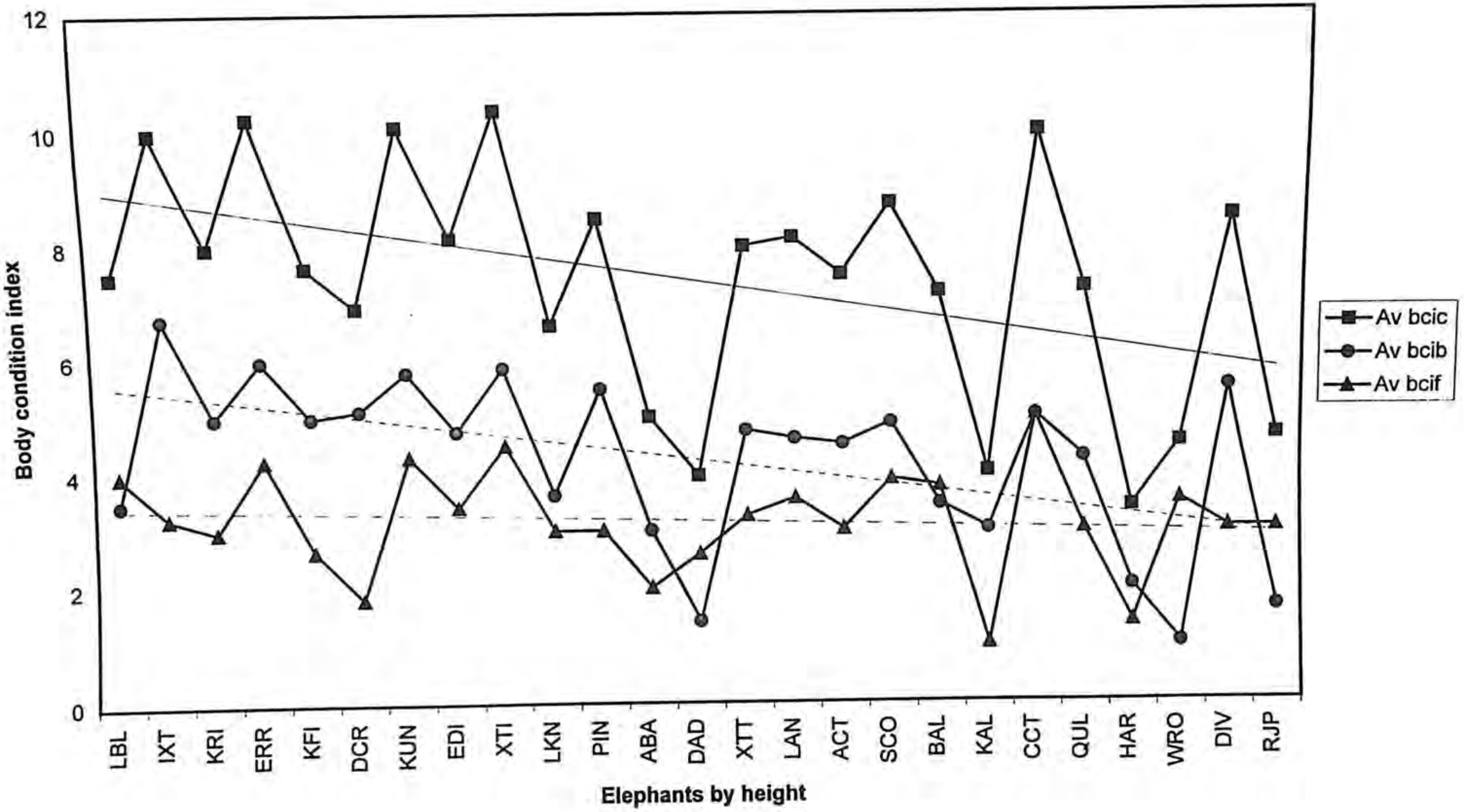


Fig.2. Age effect on average body condition index (composite (BCIC), body (BCIB) & face (BCIF))



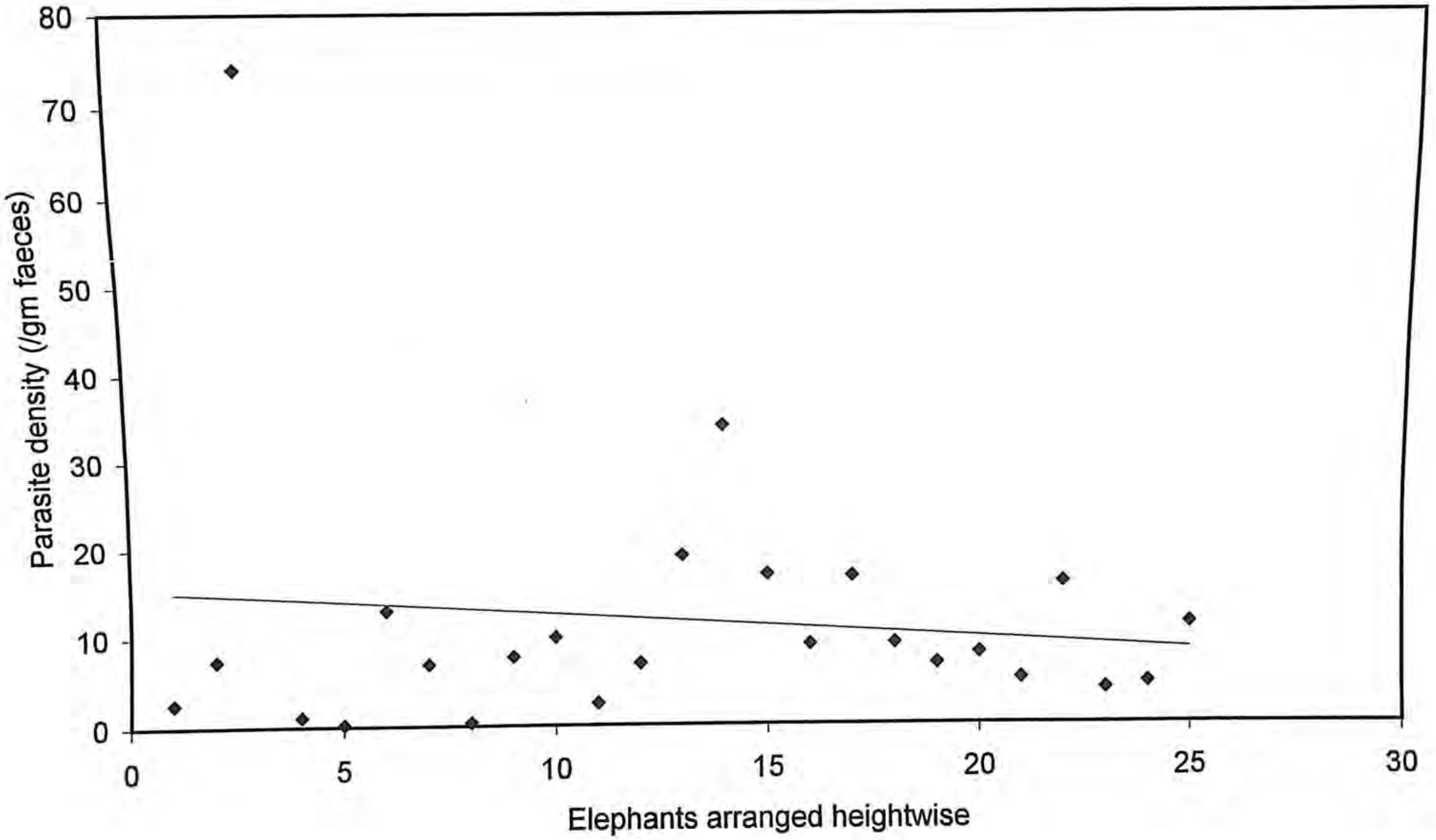


Fig. 3, Age effect on average parasite density

Fig 4. Age effect on average musth composite index (MCI)

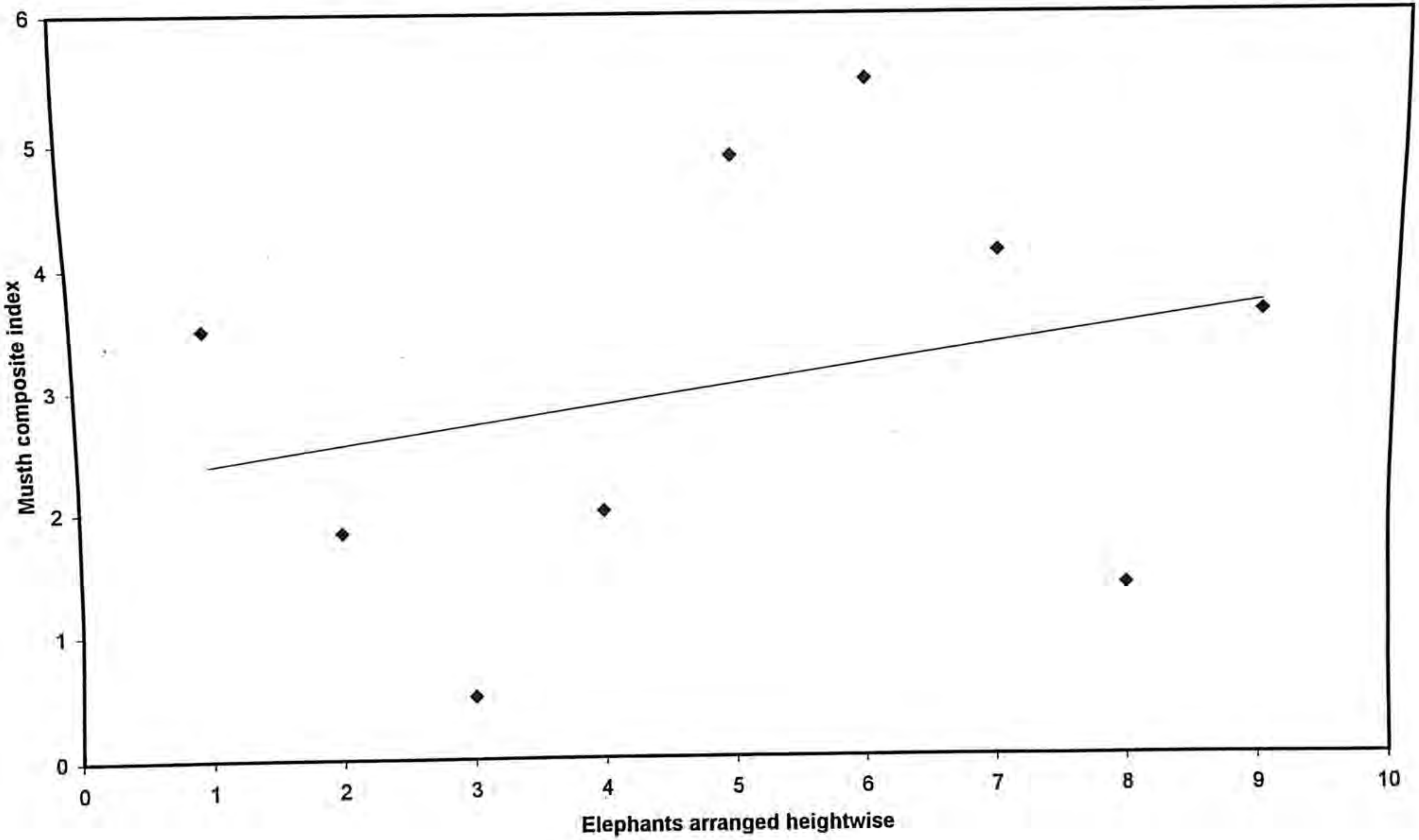


Fig. 5 Age effect on tusk length

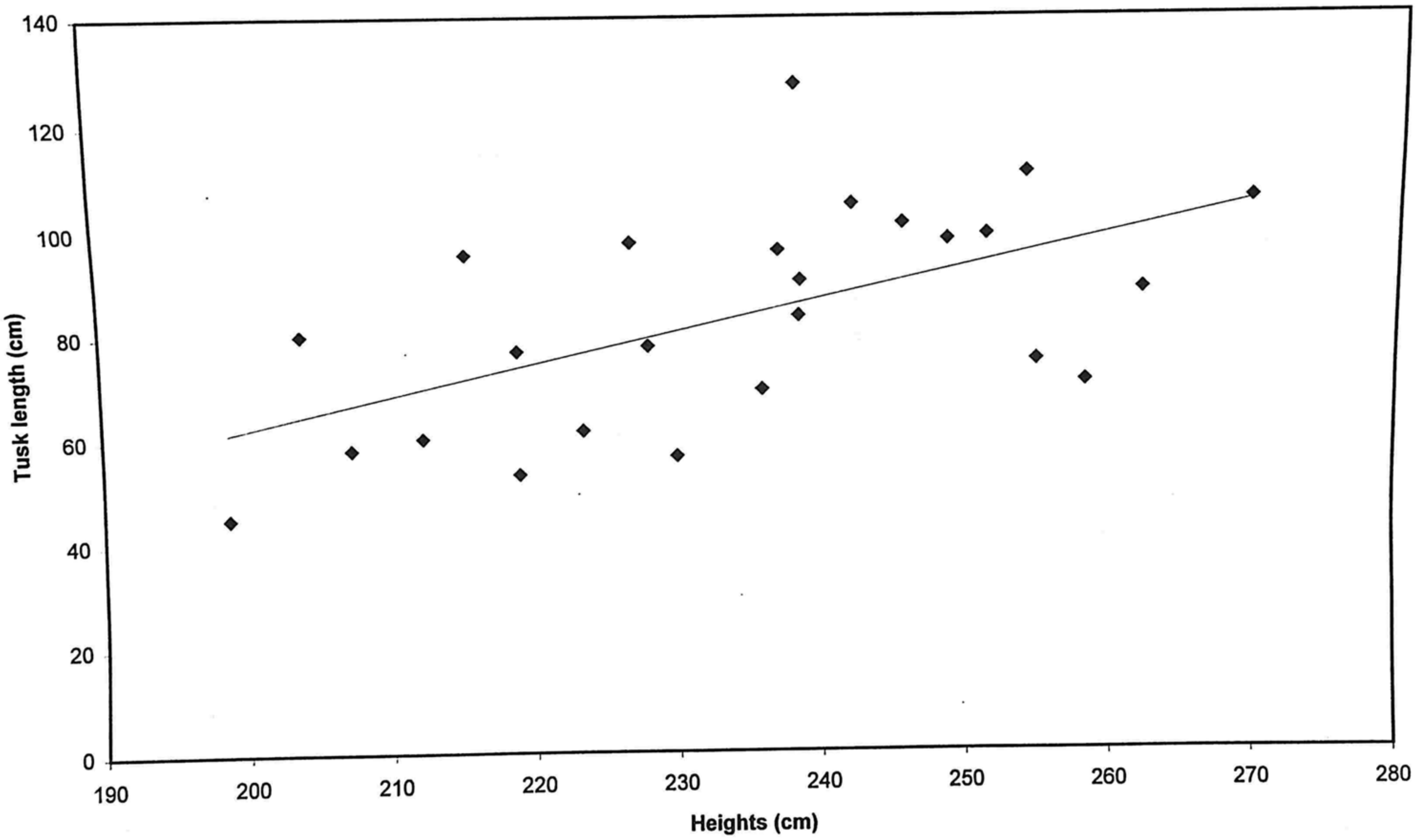
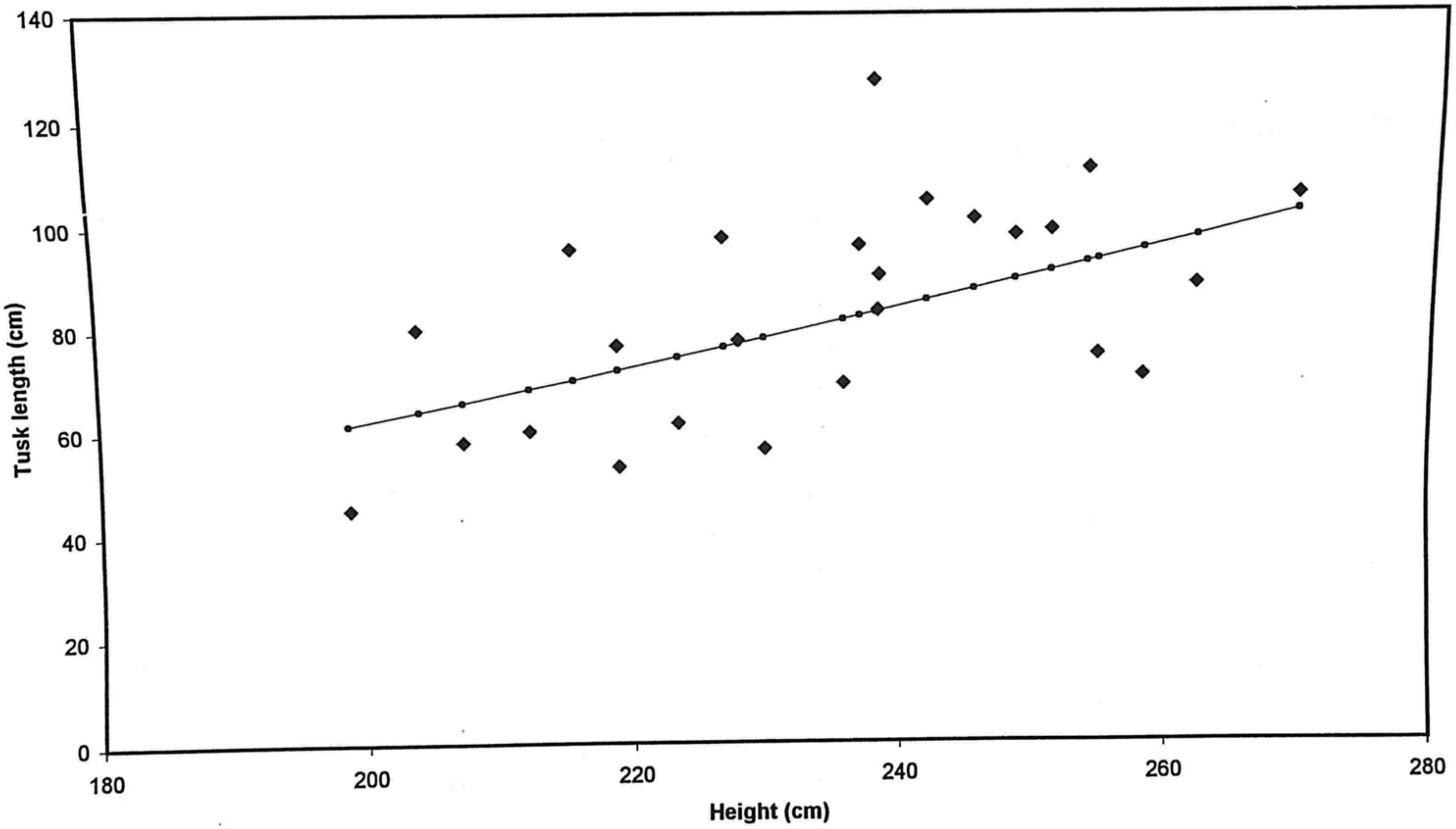


Fig. 6 Tusk lengths and fitted quadratic curve (y=-0.732+0.114x+0.001x^2), r = 0.764



Removing age effect from tusk length

Best fit was obtained by fitting a quadratic curve to the data (Fig 6), where the relationship between tusk length and height was given by the equation:

$$\text{Tusk length} = -0.732 + 0.114(\text{Height}) + 0.001(\text{Height})^2$$

This standard curve gave the best fit ($r = 0.764$) and was used to predict tusk lengths for all heights measured. The deviations of tusk lengths from this curve was then used to investigate relationships between tusk length and other parameters.

4.3 Health indicators

4.3.1 Interactions among health indicators

In order to rule out interactions among the two health indicators, individuals were separated into musth and non-musth categories and all body condition indexes were tested for correlation with parasite densities, as raw and averaged data per individual. However, no significant correlations were found in any of the combinations of BCI and parasite load, in both musth and non-musth groups. This indicated that the two health indicators were independent measures of health in this study.

4.3.2 Season effect

Another possibly confounding factor is the effect of different seasons on the health of individuals. Data on BCI and parasite load were tested in month-wise pairs using the Student's t-test for samples with unequal variances. Significant differences in parasite densities were found only between the months of January and April ($p < 0.015$). However, the sample size in January was 2 in comparison with a sample size of 23 in April, and a few very high values in April may have been responsible for the significant differences in parasite densities between the two months.

The data set was then divided into Season 1 which included the winter months of December, January and the first half of February, and Season 2 which included the summer months of the second half of February followed by March, April and early May. Tests for means between these two "seasons" yielded no significant differences either. Due to the extremely low sample size of the entire data set, no generalizations were possible regarding variations in parameters across seasons, and hence no corrections were made for this factor.

4.4 **Musth**

4.4.1 Musth intensity and age

Data from 9 males in musth were used for detailed analyses. Of these, 3 each were estimated to be in the age classes 25 – 30 yrs, 30 – 35 yrs and 35 – 40 yrs. An ANOVA performed on the average intensities of musth exhibited by these 9 individuals across 3 different age classes showed that the variance (sum of squares) between groups was not significantly different from the variance within groups (F = 0.98, p = 0.43). Hence there appeared to be no significant effect of age class, i.e., no significant trend of increase or decrease in average musth intensity with increasing age.

4.4.2 Musth versus non-musth individuals

Data were separated into musth and non-musth categories for analysis of all data parameters. Some parameters showed significant differences between musth and non-musth data sets, by Student's t-test analysis for samples with unequal means (Table 3).

Table 3. Comparison of data parameters for non-musth (“NM”, n = 16) and musth (“M”, n = 9) elephants with results of Student’s t test of difference of means

Parameter	**Average (NM)**	**Average (M)**	**T test p value**
Height (cm)	227.1	247.6	0.002*
Tusk length (cm)	78.29	92.9	0.089
Tusk length dev. (cm)	1.23	3.98	0.73
BCIC	8.55	5.35	0.000*
BCIB	5.07	2.75	0.000*
BCIF	3.48	2.61	0.018*
Parasite density (/gm)	11.09	12.92	0.37

* = indicates significance at $p<0.05$

Significant differences were found between musth and non-musth males, in all parameters except parasite load. Significant height differences between musth and non-musth individuals was explained by the age effect, since musth was observed in only the older aged animals, and not in all age classes. Tusk length differences between musth and non-musth males were also due to the age effect, because when tusk length deviations (to remove the age effect, see Section 4.2.4) in musth and non-musth males were tested against each other, there was no difference between musth and non-musth individuals.

The most interesting finding, which was foreshadowed in Section 4.2.2.a, was the significant difference in average BCI between musth and non-musth individuals (Student t, n1 = 9, n2 = 16, p < 0.001). The other health indicator, parasite density, showed no significant differences between musth and non-musth males. This indicated that while body condition indexes were significantly different between musth and non-musth males, parasite densities between the two groups were not different.

4.4.3 Musth and health indicators

a) Body condition index:

Data on musth individuals were investigated for finer resolution of patterns in health indicators during musth. There was no significant correlation between MCI and BCI when all the data on musth individuals were pooled (Fig. 7), although there was a minor trend of increasing BCIC (declining body condition) as musth intensity increases (Pearson r = 0.27, n = 15).

Health indicators were then divided into two groups based on MCI, to represent early versus late musth. Thus MCIs values from 0.5 to 3.75 (n = 8) were treated as early musth samples and MCI values from 4 to 5.75 (n = 7) were treated as late musth (or closer to peak musth) samples. These two groups were checked for significant differences in BCI. However, there was no significant difference between early and late musth samples in terms of BCI.

BCI values associated with early musth were found to be significantly different from BCI values of non-musth elephants (Student t test, n1 = 8, n2 = 48, $p<0.001$). This was an expected result following from that in Section 4.4.2, and indicates that better body condition is associated with early musth than with the non-musth state in the elephants studied in this project.

Finally, intra-individual trends during repeated sightings of musth males were studied qualitatively to determine trends or patterns, if any (Table 4). Two of the 3 musth males showed marginally increasing values of BCIC as musth progresses. However, the third male showed an increasing trend initially, in BCIC, followed by a decrease, when last seen. Due to the very low number of musth males re-sighted, and the lack of clear patterns or associations between MCI and BCIC, as well as between the number of days in musth and BCIC, it is not possible to draw conclusions with regard to changes over time in musth males.

b) Parasite load

Data on musth individuals were similarly studied with regard to parasite loads. However, as with BCI, there was no clear relationship between MCI and parasite densities when all musth data were pooled (Fig. 8). There was only a non-significant trend of increasing parasite loads (Pearson r = 0.39, n = 12) with increasing musth intensity.

Table 4. Intra-individual trends in MCI and BCI across repeated samples of musth males.

ID	Date	MCI	BCIC	# Days
RJP	22 Feb	3.75	4.25	5
	27 Feb	3.5	5	
BAL	20 March	4.75	6.25	22
	24 March	4.5	8.25	
	4 April	5.75	9	
	12 April	4.75	5.25	
HAR	22 April	4	3.25	8
	30 April	4.25	3.5	

Table 5. Intra-individual trends in MCI and parasite densities across repeated samples of musth males.

ID	Date	MCI	Par. Dens (/g)	# Days
BAL	20 March	4.75	1.5	22
	4 April	5.75	18.4	
	12 April	4.75	7.4	
WRO	1 April	1.5	0.4	4
	5 April	1.25	7.4	
HAR	22 April	4	18	8
	30 April	4.25	14	

Fig. 7 Relationship between musth composite index (MCI) and body condition index (BCIC) and (r=0.27, non signif.)

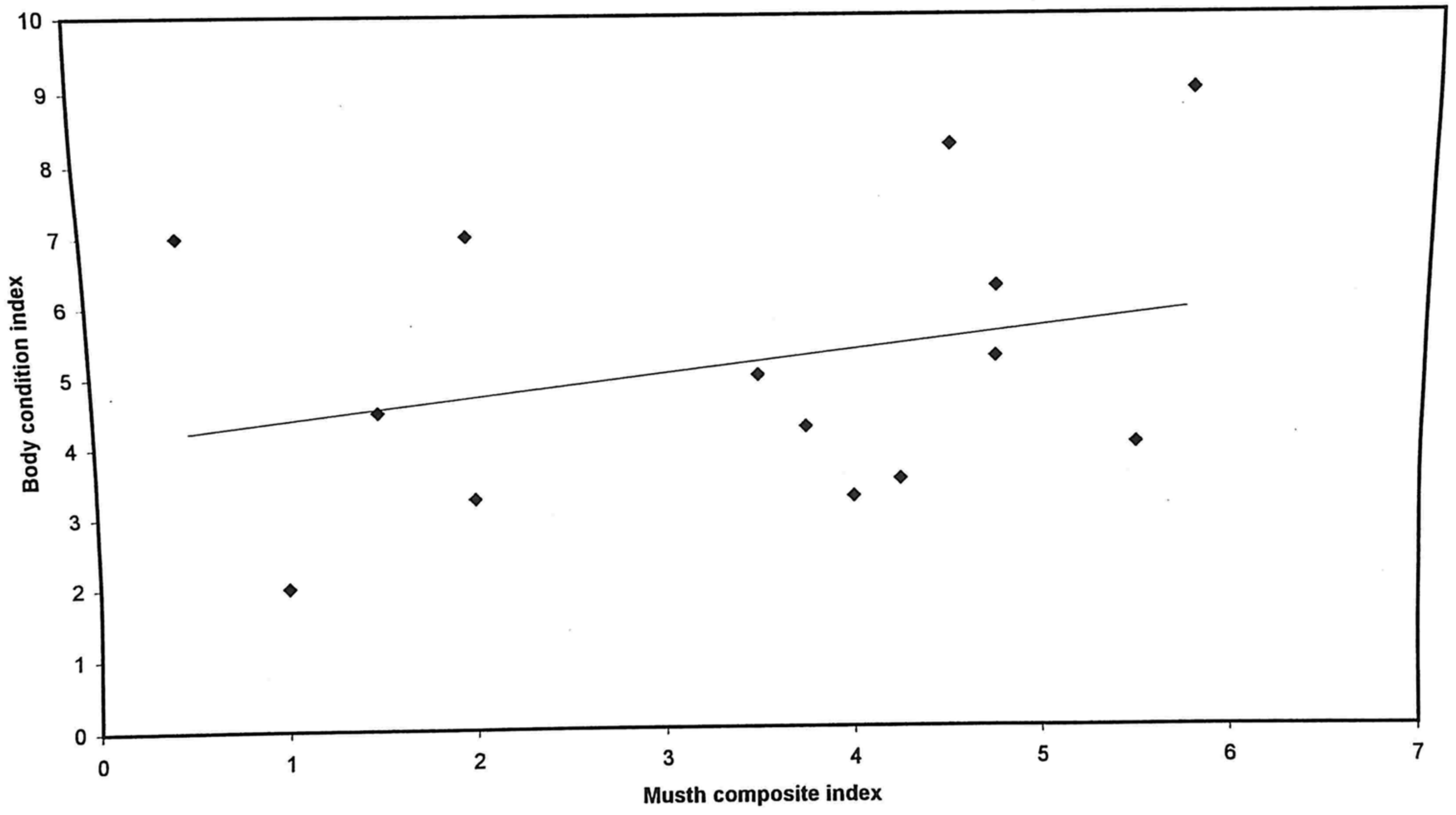
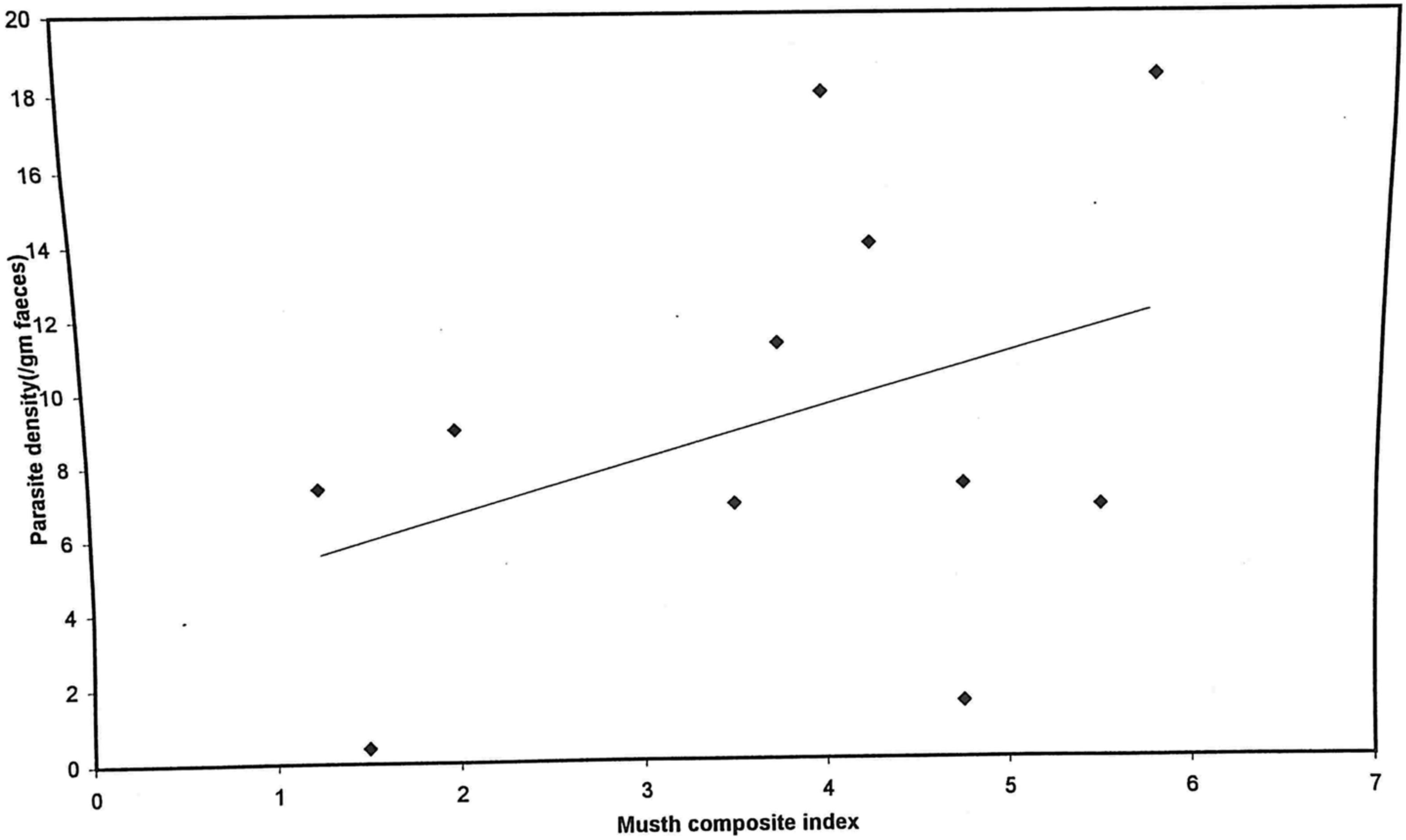


Fig. 8 Relationship between musth composite index and average parasite load
(r=0.38, non signif.)



Division of musth values into early (n = 6) and late (n = 6) stages, based on MCI values, as above, revealed no significant difference between early and late musth in terms of parasite loads.

However, another interesting result emerged, when parasite loads associated with early musth were compared against parasite loads associated with non-musth. There was a significant difference between early musth parasite densities and non-musth parasite densities (Student t test, n1 = 6, n2 = 31, p<0.05). This result is significant when considered in conjunction with the results from the MCI-BCIC analysis. Significantly lower parasite loads in early musth individuals support the findings above, of better body condition in early musth individuals, when compared with individuals not in musth.

Intra-individual trends in parasite loads of musth males during the course of their musth were examined qualitatively for patterns (Table 5). As with BCIC, there was no clear trend of increasing parasite loads with increasing intensity and progression of musth. Again, due to the very low number of musth males resighted, it is not possible to draw conclusions with regard to parasite load changes during the period of musth.

4.5 Tusk length

4.5.1 Tusk length and health indicators

a) Body condition index

Tusk length deviations calculated from the standard quadratic curve fitted to the data (Section 4.2.5) were tested for correlative association with BCI. There was a weak but non-significant positive trend when the two parameters were plotted against each other, indicating worsening body condition with increasing positive deviation of tusk length (Fig. 9).

b) Parasite load

Parasite loads showed no relationship with tusk length deviations (Fig. 10).

4.5.2 Tusk length correction using subjective age classes

It was felt at this point, that the use of height as a proxy for age may have reduced extreme trends of long or short tusks if height is genetically linked to tusk length and if heights vary greatly across ages. Hence a second standard curve was fitted to the tusk length data, using the subjective age classes (class intervals = 5 yrs.) to rank individuals. This had the effect of collapsing the data into 8 groups (described in section 4.2.1) and magnifying tusk length deviations from the standard values for each group. Best fit (r = 0.82) was achieved by using an exponential association curve with the equation:

$$\text{Tusk length} = 102.37\,[\,1 - e^{-0.474(\text{Age class})}\,]$$

Tusk length deviations obtained from this correction were then tested for relationships with BCI and parasite densities. However, tusk length deviations obtained from this curve also did not produce significant correlations with body condition or parasite load. These findings indicated that helminth parasite densities and body condition indexes were not related to tusk length deviation in the wild elephants identified during the current study.

4.6 Musth-tusk length relationship

Tusk length deviation was tested for its relationship to musth. There was no significant difference in average tusk length deviation between animals which

Fig. 9 **Relationship between tusk length deviation and average body condition index (BCIC) (r = 0.25, not signif.)**

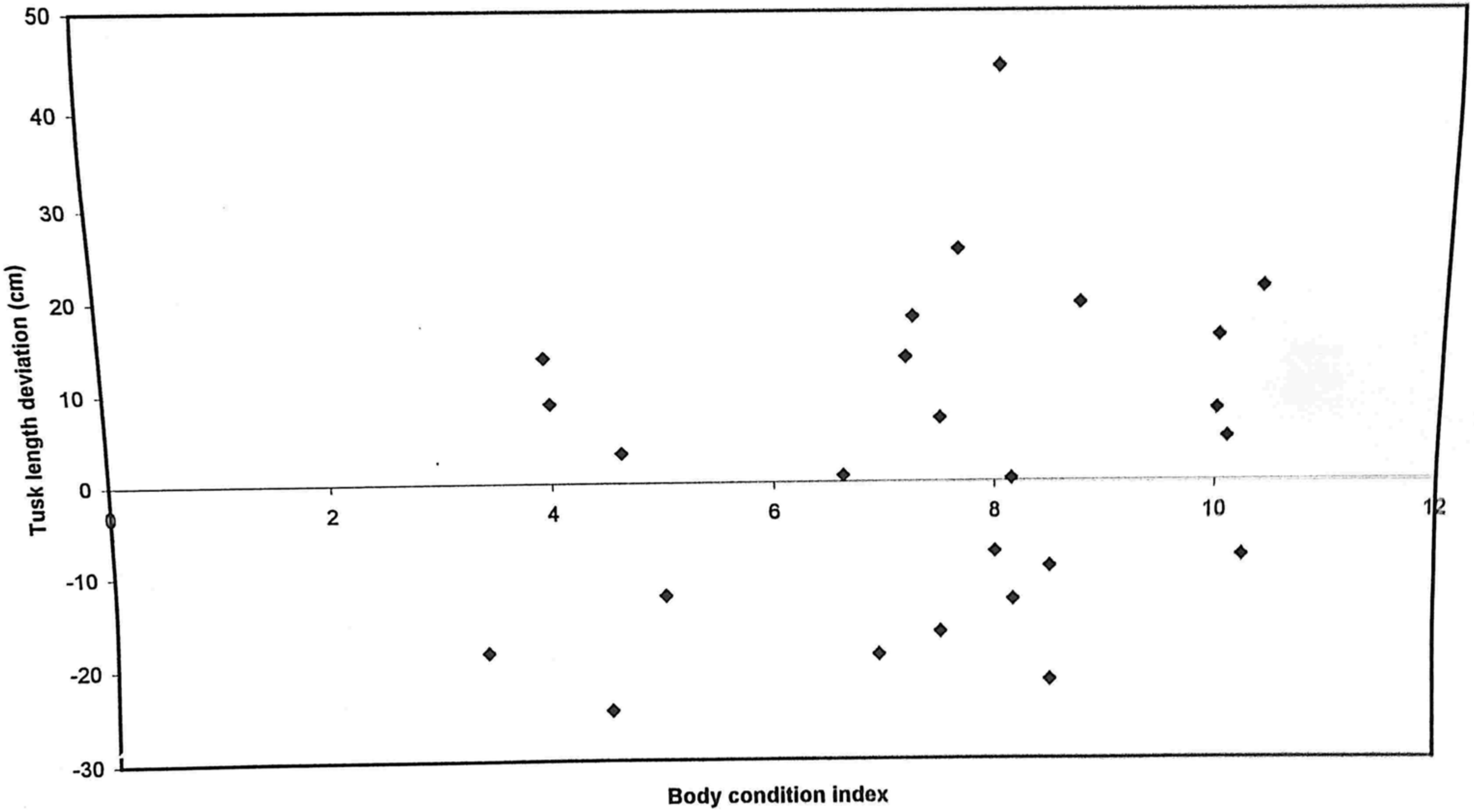


***Fig 10.* Relationship between tusk length deviation and average parasite load (r = 0.13, not significant)**

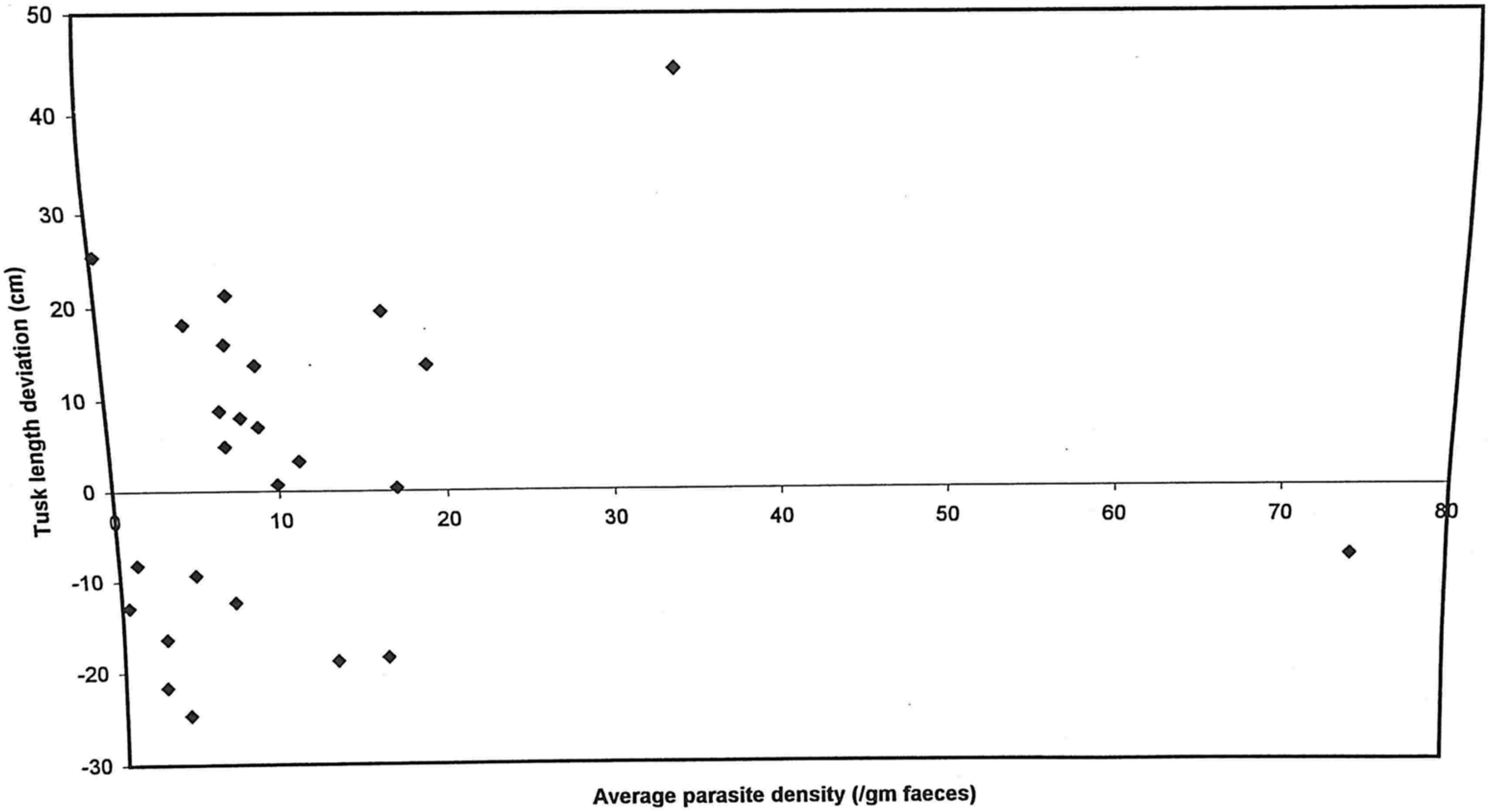
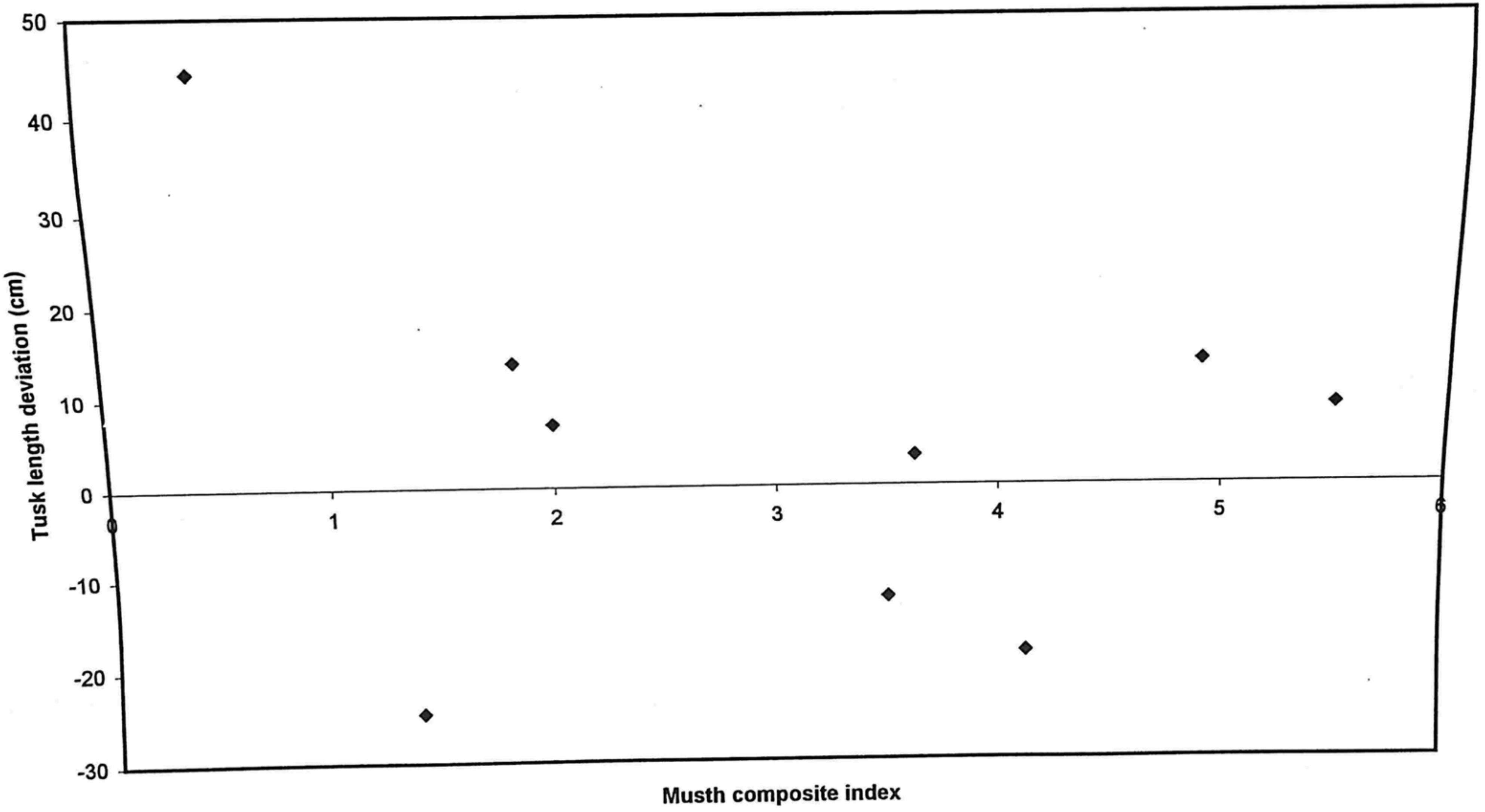


Fig. 11 Relationship between tusk length deviation and average musth composite index (r = -0.26, not signif.)



exhibited musth and those which did not come into musth during the study period (Table 3). A plot of tusk length deviation against MCI showed no significant relationship (Fig. 11). Six of the 9 musth males showed positive tusk length deviations while 3 showed negative deviations, although no significance can be associated with this finding at this stage.

4.7 Behaviour analysis

4.7.1 Dominance interactions

Nine group interactions between identified individuals were examined for dominance interactions. The chosen behaviours were subjectively designated as dominant or subordinate, *a priori*, as small sample sizes precluded a conventional dominance analysis. However, several behaviours such as approach-retreat interactions are classic indicators of dominance established in other well studied animals as well as in studies of African elephants (Poole 1987). Other behaviours, such as poking with tusks, can be reasonably assumed to represent dominance, as large and lethally dangerous animals such as elephants can be expected to exercise restraint in their interactions with each other and hence prefer to avoid aggression unless the chances of winning are reasonably high.

Of the interactions recorded, 5 were paired interactions (Dyads) and 4 interactions involved 3 males (Triads). In 2 each of the dyads and triads, a single female elephant was also present and interacting with the groups. Two of the 4 triadic interactions had a single musth male each, interacting with 2 non-musth males.

Dominant and subordinate behaviours (listed in Appendix) were tallied for each individual and dominance within dyads was assigned to the individual who demonstrated higher frequency of dominant behaviours and/or lower frequency of subordinate behaviours. Triads were analyzed for dominance in pair-wise interactions and dominance assigned as described above. The resulting set of dominant-subordinate pairs (n = 9) were then compared in terms of the parameter advantage expected to be conferred by differences (between the two interacting individuals) in the following 6 parameters: height, tusk length, tusk length deviation (from quadratic standard curve), average parasite density, average body condition index and occurrence of musth (Table 6). Lower parasite loads and better body conditions (lower scores for both measures) were considered positive or advantageous (in comparison to higher scores) in dominance interactions.

Simple calculation of proportions of dominant individuals enjoying a particular parameter advantage over their subordinates showed that the dominant individual had the advantage of musth on every interaction between musth and non-musth individuals (proportion positive = 1.00, n = 4) (Table 6). Dominant individuals also had the advantage of greater height in 89% of interactions, while the advantage of longer tusks was associated with the dominant individual in 78% of interactions. There were two dominant individuals who had only 2 (out of a possible total of 6) positive scores in terms of advantage. However, both of these individuals shared the common advantage of height over their respective subordinates. Out of the 9 dyadic pairs, only one dominant individual was shorter than his subordinate.

Table 6. Parameter advantages and disadvantages in dominant animals of dyadic interactions.

Pair (Dom-Sub)	**Hgt.**	**Tusk len.**	**Tusk dev.**	**BCIC**	**Par./gm**	**Musth**
KFI - KUN	-	+	+	+	+	
ERR – IXT	+	-	-	-	+	
LAN – DCR	+	+	+	-	-	
LAN – LKN	+	+	-	-	-	
DAD – PIN	+	+	+	+	-	
KAL – XTT	+	-	-	+	+	+
BAL – LAN	+	+	+	+	+	+
KAL – IXT	+	+	-	+	+	+
BAL - DCR	+	+	+	-	+	+
Propn. positive:	0.89	0.78	0.56	0.56	0.67	1.00
Binom. test p value	0.018	0.070	0.246	0.246	0.164	

However, this individual had positive scores, signifying advantage, in the remaining 4 possible parameters.

Tests of binomial distribution probability were carried out on the proportions of positive scores obtained for each of the parameters listed in Table 6 (except musth, which had a probability of 1.0). This was done to establish whether the proportions of positive scores obtained by dominant individuals for each parameter (if less than 1.0) was significantly different from 0.5 (equal probability of having or not having the advantage of that parameter over the subordinate animal). Only height advantage was significantly different from 0.5 in this data set (Table 6). Although tusk lengths received a positive score in 78 % of interactions, this was not significantly different from 0.5, indicating that tusk length may not be significantly linked with dominance in dyadic interactions.

From this analysis of dominance behaviours in a small sample of interactions, it appears that musth and height are linked with dominance. Other parameters such as tusk length, tusk length deviation, BCI and parasite density may not be so tightly associated with dominance in male elephants. One cannot, however, rule out the importance of these other factors in dominance, as musth is not always present in either one or both of an interacting pair of males, and there was a single case recorded, of domination by the less tall interacting individual. Actual establishment of dominance among male elephants may result from complicated interactions of several parameters. A larger data set of dominance interactions and more sophisticated analyses may provide further insight in future studies of this aspect of elephant ecology. From this limited analysis and data set, we may conclude that musth and height are significantly associated with the establishment of dominance in dyadic interactions between wild male elephants of the study area.

4.7.2 Interactions with females

Only four interactions between females and males were analysed. The qualitative findings are summarised below:

- Female (10 – 15 yrs) did not show any sexual interest in subordinate animal DCR during the dyadic interaction between LAN and DCR, although DCR approached and touched her.
- The same female presented (her rear) to an approaching dominant male in musth, BAL, spread her legs and urinated when he came close and touched her with his trunk. BAL was dominant over LAN and DCR in this interaction, having the advantage in all parameters over LAN and in all parameters except BCI over DCR.
- Female (25 – 30 yrs) appeared to be in consortship (close physical association between a male and a female over an extended period of time, independent of family group) with dominant male DAD who had the advantage of height, tusk length, tusk length deviation and body condition over subordinate male, PIN.
- However, the same female allowed PIN to show sexual interest in her by moving away from DAD and slightly towards PIN, standing with her tail cocked to the side while PIN tested her genital area while DAD was preoccupied with chasing away a third male, MAK.
- The subordinate male, PIN was ultimately chased away by DAD, who appeared to be guarding the female from all other males. This indicates an important role for dominance and mate guarding in elephant sexual behaviour.

5. DISCUSSION

5.1 Musth as an honest signal of quality

Probably the most important findings of this study were those relating to musth and health indicators. Male elephants which exhibited external signs of musth of all stages, had significantly lower average BCI scores (indicating better health) than males which did not attain musth during the study. Early musth males had slightly lower BCI scores, though not significantly different scores, than late musth males, indicating that throughout the periods of musth monitored in this study, males did not show significant deterioration of body condition as musth progressed. This could be interpreted to mean that in order to sustain musth a male must be able to retain its good body condition. It is also possible that a highly productive environment such as Nagarahole is able to provide nutrition to sustain reasonably good health in musth males despite the physiological burden imposed by this condition. Alternatively it could be an artefact of low sample size.

Inter individual parasite loads did not show any significant difference when all musth males were compared against all non-musth males. However, early musth males were found to have significantly lower average parasite loads than males which did not achieve musth. This supports the findings above that in order to attain early musth, males must be able to achieve a state of health significantly above that of non-musth individuals. Better health may correspond to a lower internal parasite load and to better external body condition. Hence musth may serve as an "honest signal of quality" (Zahavi, 1977, 1987) to female elephants as only those animals capable of sufficiently improving their health condition and reducing their parasite loads would be able to produce this signal.

The results above support the proposed hypothesis, H_A1, that individuals exhibiting early musth signals have better health indicator values than non-musth individuals. Hence we may reject the null hypothesis, H_01, that there is no significant difference in health indicators between early musth and non-musth male elephants, in the group of animals studied ($\alpha = 0.05$).

However, significant increases or decreases in health indicator values were not obtained, between early and late musth animals. Examination of individual cases, where multiple sampling of musth individuals was possible, did not reveal any clear trends in BCI or parasite load with increasing musth intensity and duration. In addition, the sample sizes were too small to draw conclusions or make projections in this regard. Hence we cannot reject the null hypothesis, H_02, that changes in BCI and parasite loads with repeated samplings of identified musth individuals during a single episode of musth are not correlated with increasing intensity and duration of musth. These findings fail to clearly establish musth as a "signal of handicap" (Zahavi 1975) in this study.

A mention has to be made regarding the assumption of interpreting low MCI scores as representative of early musth. Elephants at the end of a period of musth also may exhibit a low intensity of musth and hence receive low MCI scores. The inability to repeatedly sample all musth animals over their entire musth period is a limitation which calls for caution in interpreting intra-individual patterns seen during this study. However, it must be mentioned in support of rejecting null hypothesis

H_01, that the significantly lower BCI values of "early" musth samples were corroborated by the significantly lower parasite loads of "early" musth samples. This tends to support the assumption that low MCI scores reflect early musth.

Behavioural analysis supported the possible importance of musth as a sexual signal. Musth was observed to potentially increase a male's mating success in two ways: as a possible correlate of dominance over other males, and as a direct sexual signal to females who respond favourably towards males exhibiting this honest signal of better health. Poole (1987, 1989b) reported increased reproductive success for male African elephants through higher dominance and higher female choice of larger, older males in musth. This is similar to the behavioural patterns obtained in this study.

5.2 Tusk length as a signal of heritable true fitness

During this study there was no evidence to support the hypothesis that tusk lengths were negatively correlated with average BCI and parasite loads. Hence we cannot reject the null hypothesis, H_03, that there is no significant negative correlation between tusk length and average BCI and between tusk length and average parasite loads. Consequently, there is no evidence from this study of wild male elephants that tusk length serves as "an indicator of heritable true fitness" (Hamilton and Zuk 1982), as proposed earlier.

Again, caution would be advised in the interpretation or extrapolation of the results of this study. There are several possible reasons why the findings of this study do not corroborate those of Watve and Sukumar (1997):

- intra-individual variation was not controlled for adequately in either of the two studies. A better understanding of intra-individual variation is required before any conclusions can be drawn. Watve and Sukumar (1997) did, however, control for seasonal variation in parasite loads, which was not possible in this study due to limited background data on seasonal parasite load variations across seasons. This is a possible source of intra-individual variation, especially since the study extended through the hot dry summer, which may have stressed some animals more than others and exaggerated differences in their average parasite loads as well as in their BCIs.

- Host-parasite interactions between elephants and their helminth parasites may show variations in different habitats. Fluke and sprirorid nematode ova were detected in the Nagarahole samples, which were not reported from the Mudumalai population. There may be some variations in host-parasite ecology between these two study areas which may need to be corrected for before comparing the two populations.

The lack of significant association between the two chosen sexual "signals" was not surprising given their very different associative tendencies with the two health indicators. Hence hypothesis $H_0 4$, that musth and tusk length are not correlated with each other, could not be rejected.

Finally, behavioural analysis showed that dominant individuals were more likely than subordinates to attain musth and to have the advantage of height in male-male encounters. The dominant individual had longer tusks in a high proportion of interactions studied, although this was not shown to be a significant association with dominance. Hence the null hypothesis, $H_0 5$, that dominance in male-male interactions is not associated with greater ability to come into musth, can be rejected ($\alpha = 0.05$). However, in the case of tusk lengths, we cannot reject the null hypothesis, $H_0 5$, that dominance in male-male interactions is not associated with longer tusks.

5.3 Appropriateness of health indicators

Tusk lengths hence did not appear to signal "heritable true fitness" in male elephants in this study area during this short study period. However, the use of tusk length as a signal cannot be completely rejected, because longer tusks were associated with dominance in 78% of interactions, and dominance may influence female choice. It is possible that longer time periods are required to assess the role of tusk lengths in sexual signaling and dominance, and a more appropriate health indicator may be required, than external body condition and helminth parasite loads which may tend to fluctuate greatly over short intervals of time. These short term fluctuations would not be reflected immediately in tusk length growth, and hence may lead to incorrect conclusions about their value as sexual signals. It appears more likely that tusk length may serve as an indicator of long term fitness and health of individuals, whereas musth may serve as a reference to a male's ability to interact with the immediate environmental conditions. This may explain why patterns associated with musth were better reflected in the two chosen health indicators while differences in tusk lengths failed to show correlations with the same health indicators.

5.4 Significance of study

All interpretations of results in this study are subject to verification in future studies, due to the small sample sizes. Given this limitation, though, this study can still be of value to conservationists interested in promoting long term viability of the species and of small threatened populations of wild elephants. The following are possible applications of the results of this study:

1. It is sometimes felt that a low sex-ratio of male to female elephants is not of great concern as long as there are a few males available to mate with all the receptive females in a given year. However, in light of the findings that males which are able to achieve musth condition may be of greater value to females, given a choice, it may be important to monitor the "quality" of the males available. This could have long term genetic consequences for the population.
2. A simple non-invasive method of assessing the health of populations over regular intervals may be developed by using a combination of BCI and parasite density values. As seen in the case of musth versus non-musth, there are significant measurable differences in these two health indicators over short intervals, which may serve as sensitive indicators of declining or improving health trends in individuals and populations over different seasons and years.
3. Often crop raiding, in agricultural fields surrounding protected wildlife sanctuaries, is carried out by lone male elephants. Sukumar & Gadgil (1988) had suggested that this could be viewed as an adaptive strategy of "high-risk, high-gain" followed by male elephants, in order to attain better body condition, increase their chances of attaining the musth condition and thus increasing breeding success. The current study lends support to this

speculation, by demonstrating the relationship between musth (especially early musth) and better health indicators.

4. Sukumar (1991) also suggested that selective removal by capture of such frequent offenders which tended to develop a propensity to raid crops, may alleviate human-elephant conflict and thus reduce a serious conservation problem. However, in light of the possible implications of crop raiding on increased reproductive success of male elephants, removal of frequent crop raiders from a small pool of males elephants may not be advantageous in the long run, as it would possibly remove the most healthy males favoured by females. In addition, other males will probably quickly fill in the void left by the previous raider, since crop raiding may prove to be the most cost-effective strategy available, as suggested by Sukumar & Gadgil (1988). Hence capture of habitual raiders may not be the most effective strategy for dealing with crop raiding bulls under all circumstances of crop raiding, in light of these ramifications for reproductive success of wild elephant bulls.
5. Since tusk lengths showed slight association with dominance, it lends support to the argument of Watve and Sukumar (1997), that poaching of bulls with long tusks may remove some of the better and more genetically fit individuals from the population. This may have implications for protection of long tusked male elephants from poaching by ivory hunters.
6. The greater significance of association between musth and height in determining dominance may have important implications for reproductive success of makhanas (tuskless male Asian elephants), a hitherto neglected

subgroup among Asian elephants in India. There is anecdotal evidence from several field studies that makhanas tend to be taller on average and more physically fit than tusked males. This may be reflected in their overall physical heath and ability to attain musth. In light of the changing ratios between tusked and tuskless male elephants due to poaching for ivory in several protected areas of our country, makhanas may gain selective advantage over tusked males in terms of reproductive success and this could further skew the ratios in favour of makhanas in the future. This could be an interesting topic of investigation in future scientific studies, especially in areas where the proportions of tusked and tuskless males in the population are more equal.

6. CONCLUSION

This study of health and sexual signals in male Asian elephants produced some interesting patterns. The important findings were:

1. Individuals exhibiting signs of early musth had significantly better body conditions and lower parasite loads than individuals exhibiting no signs of musth.
2. Longer tusks were not significantly correlated with better health indicators.
3. Dominance behaviours recorded in dyadic interactions among male elephants indicated that dominance was associated with musth, height of the animal and tusk length in a high percentage of interactions.

The most significant result indicated by this study was that musth has potential to be considered as an honest signal of better-than-average health in males. This information may be used by female elephants in choosing mates. Social interactions among males corroborated this speculation by showing that musth may be an important determinant of dominance in male-male interactions. Social interactions also indicated that height (or age) and tusk length may favor dominance. Limited samples of male-female interactions suggested that females discriminate between different males, and that male-male dominance interactions may influence female choice. However, small sample sizes limit the extent to which these findings could be extrapolated to other wild elephants in this and other populations.

Despite its limitations, though, this study is significant as it provides a basis for future investigations of musth as a signal of genetic quality and as an honest signal of handicap to female elephants and to humans trying to conserve the genetic fitness of this species in the long run.

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APPENDIX

Ethogram of social behaviours of wild elephants recorded at Nagarahole National Park, November 1998 – May 1999:

I. Dominance and threats

- Approach of dominant followed by or accompanied by turning away/walking away/running away by subordinate
- Approach by dominant to subordinate with head swinging up and down or with trunk slung over tusks
- Placement of trunk on face/back/rump/tail of subordinate
- Pushing subordinate with tusks, with trunk base, with head butt, with body side
- Hit subordinate with trunk
- Mount subordinate from behind
- Placement of trunk into mouth of subordinate
- Throwing mud on the head in a slow "ritualised" manner facing subordinate
- Rubbing forefoot or swinging forefoot just above the ground forward and backward while facing subordinate
- Swing trunk out forcefully towards subordinate
- Sensing directly and overtly towards other elephants with trunk
- Lock tusks with subordinate and push him backwards
- Kick subordinate with hind foot
- Approach with head up and tusks pointing forward at subordinate
- Move close to subordinate from further away
- Displacement of subordinate for feeding

II. Subordination:

- Passive receipt of dominance behaviours without retaliating
- Turning away/moving away from dominant elephant's approach
- Penis descent in response to dominant animal's approach
- Urination or defecation in response to dominant animal's approach

III. Musth

- Frequent tests of female genital area
- Stand still & alert >5 seconds
- Dig tusks in shallow water
- Walk with head swinging up and down

IV. Female interest in / preference for male:

- Approach male
- Turn around, and present posterior when male approaches
- Spread legs when male tests genital area

- Urinate/defecate when male approaches female posterior
- Passively accept male dominance behaviours (such as placement of tusks on her back, mounting, etc.)
- Move along with male when he leaves the female group

V. **Female rejection of male interest:**

- Move away when male approaches or attempts to mount
- Run away with /without vocalisation when male persistently tries to approach her