

SHORT COMMUNICATION

Life-history traits of gaur *Bos gaurus*: a first analysis

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ABSTRACT

In this first detailed analysis of gaur *Bos gaurus* life-history traits, data were collected from a 20-month field study in South India and from captive gaur populations. Mean age of females at first parturition was 3 years; females remained fertile beyond the age of 15 years. Adult females were three times more abundant than adult males in the wild; survival of females was greater than males beyond three years of age. Life span of both sexes has not exceeded 24 years in captivity. Gaur life-history traits are similar to those of other similar-sized Bovini species.

Keywords: Bovidae, demography, India, mortality, reproduction

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INTRODUCTION

Large herbivores exhibit life-history traits of the slow pattern: recruitment is low, maturity occurs late and generation times and life spans are long (Millar & Zammuto 1983). Also, survival is low in the pre-weaning stage, high in the prime adult stage and decreases in old age (Spinage 1972, Gaillard et al. 2004), and often, adult females have higher survival rates than adult males (Gaillard et al. 2000, Toïgo & Gaillard 2003).

Bovini tribe (family: Bovidae, sub-family: Bovinae) species such as the banteng *Bos javanicus* (Hoogerwerf 1970, Choquent 1993), African buffalo *Syncerus caffer* (Grimsdell 1969, Sinclair 1977, Prins 1996), American bison *Bison bison* (McHugh 1958, Fuller 1961, Vuren & Bray 1986) and European bison *Bison bonasus* (Kraśnińska & Kraśniński 2007) have life-history characteristics of the slow pattern. However, little

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is known of the life history of Asia's largest Bovini species, gaur *Bos gaurus*, apart from the opportunistic observations and interpretations of Schaller (1967).

Based on a 20-month field study of a wild gaur population in South India and data from the world's largest captive gaur population (Omaha's Henry Doorly Zoo) and India's largest captive population (Mysore Zoo), we present the first analysis of gaur life-history traits. Life-history traits correlate to body size (Calder 1996); allometric scaling of life-history traits is documented within large mammalian herbivores (Western 1979). Furthermore, phylogenetically similar species exhibit similar life-history traits (Fairbairn 1997). We therefore compared life-history traits of gaur with those of other Bovini species for which data were available: the banteng, African buffalo and American and European bison.

METHODS

Reproductive traits and life span

Data of captive gaur were compiled from: (i) gaur ($n = 41$) that were part of the captive gaur population at Mysore Zoo, South India (1994–2006); and (ii) gaur ($n = 130$) that lived their entire lives at Omaha's Henry Doorly Zoo, Omaha, USA (1968–2006). These combined zoo data were used to derive sex ratio at birth and life span of both sexes. Since mating was controlled by staff in Omaha Zoo, reproductive traits like age at first parturition and inter-birth interval were estimated using only Mysore Zoo data.

Age-sex structure and survival

To determine free-ranging gaur population structure by age and sex, two contiguous tiger reserves in South India – Mudumalai (329km²; 11°32'–43'N, 76°22'–45'E) and Bandipur (880km²; 11°36'–57'N, 76°13'–52'E) – were surveyed between January 2006 and August 2007. Most data were collected from a 200km² study area that was split equally between the two reserves. Given the difficulty in observing gaur in forested areas, and because gaur were more tolerant of humans in vehicles than on foot, the majority of data were collected by systematically sampling from over 3750km of the road network within the study area at dawn and dusk using an open-topped jeep.

Gaur were classified into three unsexed age classes below the age of 1 year (0–2, 3–5 and 6–12 months) and four (1–2, 2–3, 3–10 and >10 years) and five (1–2, 2–3, 3–5, 5–8 and >8 years) age classes for females and males, respectively, above the age of 1 year, based on methods described by Ahrestani (2009). Individuals were sexed and aged taking into account a combination of the size, shape and colour of the body, the ratio of white to black and the shape and size of the horns. A total of 1620 observed gaur were classified during the study. Despite pseudoreplication (Hurlbert 1984), the large sample size, the different habitats (dry deciduous and moist deciduous) sampled and the fact that different herds were sampled (based on comparisons of photographs of the animals sampled) meant that the data reflected a valid age-sex distribution of the gaur population.

Since information on sex ratio at birth from captive populations of gaur remained inconclusive (this study), reference was made to studies of other Bovini species that showed that sex ratio at birth did not differ significantly from parity: African buffalo, 1.00 (Grimsdell 1969, Sinclair 1977, Prins 1996); American bison, 1.00 (Green & Rothstein 1991, Fuller et al. 2007); European bison, 0.98–1.00 (Kraśińska & Kraśiński 2007, Mysterud et al. 2007); and banteng, 1.00 (Hoogerwerf 1970, Choquent 1993).

The lack of any size-based sexual dimorphism between the sexes in the first year of age (Ahrestani 2009) led us to assume that survival for both sexes of gaur through the first year is the same in the wild. Numbers of free-ranging male and female gaur in the first year were therefore calculated as half the number of gaur found below 1 year.

As a standardized age classification system was not used in previous gaur population studies, data from these earlier studies were compared to data from this study by grouping population structure data into gaur calves (C, <1 year), males (M, > year) and females (F, >1 year).

Data on age at death of 72 male and 58 female gaur from Omaha Zoo (1968–2006) were used to construct life tables and compare survival between both sexes.

RESULTS

Reproduction and life span

In Mysore Zoo, the mean age at first conception (primiparity) for females was 37.6 months (standard deviation = 3.8; $n = 5$). The mean inter-birth interval of seven births for three young females (<6 years old) was 398 days, and the oldest female in Mysore Zoo, who lived to about 18 years, reproduced 14 times during her lifetime with a mean inter-birth interval of 373 days.

The ratio of males to females at birth was 0.86 ($n = 41$) in Mysore Zoo and 1.36 ($n = 180$) in Omaha Zoo. Records from Omaha Zoo showed that the life span of females was greater than that of males: 17% of females ($n = 58$) lived beyond 15 years, the oldest reaching the age of 22.5 years; only one male (of 72) lived beyond 15 years, but this male lived the longest (23.6 years) of all 130 individuals sampled.

Age-sex structure

Adult females made up 50% of the free-ranging gaur population and were three times more abundant than adult males (Figs 1 and 2). This was consistent in three consecutive 6-month periods of the study: in January–June 2006 (male : female = 26.1:73.9), July–December 2006 (26.2:73.8), and January–June 2007 (24.4:75.6). Similar female-biased adult sex ratios were shown in other studies in India (Fig. 3).

Survival

The percentage of both male and female free-ranging gaur in each age category decreased from the age of one to three years: males decreased from 8.7% (1st year) to 4.7% (2nd year) to 3.0% (3rd year); females decreased from 8.7% (1st year) to 4.8% (2nd year) to 2.5% (3rd year; Fig. 2). Analysis of the captive gaur data from Omaha Zoo showed that females have higher survival than males through much of their life span (Table 1; Fig. 4).

DISCUSSION

Reproduction

The estimated 3 years of age at primiparity for captive gaur (Mysore Zoo, this study) cannot be directly applied to free-ranging female gaur. Our data, however, do suggest that female gaur become sexually mature at around 26 months. The average age at primiparity observed in free-ranging populations of other Bovini species like the banteng, American and European bison (Table 2) is 3 years (although ovulation

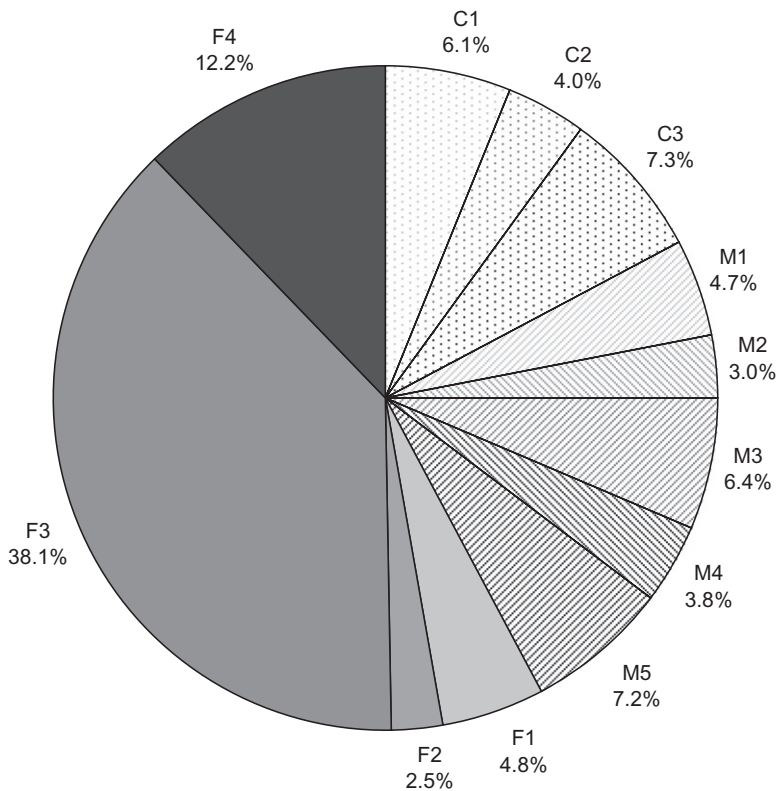


Fig. 1. Structure of gaur population found in contiguous Mudumalai and Bandipur National Parks, South India, between January 2006 and August 2007. Age-sex classes: C1 = calves 0–2 months; C2 = calves 3–5 months; C3 = calves 6–12 months; M1 = males 1–2 years; M2 = males 2–3 years; M3 = males 3–5 years; M4 = males 5–8 years; M5 = males >8 years; F1 = females 1–2 years; F2 = females 2–3 years; F3 = females 3–10 years; F4 = females >10 years.

in African buffalo can begin as early as 18 months, they have been observed to calve only at 4–5 years in the wild, making them the Bovini species that begin recruitment at the oldest age; Table 2). Our data on captive gaur together with the average age at primiparity of other Bovini species suggest that the age at primiparity for free-ranging female gaur is probably 3 years.

It appears that female gaur remain fertile in old age; an 18-year-old female in Mysore Zoo gave birth to her fourteenth calf a few months before her death. Old females of other Bovini species (Table 2) have also been observed to calve, and American bison females of over 40 years old have been seen accompanied by calves (McHugh 1958).

Data from Mysore Zoo showed that captive female gaur are capable of one birth a year, because the gestation period for gaur is ~ 9.5 months (Joe Sheppard, Omaha Zoo, USA & Dr Nanjappa, Mysore Zoo, India, personal communications; Hubback 1937, Schaller 1967). The calving interval between successive births for free-ranging gaur can be calculated from 'gestation time/fertility rate' (Sinclair 1977) and was found to be 838 days; the fertility rate was estimated as 0.34, which was the calves: 100 females ratios (Table 2). It is not unexpected for free-ranging gaur to have a

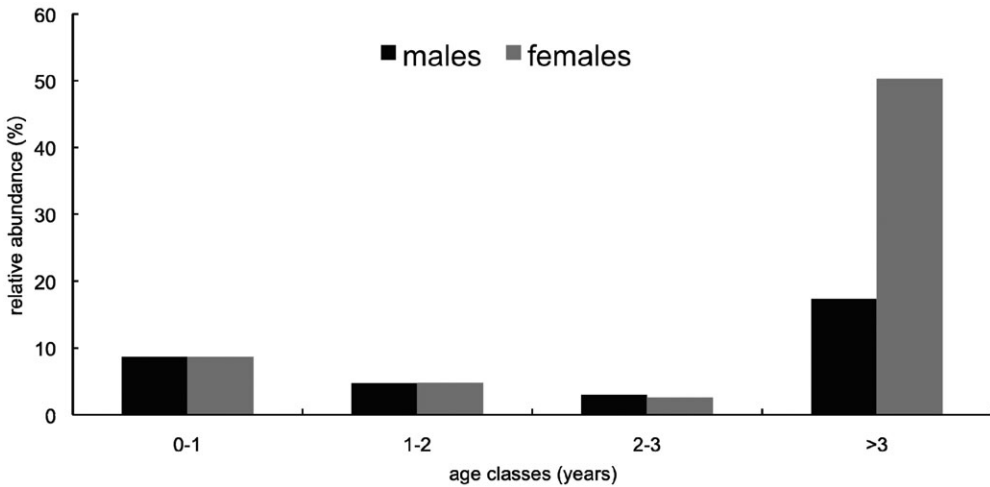


Fig. 2. Relative abundance of male and female gaur in four age classes found in Mudumalai and Bandipur National Parks, South India, January 2006–August 2007. Note: Gaur that are 0–1 years old are difficult to sex. Therefore, the relative abundance (%) of males and females in this age-class were each estimated as half the number of gaur found below 1 year.

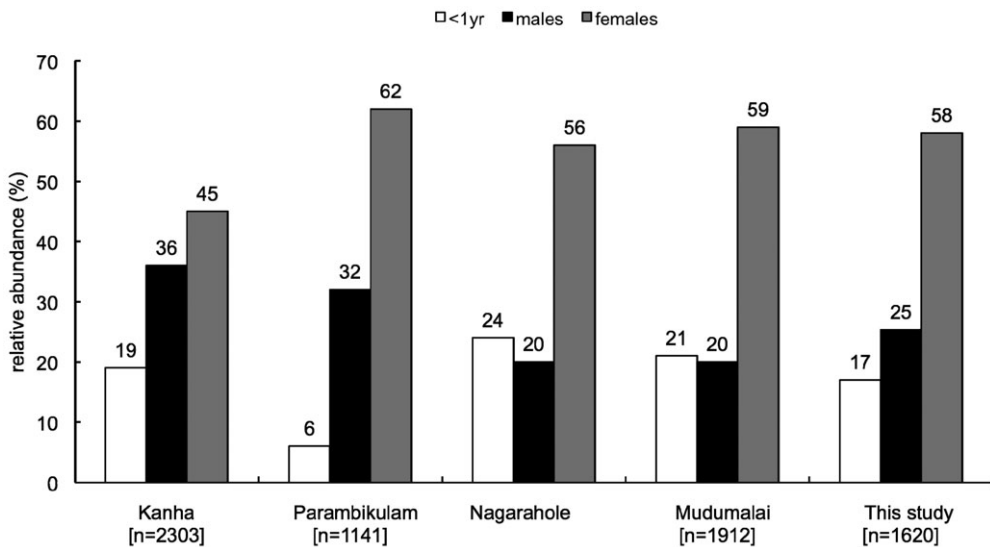


Fig. 3. Relative abundance of calves (<1 year), males (>1 year) and females (>1 year) found in the field study in comparison with four other gaur studies in India. Literature sources are: for Kanha National Park, Madhya Pradesh – Schaller (1967); for Parambikulam Wildlife Sanctuary, Kerala – Vairavel (1998); for Nagarahole National Park, Karnataka – Karanth and Sunquist (1995); for Mudumalai National Park, Tamil Nadu – Kumar et al. (2004); This study: Mudumalai and Bandipur National Parks, South India.

lower fertility rate than captive gaur, and our estimate was similar to what Schaller (1967) found for free-ranging gaur (Table 2). Also, it appears that gaur have a fertility rate higher than that of banteng, but half of that of free-ranging African buffalo and American bison (Table 2). We may have underestimated the fertility rate

Age	$l(x)$ males	$l'(x)$ males	$l(x)$ females	$l'(x)$ females
0	72	1000	58	1000
1	41	569	43	741
2	40	556	41	707
3	34	472	36	621
4	33	458	34	586
5	31	431	33	569
6	21	292	32	552
7	16	222	30	517
8	12	167	26	448
9	9	125	25	431
10	6	83	25	431
11	4	56	22	379
12	2	28	17	293
13	2	28	15	259
14	2	28	12	207
15	1	14	11	190
16	1	14	10	172
17	1	14	8	138
18	1	14	4	69
19	1	14	2	34
20	1	14	2	34
21	1	14	2	34
22	1	14	1	17
23	1	14	0	0
24	0	0	0	0
25	0	0	0	0

Table 1. Life table for gaur *Bos gaurus*

Source: Captive population data from Omaha Zoo.

$l(x)$ = number of individuals surviving to age x (years).

$l'(x) = l(x)$ transformed to an initial population of 1000 individuals.

in free-ranging gaur; calves could have been missed during surveys because of their small size, their light brown colour that makes them blend in well with the undergrowth, and their habit of sitting concealed in undergrowth (Hubback 1937).

Although the average inter-birth interval of free-ranging female gaur is unknown, if it is assumed to be equal to the highest inter-birth interval found in other wild Bovini species – 52–54 weeks for American bison (Green & Rothstein 1991) and European bison (Kraśnińska & Kraśniński 2007) and 1–2 years for African buffalo (Grimsdell 1969, Prins 1996) – gaur females reaching the age of 20 years can be expected to produce ~ 8–10 calves in their lifetime.

Survival

Adults

The higher percentage of adult females found in gaur populations is also found in many other large herbivore species (Berger & Gompper 1999). Although the probability of detecting solitary animals, usually adult male gaur, might have been less than that of detecting herds mainly composed of adult females, we are confident that the adult gaur sex ratio in our field study area is female biased, because (i) despite their solitary nature, the probability of detecting adult males in the field was high because of their large size and their indifference to human presence; (ii) all four

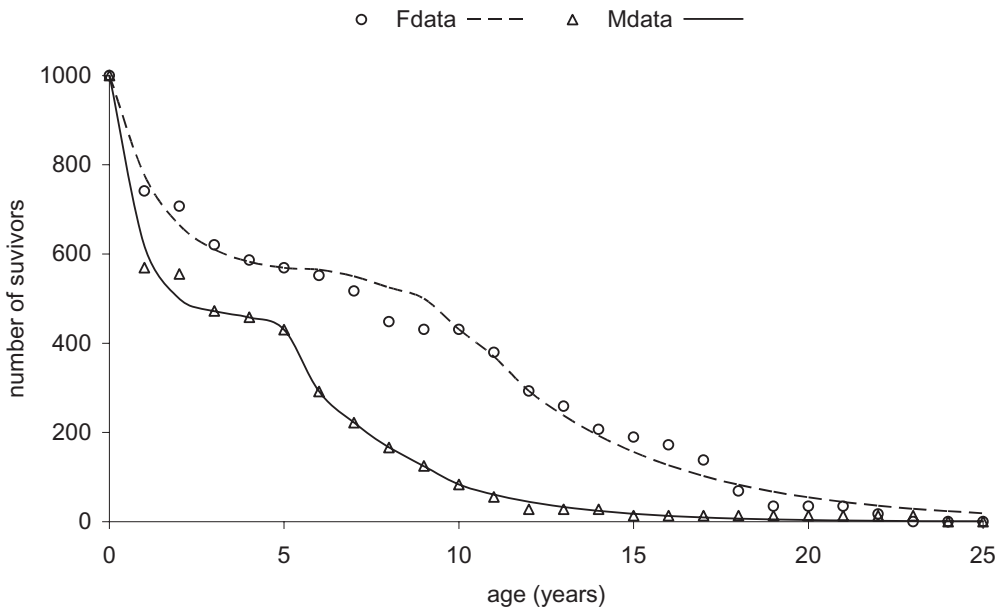


Fig. 4. Survival curves fitted to data of age at death for female (Fdata, $n = 58$) and male (Mdata, $n = 72$) gaur in the world's largest captive gaur population at Henry Doorly Zoo, Omaha, Nebraska, USA, 1968–2006. The data were adjusted to an initial population of 1000 individuals for each sex.

Table 2. Life-history traits of gaur *Bos gaurus* compared to those of other Bovini species

Species	Primiparity	Oldest age at conception (years)	Calves:100 adult females	Maximum longevity
<i>Bos gaurus</i>	3 years ¹	18 ¹	34:100 ¹ 35:100 ⁹	F : 24 years ¹ M : 23.6 years ¹³
<i>Bos javanicus</i>	3 years ²	24 ²	23:100 ²	20–25 ²
<i>Bison bison</i>	92% pregnant at 3 years ³ 82% pregnant at 3 years ⁴	40+ ³	62:100 ¹⁰ 76:100 ¹¹	F : 40+ years ³ M : 20+ years ³
<i>Bison bonasus</i>	3–4 years ⁵	24 ⁵	48:100 ⁵	F : 23–27 years ⁵ M : 20–22 years ⁵
<i>Syncerus caffer</i>	4 years ^{6,7,8}	16 ⁷	70:100 ⁶ 74:100 ¹²	23–25 years ^{6,8,14}

Sources: ¹this study; ²Hoogerwerf (1970); ³McHugh (1958); ⁴Green and Rothstein (1991); ⁵Krasińska and Krasiński (2007); ⁶Sinclair (1977); ⁷Grimsdell (1969); ⁸Prins (1996); ⁹Schaller (1967); ¹⁰Vuren and Bray (1986); ¹¹Bradley and Wilmshurst (2005); ¹²Jolles (2007); ¹³Crandall (1964); ¹⁴Spinage (1972).

other studies of wild gaur populations in India show a similar result (Fig. 3); and (iii) female-biased adult sex (M:F) ratios were reported in all studies of other Bovini species: banteng, 0.32 (Hoogerwerf 1970); domestic cow *Bos taurus*, 0.61 (Berteaux 1993); American bison, 0.56–0.84 (Vuren & Bray 1986, Gates et al. 1991, Berger & Cunningham 1994); European bison, 0.68 (Krasińska & Krasiński 2007); African buffalo, 0.22–0.63 (Sinclair 1977, Prins & Iason 1989, Aremu et al. 2007).

In most extant ungulate populations, males die disproportionately to their abundance, probably because enhanced growth rates in males predispose them to greater mortality than females; solitary males dispersing from mixed herds experience greater mortality; and the intensity of intra-male competition results in greater male mortality (Berger & Gompper 1999). Karanth and Sunquist (1995) found that adult female and adult male gaur comprised 23% and 15% of tiger *Panthera tigris* kills, respectively, in Nagarahole National Park, South India. This 1.5:1 mortality ratio was reported with a 3:1 (56:20) adult female: adult male ratio, suggesting higher mortality due to predation of male than female gaur. In Omaha Zoo (Fig. 4), where gaur were free from predation, males had lower survival than females. This finding is supported by the comprehensive captive animal populations review by Kohler et al. (2006), who found female hoofstock survival to be higher than male survival by 38%. Both zoo results suggest that males are probably physiologically predisposed to a shorter life span than females. While injuries sustained during fights between large herbivore males may cause death directly or indirectly (Geist 1986), fights are rare between adult male gaur (Schaller 1967, FSA, personal observations) as well as between males of other Bovini tribe species (Hoogerwerf 1970, Prins 1996, Krawińska & Krawiński 2007).

Research on the diets of the three major predators that overlap in range with gaur in India, the tiger, leopard *Panthera pardus* and dhole *Cuon alpinus* (Johnsingh 1992, Karanth & Sunquist 1995, Venkataraman et al. 1995, Ramakrishnan et al. 1999, Andheria et al. 2007), indicates that tigers are the most significant predators of gaur: gaur constitute 8–24% of tiger diet, less than 3% of leopard diet and less than 2% of dhole diet.

Calves

Karanth and Sunquist (1995) found that young (<1 year) gaur made up nearly 60%, 88% and 100%, respectively, of tiger, leopard and dhole gaur kills. Furthermore, mortality of African buffalo calves has been found to be as high as 50% (Sinclair 1977), mortality of banteng in the first 6 months has been reported to be 26% (Choquent 1993), and mortality of gaur calves in Omaha Zoo was 36% (this study). This suggests that wild gaur calf mortality may be high in India.

CONCLUSIONS

Gaur, in accordance to their large body mass, exhibit life-history traits of the slow pattern similar to other Bovini species: females begin recruiting for gaur populations after the age of 3 years, but remain fertile in old age; survival of adult female gaur is higher than that of adult males, beyond the age of three; and gaur are long-lived species, maximum lifespan in captivity reaching 24 years. It is important to note that environmental and ecological factors, such as carrying capacity, food availability, drought and predation rate, may significantly affect the life-history traits of individuals.

There is a need for further studies that include monitoring animals of known ages in the wild to make better estimates of age-specific vital rates of this vulnerable species.

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