Original Investigation

Decreasing reservoir water levels improve habitat quality for Asian elephants

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ABSTRACT

Population health and habitat quality are intimately related and seasonal changes in habitat quality are likely to be reflected in the body condition of animals. We studied seasonal variation of body condition in free ranging Asian elephants (*Elephas maximus*) in Udawalawe National Park, Sri Lanka based on visual scoring of individually identified elephants. We assessed the body condition of 218 adult females and 329 adult males from January 2008 to November 2012 and examined its relation to monthly rainfall and water level of the Udawalawe reservoir. Contrary to expectations, body condition of elephants was higher in the dry season, when primary productivity decreases due to lack of rainfall. However, the body condition showed both a seasonal and inter-annual negative co-relation with reservoir water level. A possible explanation for improved body condition in the dry season is the greater availability of fresh grass due to the emergence of reservoir bed grasslands with the drawdown of water. Our results underscore the importance of water management of large irrigation reservoirs in elephant conservation in Sri Lanka.

Introduction

The main regulator of large herbivore occurrence and densities arguably is fodder availability hence primary productivity (Mduma et al., 1999). Key factors affecting primary production are photoperiod, temperature, soil nutrients (McNaughton et al., 1988; Burke et al., 1990), rainfall (Deshmukh, 1984) and soil moisture (Nippert, 2006). In a given area in the tropics, seasonal and inter-annual variation in photoperiod, temperature and soil nutrients is minimal. However, changes in rainfall, hence soil moisture and its temporal variability significantly affect productivity even in the tropics (McNaughton, 1985; Weltzin et al., 2003). In seasonal habitats, primary production decreases drastically and high quality forage biomass accumulated during the wet season rapidly converts to low quality in the dry season (Sinclair, 1975; McNaughton, 1985). Therefore a positive relationship exists between large herbivore biomass and rainfall in seasonal habitats (Coe, 1976; Mduma et al., 1999).

Body condition is an indicator of an animal's health and fitness (Gerhart et al., 1996). Body condition of free ranging Asian elephants (*Elephas maximus*) may be influenced by a variety of factors. Differences in resource availability among localities may cause variance in body condition among populations. Climatic variations have a direct bearing on food availability and quality, hence are reflected in seasonal and long-term body condition changes of a given population (Sukumar, 1989; Desai, 1991). Elephants are hindgut fermenters with rapid food passage times, low digestibility and energy intake, and are inefficient in dealing with plant toxins (Clauss et al., 2003; Dumonceaux, 2006). They require about 150-300 kg of fodder daily to sustain themselves (Vancuylenberg, 1977) and have evolved to be generalized herbivores consuming over a hundred plant species in any given location (McKay, 1973; Sukumar, 1990; Samansiri and Weerakoon, 2007; Campos-Arceiz and Blake, 2011).

Ungulates require an average of 4-5% of crude protein to maintain their body weight (Sinclair, 1975). Grass is preferred by many mammalian herbivores, as it is easy to gather and process and has few secondary compounds. With the onset of dry season, crude protein in grasses reduces from 8% to 1-3% and ungulates can obtain their required crude protein only through active selection of food material (Sinclair, 1975). Similarly, the preferred food of elephants is fresh grass, which is high in protein and low in silica and fibre (Sukumar, 1990). As grass matures, its protein content decreases and silica and fibre increase, and elephants shift to browse (Sukumar, 1990). Fresh grass is present only in the wet season and early dry season in the tropical habitats of Asian elephants (Fernando, 2015) hence its availability can be expected to have a major impact on elephant body condition. Sri Lankan elephants do not migrate and are non-territorial with comparatively small overlapping home ranges (Fernando et al., 2008b). Elephant density in Sri Lanka is about ten times that of any other range country (Fernando and Pastorini, 2011). Therefore in Sri Lanka, it can be expected that elephants will use habitat intensively and habitat quality will have a major influence on their body condition.

Behavioural aspects such as sociality (Pinter-Wollman et al., 2009) and ranging patterns (Fernando et al., 2008b) may influence the body condition of groups and individuals differently. Female elephants live in social groups (e.g. Fernando and Lande, 2000) hence experience intra- and inter-group competition for resources (Janson, 1988). Males remain with their natal groups until puberty and become solitary thereafter (Lee, 1991). Therefore, adult males can be expected to experience less resource competition than adult females hence better body condition.

Unlike female elephants, which cease growth once reproductively active, males continue to grow well beyond puberty (McKay, 1973). Thus, adult males can be divided into three age-size classes; sub-adult, young-adult and mature-adult, which also correlate with behavioral aspects influencing body condition. ‘Sub-adult’ males leave their natal herds and go through a transition period of adaptation, which may result in decreased body condition. Once they adapt to a solitary lifestyle, as 'young-adult' males they are likely to have higher resource acquisition hence better body condition. 'Mature-adult' males experience an annual 'musth' period (Poole, 1987) with associated increase in ranging and loss of body condition as musth progresses (Poole, 1989; Fernando et al., 2008b).

Reproductive, physiological, health status and behavioural differences may cause individual variation in body condition. Reproductive females invest heavily in bearing and rearing of calves. Some males take risks in raiding crops (Chiyo et al., 2011; Ranjeewa et al., 2015) and may gain in body condition. However, stress and injuries sustained in raiding may impact body condition negatively. Additionally, management actions taken to mitigate the human-elephant conflict such as elephant drives, electric fencing and translocation may have severe repercussions on the wellbeing of elephants (Fernando et al., 2008a).

Thus, body condition assessment of free ranging elephants can help understand the impact of environmental, behavioural and management actions on elephant health, hence is of importance for elephant conservation.

The body condition index (BCI) of an animal is a numerical indicator of fat deposition in different regions of the body (Riney, 1960; Wemmer et al., 2006; Fernando et al., 2009). Body condition assessment is widely used in dairy herd management to monitor the nutritional status of cows by direct measurement of subcutaneous fat (Wildman et al., 1982; Otto et al., 1991) and ultra-sound scanning (Brethour, 1992). Body condition of wild animals cannot usually be assessed through direct measurement due to logistical, legal and ethical constraints, which preclude capture and slaying. An alternative is body condition scoring through visual assessment (Riney, 1960). Visual body condition scores and ultra-sonic measurements of subcutaneous fat in dairy cows show a highly significant correlation, suggesting that visual body condition scores accurately reflect the amount of subcutaneous fat deposits (Edmonson et al., 1989; Zulu et al., 2001). Visual body condition scoring has been used in the study of mice (Ullman-Cullere and Foltz, 1999), pigs (Chikwanha, 2007), cows (Wildman et al., 1982), goats (Villaquiran et al., 2004) and reindeer (Gerhart et al., 1996). A few studies have also assessed the body condition of free ranging and captive elephants (Godagama et al., 1998; Wemmer et al., 2006; de Klerk, 2009; Pinter-Wollman et al., 2009; Ramesh et al., 2011). In this study we use an adaptation of the visual body condition scoring of Wemmer et al. (2006).

The objectives of this study were to assess the body condition of adult male and female elephants in the Udawalawe National Park (UWNP), determine its seasonal variation and to identify the possible factors influencing it. We hypothesized that 1. Primary productivity will have a major influence on elephant nutrition and hence the body condition of elephants would vary seasonally, being higher in the wet season and 2. The body condition of males will be higher than that of females, and it would differ between age-size classes of adult males with sub-adults showing the lowest and young-adults highest condition.

Material and methods

Study area

Udawalawe National Park is 308 km^2 in extent and is administered by the Department of Wildlife Conservation. It is located in southern Sri Lanka between 6º 25' and 6º 35' N and 80º 45' and 81º 00' E. It encompasses the Udawalawe irrigation reservoir built in the 1960's and the Mau Ara reservoir built in the 1990s (Fig. 1). Road accessibility is limited to the central one third of the park.

The annual average temperature is 32ºC and the average annual rainfall 1,329 mm. Rainfall is characterized by a bimodal pattern, a small peak occurring during the south-west monsoon from April to May and the main rainfall occurring during the north-east monsoon from October to December. A prolonged dry season occurs from June to September (Fig. 2).

The natural vegetation in Udawalawe is tropical dry evergreen forest. Prior to declaration in 1972, the park area was under extensive logging and slash-and-burn cultivation, which converted it to grassland-savannah habitat dominated by *Megathyrsus maximus*, a naturalized perennial fodder grass. Since declaration, the grassland-savannah habitats have undergone succession, becoming scrub and secondary forest (Fernando and Leimgruber, 2011). In the dry season, most grasses dry up and patchy fires occur in grassland and scrub areas. The water level of the reservoir decreases in the dry season as the water is let out for cultivation and fresh grass habitat composed of native short grasses, emerges in the draw-down area.

Data collection

The study extended from January 2008 to November 2012. Data on males were collected from 2008 to 2012 and on females from 2009 to 2012. No fieldwork was conducted in February and April 2008 due to logistic issues. A total of 531 days were spent in the park. Observations were carried out from 6:00 am to 11.30 am and 2.30 pm to 6:00 pm from a 4WD vehicle. In each of the 57 months, 1 to 16 days (average 9.3 ± 3.1) were spent in the field.

Photographs of elephants were taken with a digital camera (Panasonic dmc-fz18). Individual elephants were identified using characteristics such as ear shape and tears, wounds, lumps, tail, body shape etc. (Fernando et al., 2010; de Silva et al. 2011; Vidya et al., 2014). Adult males were categorized as sub-adult, young-adult and mature-adult, to assess variation in body condition among male age-size classes. Females with dependent calves or pregnant were considered 'adult'. All adult males identified during the study period were categorized based on morphology and comparison with female height. Males taller than an adult female and with well-developed secondary sexual characteristics such as prominent frontal domes, broad trunk base, marked nasal prominence, and bulky penis/penis sheath, and/or showing full musth as indicated by copious temporal discharge and continuous urine dribbling, were considered 'mature-adult'. Males with developing secondary sexual characteristics and somewhat taller than an adult female were categorized as 'young-adult' and males equal in height to an adult female without development of secondary sexual characteristics 'sub-adult' (also see Appendix 1).

A modification of Wemmer et al. (2006) was used for scoring of body condition as the stipulated observation conditions could not be met with free ranging elephants. We assessed seven body areas in scoring body condition; head, scapular, thoracic, flank, thoracic spine, lumbar spine and pelvic areas (Table 1, Appendix 2). Scoring was done by observing the elephant's profile from a vehicle at a distance of up to 50 m. Identified individuals were observed with the naked eye, and a score given for each body area ranging from 0 to 2 (Table 1). A score of 0 indicated 'poor', 1 'moderate' and 2 'good' body condition. Scores for the seven body areas were then added to give a body condition index from 0 to 14 for each animal.

Daily rainfall data was collected using a standard U.S. Weather Bureau rain gauge. Data on monthly water levels of the Udawalawe reservoir were obtained from the Mahaweli Authority of Sri Lanka.

Data analysis

Only a single body condition score was taken per individual per day. In 622 cases, an individual was observed more than once within the same month. To assess the reliability of the BCI assessments, we calculated Cohen's kappa with quadratic weighting (Bakeman and Gottman, 1997) for the first two observations in a month. For further analysis, if an individual was seen more than once in a given month, daily scores were averaged over the month, giving a monthly body condition index (BCI) for each individual.

Data was analyzed using the computer program JMP 13.1.0. A general linear mixed model (GLMM) was conducted to compare the body condition of different sex and age classes, with individual as a random factor. To identify which sex-age classes differed from each other, we carried out post hoc Tukey-Kramer HSD tests. Analogous analyses were conducted to compare the BCI across different years. For comparing individual variation of BCI between sex-age classes for those individuals that were observed in two or more months, we used ANOVA with post hoc Tukey-Kramer HSD tests.

To determine the influence of rainfall and water level in the Udawalawe reservoir on BCI, we conducted a GLMM for each sex-age class separately, using BCI as the response variable, rainfall and water level as fixed effects and individual as a random factor. An interaction effect between water level and rainfall was retained in the model if this decreased the model's AIC value as compared to a model without the interaction effect.

Results

We recorded a total of 4009 body condition scores of 526 individual elephants during the study period with an average of 7.55 ± 5.61 (range 1-32) scores/day and 70.33 ± 34.11 (range 2-144) scores/month. One fifth of the elephants were seen multiple times in a month (Table 2). For the first two observations within a month, Cohen's kappa with quadratic weighting was 0.663 (N = 622), indicating good reliability of the BCI assessments.

After correcting for multiple encounters within each month, we recorded 3175 BCI at an average of 55.70 ± 26.42 (range 2-122) BCI/month.

A total of 218 adult females, 74 sub-adult males, 47 young-adult males and 208 mature-adult males were identified. The total number of sightings and computed numbers of monthly BCI respectively for each category were: Adult females 944 and 902; sub-adult males 409 and 329; young-adult males 387 and 302; mature-adult males 2269 and 1642.

The average BCI in all 4009 encounters was 7.83 ± 3.03 (range 0-14) and corrected for multiple sightings within a month 7.68 ± 3.04 (N = 3175). The most common BCI were 8 (386 elephants), 9 (482 elephants) and 10 (445 elephants), adding to 41.4% of all BCI (Fig. 3).

Of the 385 individuals that were observed more than once, most were observed 6 times (interquartile range 3-10, range 2-35). The minimum BCI was 5 or lower for 60% (interquartile range 3-7, range 0-12), and the maximum BCI was 10 or higher for 59% of these individuals (interquartile range 8-12, range 1-14). For 63% of individuals, the range of BCI was at least 4 (interquartile range 3-6.5, range 0-13). Overall, the range of BCI per individual was positively correlated with the number of observations ($r^2 = 0.31$, $P < 0.0001$, N = 385), but only for up to 10 observations (11 observations or more: $r^2 = 0.04$, $P = 0.074$, N = 86).

Comparing sex and age classes

The mean BCI of the 902 female scores for the study period was 5.44 ± 3.01 (range 0-13) and that of the 2273 male scores 8.56 ± 2.56 (range 0-14). With respect to the three classes of males, the 329 sub-adult male scores had a mean of 9.42 ± 2.20 (range 3-14), the 302 young-adult male scores a mean of 9.74 ± 2.00 (range 2-14) and the 1642 mature-adult male scores a mean of 8.17 ± 2.61 (range 0-14) (Fig. 4). There was a significant difference in BCI across the four categories (GLMM, P < 0.0001). Pair-wise comparisons revealed significantly different BCI between adult females, mature-adult males and both, young-adult or sub-adult males (Tukey-Kramer HSD, all P < 0.0001, Fig. 4). The BCI did not differ significantly between young- and sub-adult males (P = 0.8).

For the 157 adult females that were observed more than once, the mean, minimum and the maximum BCI were lower than for the male age groups (ANOVA, Tukey-Kramer HSD, all P < 0.0001), but the range of BCI was only smaller than in mature-adult males (p=0.0003). Further, mature-adult males showed a significantly larger range of BCI than sub-adult males (Tukey-Kramer HSD, P < 0.0001).

Annual variation of BCI

Pooled data for all scores showed significantly different BCI over the five study years (GLMM, P < 0.0001).

Adult females had significantly higher BCI in 2009 and 2012 compared to 2010 or 2011 (Tukey-Kramer HSD, $P \leq 0.0001$, Fig. 5). There was no significant difference in BCI between 2009 and 2012 (P = 0.617) or between 2010 and 2011 (P = 0.985) for adult female scores.

Mature-adult males had significantly higher BCI in 2008 than in any of the following four years ($P \leq 0.002$) and had lowest BCI in 2010. The BCI of adult males was significantly higher in 2009 and 2012 compared to 2010 or 2011 ($P \leq 0.0001$, Fig. 5).

In young-adult males the lowest BCI was found in 2010 (Fig. 5), which was significantly lower than in 2008 and 2009 (both P < 0.0001). Their BCI was highest in 2008, which was significantly higher than in 2010 (P < 0.0001), 2011 (P = 0.027) or 2012 (P = 0.045).

In sub-adult males the lowest BCI was found in 2011 and the highest in 2009 (Fig. 5), the latter was significantly higher than in 2011 (P = 0.005) and 2012 (P = 0.016).

Monthly variation of BCI

Adult females showed significant differences in BCI over the 12 months (GLMM, P < 0.0001). Overall adult female BCI was higher from January to August and lower from September to December (Fig. 6). BCI was significantly higher in April, May, June and July than in September, October or December (all P < 0.035).

Mature-adult males showed much less monthly variation in BCI (P = 0.022, Fig. 6). BCI was higher in June than in September (P = 0.018) or January (P = 0.022). No differences between months were found in young-adult males (P = 0.37). However, BCI of sub-adult males differed significantly across the months (P = 0.0007), showing a pattern similar to adult males (Fig. 6). Sub-adult males' BCI was significantly higher in June than in September (P = 0.004) or December (P = 0.002). All other monthly comparisons were not significant.

Water level of the reservoir and rainfall

In adult females, BCI was higher in months with lower water levels (GLMM, P = 0.029) and those with less rainfall (P < 0.0001; Fig. 7), the interaction between rainfall and water level was not significant (P = 0.403).

In mature-adult males, BCI was higher in months with low water level (P<0.0001), whereas rainfall did not influence BCI (P = 0.967, interaction with water level not significant). In young-adult and sub-adult males, neither water level nor rainfall exerted an influence on BCI (young-adult: both P > 0.286, sub-adult: both P > 0.077).

Discussion

We found the body condition of adult elephants in Udawalawe to vary seasonally. Thus, the observed results are consistent with a hypothesis of habitat quality having a major influence on elephant body condition. Contrary to expectations from rainfall and primary productivity, we found the body condition of elephants to be higher in the dry season than in the wet season. The opposite pattern was recorded in elephants at Mudumalai, India (Ramesh et al., 2011) and Eastern Cape, South Africa (de Klerk, 2009), in agreement with the expected positive relationship between rainfall and primary productivity. Thus, the pattern of body condition variation in Udawalawe is contrary to expectations and indicative of greater resource availability in the dry season. A sufficient explanation for this anomaly may be provided by the water level fluctuation in the Udawalawe reservoir and its effect on grass availability. The Udawalawe reservoir created by damming a major river, fills up with monsoonal rains in the wet season. With progression of the dry season, the water is gradually released for cultivation and the draw-down area becomes a lush grassland, which is heavily utilized by elephants. Therefore, elephants in Udawalawe experience a boon time with abundant fodder during the dry season, which is the opposite of resource availability patterns in 'natural' habitats. The body condition of adult elephants also showed inter-annual variation negatively correlated with the mean annual water level of the reservoir. The lowest BCIs in the study period coincided with the highest water level of the reservoir in 2010, providing additional support for the defining impact of reservoir water level on the body condition of elephants.

Differences between sexes and age classes

Adult female elephants in our study had lower average body condition than adult males. A marginal difference between males and females was observed in Mudumalai with 94.8% and 93% of adult males and females respectively having 'good' body condition and 2.9% of females but no males having 'poor' body condition (Ramesh et al., 2011). A study of translocated and non-translocated African elephants in Tsavo, Kenya found females to have significantly poorer body condition than males (Pinter-Wollman et al., 2009). Studies of captive elephants in India found no significant difference between the sexes (Wemmer et al., 2006), while in Sri Lanka females had significantly higher body condition (Godagama et al., 1998). Our results are consistent with the findings of other studies on free ranging elephants that have found males to display better body condition.

Elephants have a distinct social organization with group-living females and young, and solitary adult males (Douglas-Hamilton, 1972; Moss and Poole, 1983). Resource competition between members is one of the obvious costs of group living (Janson, 1988; O'Connell-Rodwell et al., 2011) and maybe particularly an issue for mega-herbivores. Asian elephants show sexual dimorphism in body size with adult males being around 3302 ± 430 kg and 262 ± 15 cm in height and adult females 2593 ± 298 kg and 235 ± 11 cm in height (Kurt and Kumarasinghe, 1998). The height and size advantage of males enables them to feed in a wider range of strata and access fodder that is not available to the smaller females. Males also tend to raid crops, which are far better in nutrition and energy content than any wild fodder, while females rarely raid (Chiyo et al., 2011; Ekanayaka et al., 2011; Ranjeewa et al., 2015). The average age at first reproduction in Udawalawe is 13.4 years and inter-birth interval 4 - 6.5 years (de Silva et al., 2013). With a gestation period of 22 months, nursing of young for 3-4 years (Lee, 1986) and possibly no reproductive senescence (Freeman et al., 2013; Mar, 2013) most adult females are either pregnant or nursing throughout life. Thus, the poorer body condition of females is likely a reflection of higher competition from conspecifics, greater energetic costs, and lower resource access. The patterns observed in the two studies of captive elephants, that of no difference between the sexes (Wemmer et al., 2006) and higher body condition in females (Godagama et al., 1998), likely reflect the non-reproductive status of most captive females and absence of sex biased variation in resource access under captive conditions.

We failed to find any previous studies that assessed body condition of elephants in relation to age/size categories. Of the three categories of males assessed in our study, mature-adults would be expected to have the highest BCI in consideration of resource access, due to their larger size. However, the lowest BCI was observed in mature-adults and the highest in young-adults. The BCI of sub-adult males lay in-between. Additionally, mature-adult and young-adult males did not show intra-annual variation in body condition, while sub-adult males displayed the same pattern as females.

A possible reason for the lower body condition of mature-adult males may be the annual expression of 'musth' by them. 'Musth' is similar to rutting behaviour of ungulates (Eisenberg et al., 1971) and its expression is age related with more mature and dominant individuals displaying more regular and extended periods of 'musth' (Poole, 1987). Males in 'musth' range over larger areas, incurring greater energetic costs (Fernando et al., 2008b) and lose body condition (Poole, 1982). Thus the advantage in resource access by mature-adult males may be offset by the greater costs of musth, leading to a lower BCI over the year. However, such an explanation is at odds with the observed lack of intra-annual variation in mature-adult males. Additional confounding factors could be male-biased crop raiding and movement of musth males in and out of the park. The patterns observed likely reflect a complex interaction of the different social, ranging and raiding behaviour and physical attributes of the size/age classes of male elephants, which influence costs, benefits and resource access.

The distribution of BCI scores in our study approximated a normal distribution with a total mean BCI close to the median of the scale. A study on wild elephants in Mudumalai India, using similar methodology but without individual identification, found most elephants to have 'good' body condition scores. Although comparison is limited because only categorical data was presented and not the actual scores, the Mudumalai study found 96.2, 2.4 and 1.4% of elephants having 'good', 'moderate' and 'poor' scores respectively (Ramesh et al., 2011), approximately corresponding to our scores of 9–14, 4–8 and 0–3 respectively. A study of wild elephants in South Africa using a visual scale of 0–8 found the majority of scores clustered around the median of the scale (de Klerk, 2009). Studies of captive elephants according to the methodology of Wemmer et al. (2006), using a scale of 0–12 found scores of 7.3 ± 0.02 in a pooled sample from India, Nepal and Myanmar (Wemmer et al., 2006) and a study in Sri Lanka using similar methodology found a score of 6.95 ± 0.26 (Godagama et al., 1998). The pattern of BCI scores we observed is comparable to most other studies in that the majority of scores clustered around the median of the scale, but not to Ramesh et al. (2011) where the scores were uniformly high. In any natural population the expectation would be an approximately normal distribution of scores. The difference in the Mudumalai study may be due to error in assigning scores, as completely subjective visual assessment is very sensitive to observer bias, or repeat sampling of individuals with high scores, due to non-identification of individuals.

Conservation implications

Irrigation reservoirs are a distinct feature of the dry zone of Sri Lanka with 30 major reservoirs such as Udawalawe and about 25,000 small reservoirs scattered across the landscape. Annual filling and emptying of the reservoirs prevent vegetative succession and promote grass growth in the fertile reservoir beds. The findings of our study highlight the importance of these reservoirs in providing valuable fodder for elephants in the normally resource poor, dry season. The ubiquity of reservoirs and the annual flux in water levels that create lush grasslands at the height of the dry season is likely a major factor in the very high density of elephants in Sri Lanka. Therefore, maintaining the *status quo* in terms of access of reservoir beds by elephants in the dry season and perpetuation of the established patterns of water level flux, is critical for elephant conservation in Sri Lanka.

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Appendix A. Supplementary data

Supplementary data (Appendices 1 and 2) associated with this article can be found, in the online version, at http://dx.doi.org/XXXXXXXXXX.

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Table 1
Criteria and scores used to assess body condition – modified from Wemmer et al. (2006).

Body area	Character	Score	Criteria
Head	Appearance of the temporal depression	2	Full (convex or flat)
		1	Slight to moderately concave; rim of temporal depression not well defined
		0	Deeply concave; rim of temporal depression sharply defined
Scapular	Prominence of the shoulder blades	2	Spinous process of the scapulae not visible, or slightly visible
		1	Spinous process and posterior edge of scapula visible as ridges
		0	Spinous process and posterior edge of scapula pronounced and bladelike with the acromian visible as a pronounced knot
Thoracic	Visibility of ribs	2	Ribs not visible, barrel smooth
		1	At least one rib visible, but the extent and demarcation not pronounced
		0	At least three ribs strongly demarcated with pronounced intercostal depressions
Flank	Appearance of area immediately in front of pelvic girdle	2	Convex
		1	Slight-moderately depressed
		0	Deeply depressed visible as a sunken area
Thoracic spine	Appearance of spine between shoulder and pelvic girdles	2	Not visible or very slightly visible as a ridge elevated from the body contour
		1	Visible as a clear ridge
		0	Visible as a prominent ridge
Lumbar spine	Appearance of spine between the pelvic girdle and base of tail	2	Smooth and rounded
		1	Bones slightly visible and more convex near the pelvis and the middle
		0	Bone segments clearly visible and more convex near the pelvis and the middle
Pelvic	Prominence of the pelvic girdle	2	Pelvic girdle not visible or slightly visible; area between the iliac crest and caudal vertebrae filled with tissue (and not forming a depressed zone)
		1	Visible but not pronounced; the rump is a slightly depressed zone between the ileum and the caudal vertebrae
		0	Visible as a jutting bone; rump is a pronounced sunken zone between ileum and the caudal vertebrae

Table 2

Number of times (N) an elephant was encountered within a month.

N	# encounters	%
1	2551	80.3
2	467	14.7
3	116	3.7
4	31	1.0
5	8	0.3
6	2	0.1

Figures

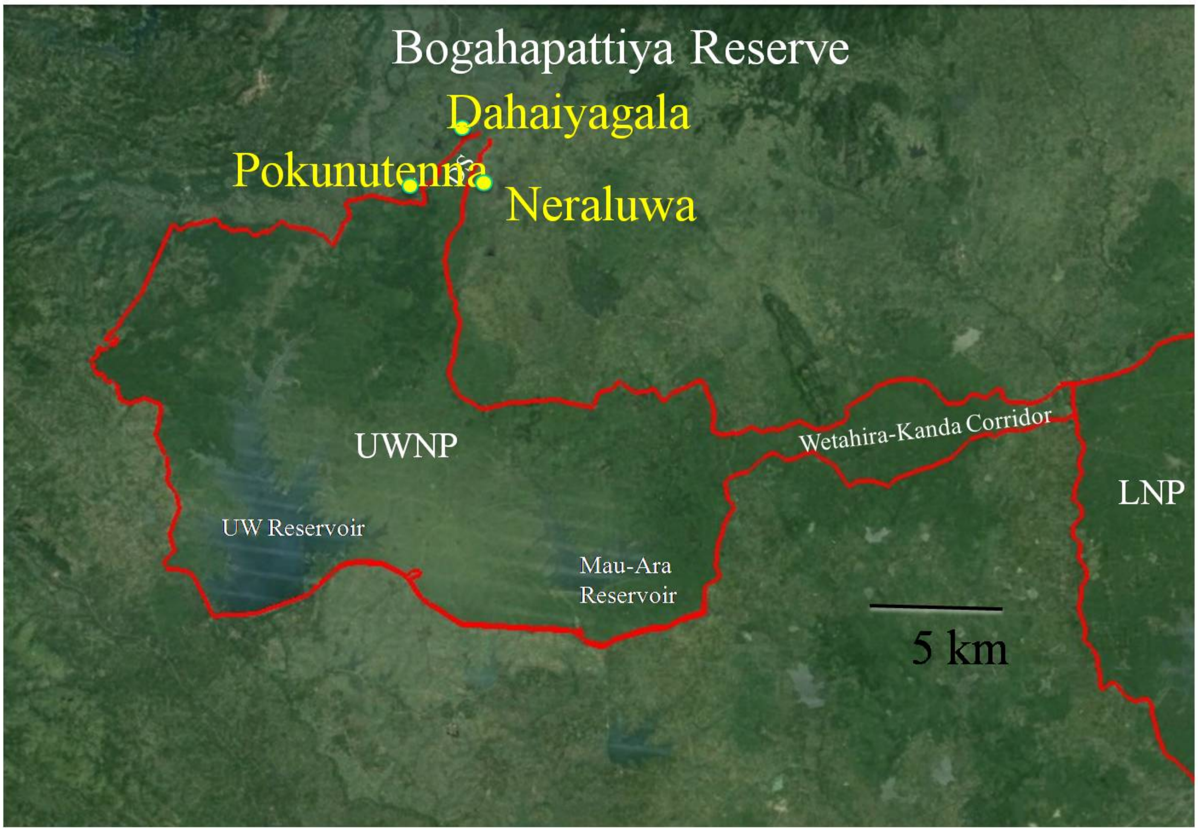

Fig. 1. Map of the Udawalawe National Park (UWNP), Dahaiyagala Sanctuary (DS) and parts of Lunugamwehera National Park (LNP). Electric fences at the park boundaries are marked with a red line. Image © 2011 Google Earth / Landsat / Copernicus.

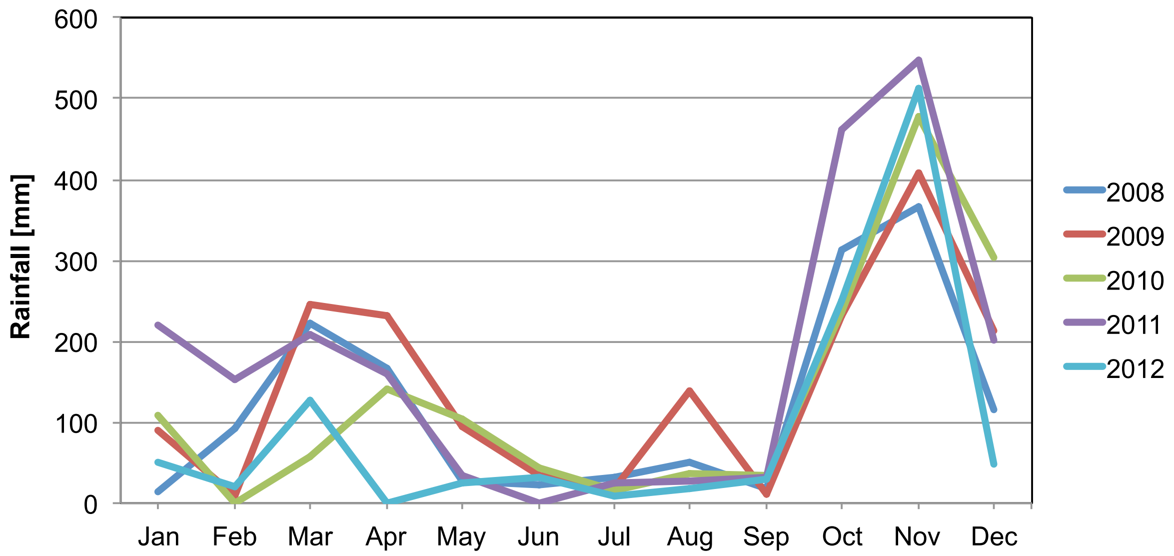

Fig. 2. Monthly precipitation from 2008-2012 in Udawalawe National Park.

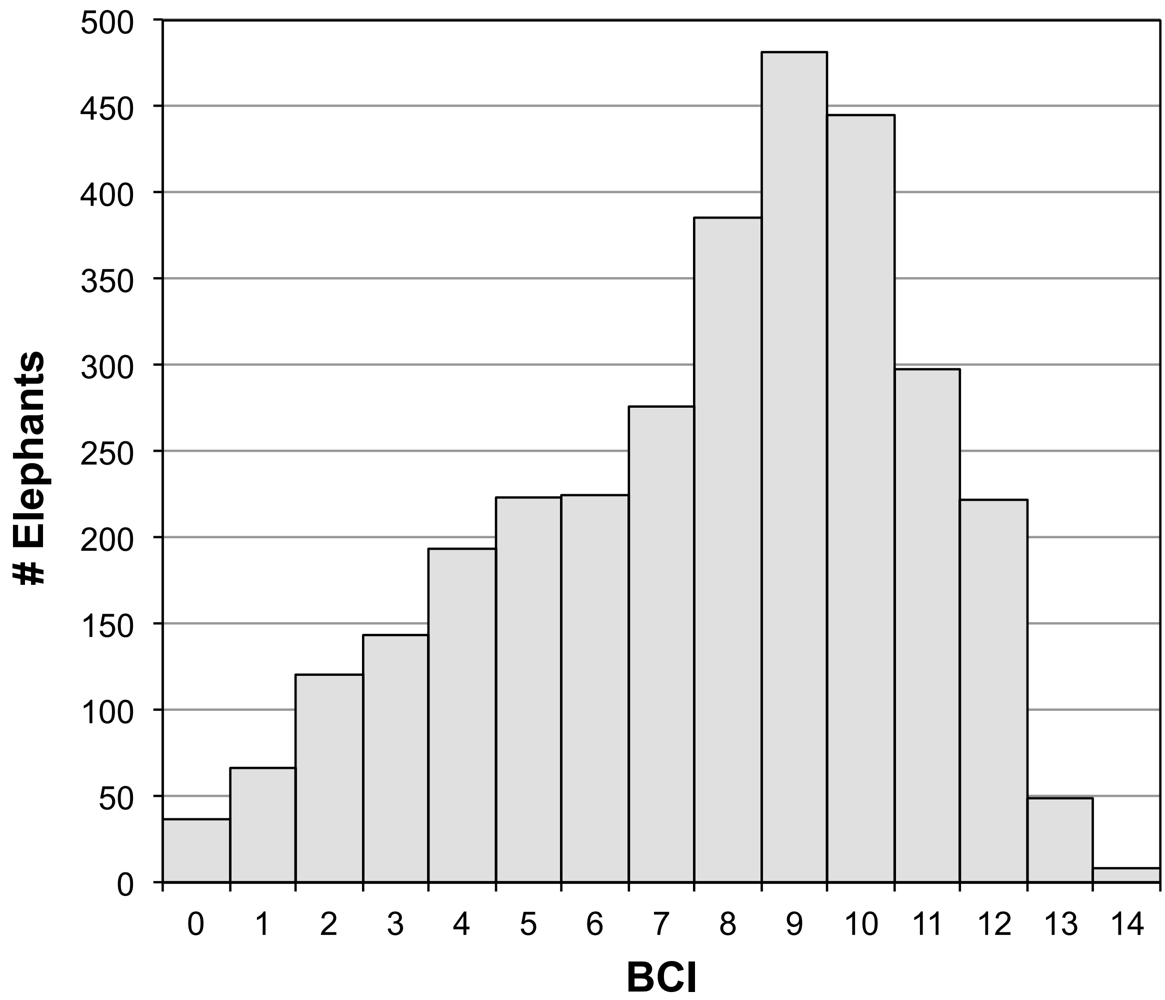

Fig. 3. BCI for 3175 elephant encounters. Each individual was only counted once per month.

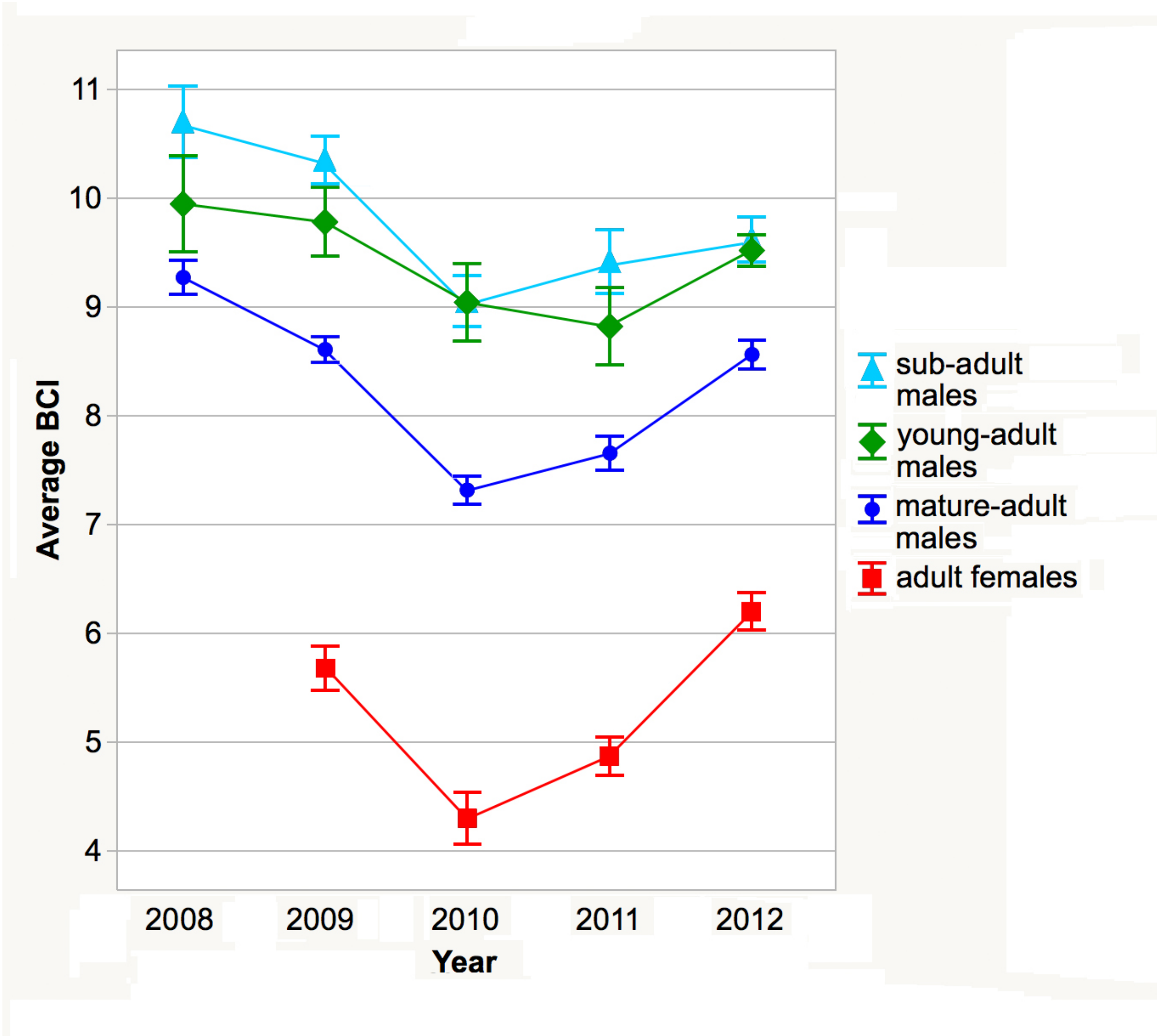

Fig. 4. BCI box plots for four sex and age classes. The horizontal line represents the grand mean. The comparison circles on the right visualize whether or not the mean values for the four categories are significantly different (no overlap) from each other.

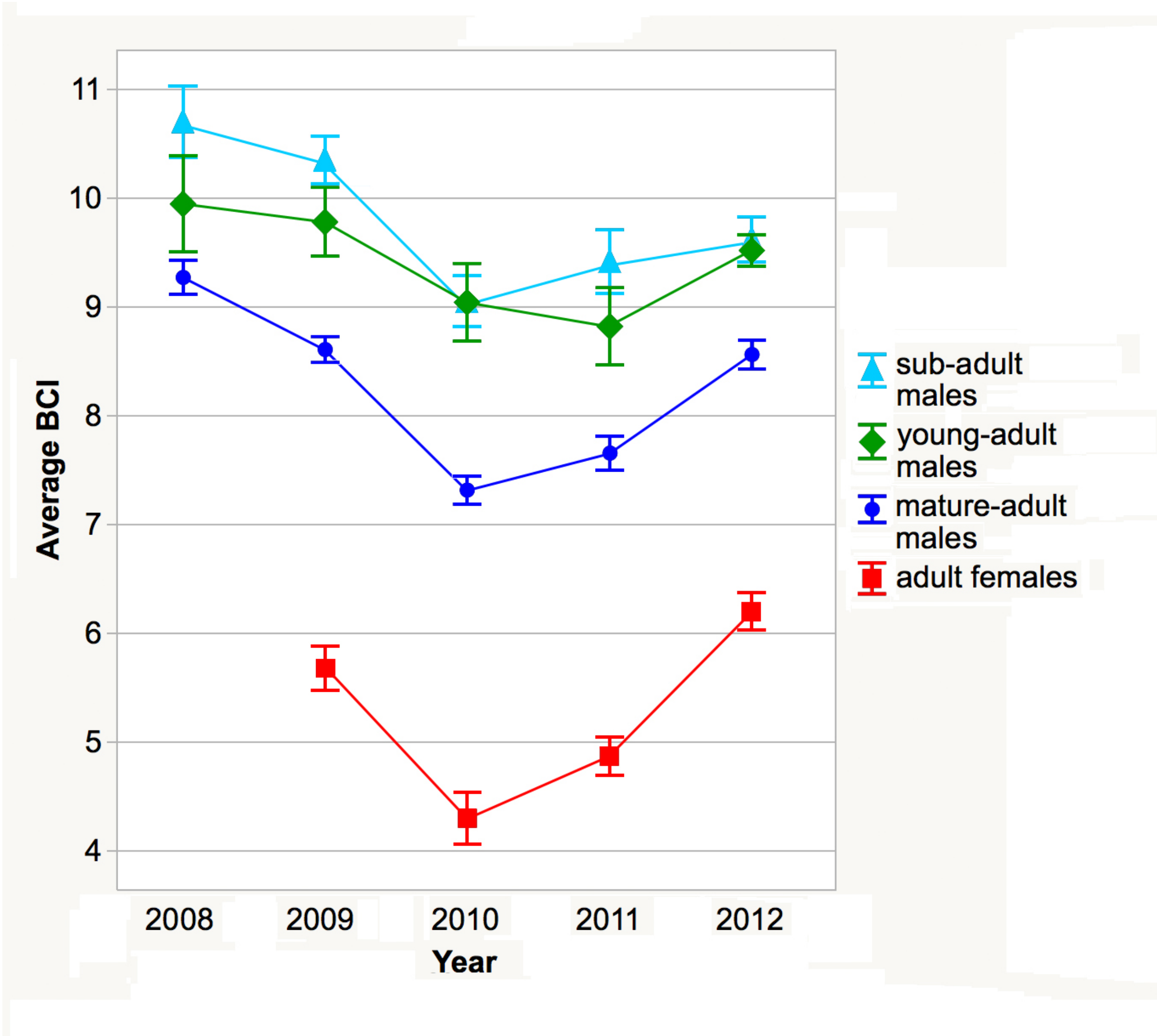

Fig. 5. BCI variation across years for each sex and age class. Standard error bars are provided.

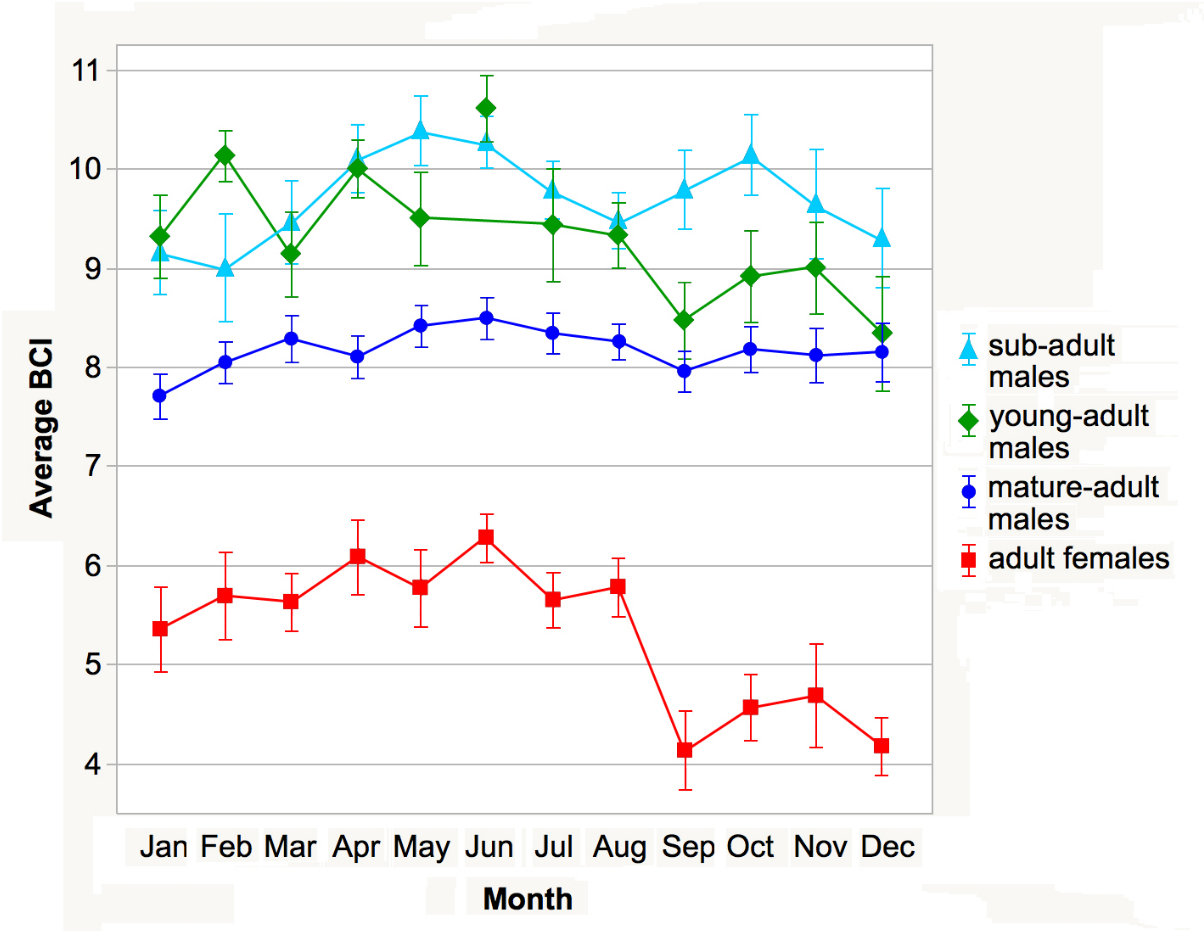

Fig. 6. Average BCI (with standard errors) across months for each sex and age class.

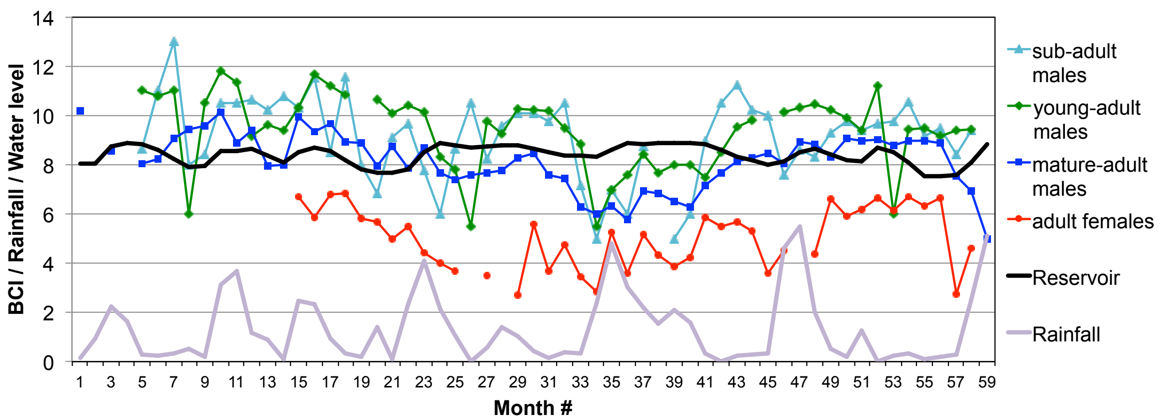

Fig. 7. Average BCI for each sex and age category in each month, monthly rainfall (x100 mm) and monthly water level of the reservoir (x10 m) from 2008-2012.