

## Reproductive seasonality and rate of increase of wild sambar deer (*Rusa unicolor*) in a new environment, Victoria, Australia

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### ABSTRACT

Sambar (*Rusa unicolor*) are the most numerous and rapidly expanding of Australia's six introduced deer species, however, there is little information about the reproductive biology of sambar deer in their natural habitat. To better predict and manage wild sambar populations in Australia it is important to understand their reproductive seasonality and rate of population growth. From results of the present study, there is reporting of field estimates of age at first breeding, reproductive lifespan, juvenile survival, adult bodyweights and fecundity to derive estimates of the current and intrinsic rates of increase for sambar in Victoria, Australia. Mean age of first reproduction was estimated to be 1.8 years, approximately 80 % of hinds calved between April and August, juvenile survival was estimated as 0.81 and age of last reproduction 12.75 years. Seasonality of reproduction is apparently compressed at 36° latitude compared to sambar at the equator indicating a response to photoperiod. Demographic data were used to estimate the current rate of growth of the Victorian population using the two stage Lotke-Euler equation and age-specific schedules of survival and fecundity in a life table. These estimates of  $r$  were 0.21 and 0.14, respectively, inferring annual rates of population increase of 24 % and 15 %. These data are in the context of a population which, even though there is a marked harvesting, is reportedly growing and dispersing northwards. Suggestions for how this information can inform management decisions directed at the conservation for sustainable use and/or population reduction in Australia are made.

### 1. Introduction

Sambar (*Rusa unicolor*) are the largest and most widespread of the Asiatic deer species comprising seven subspecies that occupy a range of native habitats from west India to Malaysia (Leslie, 2011). In Australia where 21 animals of a founder population were released between 1862 and 1873 (Bentley, 1978) sambar deer have colonised more than 70,000 km<sup>2</sup> of Victoria and lesser areas of two other states (Forsyth et al., 2015). Sambar are considered both a game hunting resource and a potential threat to agriculture and native biodiversity (Bennett and Coulson, 2010; Davis et al., 2016). In Victoria, approximately 40,000 licensed hunters killed almost 90,000 sambar in 2016 (Moloney and Powell, 2019) and contribute more than AU\$100 million annually to the local economy (Henderson

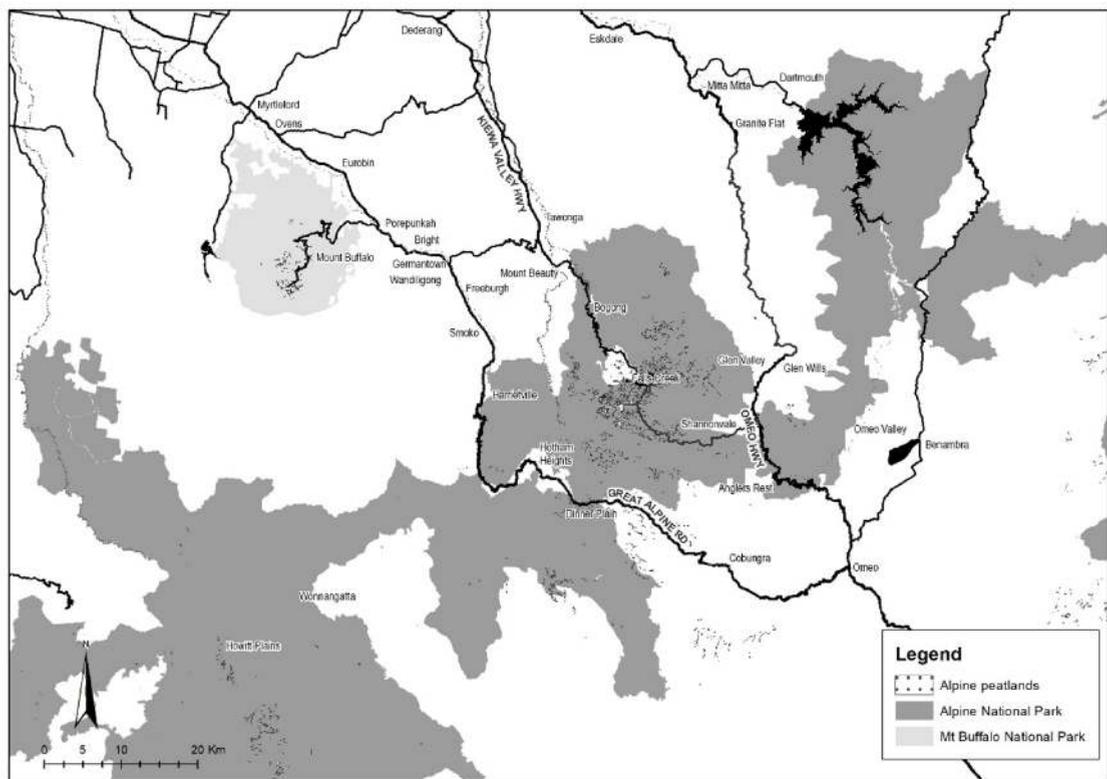
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a.



b.

Fig. 1. (a). Map of Australia with inset 1(b). Location of study site in Victoria (ArcMap, 2020).

et al., 2014). The contrasting view of sambar as a pest species is based on their effects on primary production (Lindeman and Forsyth, 2008), and negative effects on the environment through herbivory, wallowing and antler rubbing behaviour (Bennett and Coulson, 2010). Although estimates of sambar numbers are imprecise there is general agreement that the distribution and abundance of sambar in Australia is increasing and that there is a paucity of information describing their reproductive characteristics (Lincoln, 1992; Loudon and Brinklow, 1992) and current rate of increase in numbers.

Although a principal factor for expansion of wild populations is successful reproduction, data sets on the reproductive biology of wild sambar are scarce (Loudon and Brinklow, 1992; Asher, 2011) probably due to the logistical difficulties of studying this shy, cryptic and largely nocturnal animal (Matsubayashi et al., 2007; Leslie, 2011). From previous studies, there is acknowledgement that there are some observational bias and lack of precision in data collection (Eisenberg and Lockhart, 1972; Mishra, 1982; Flynn, 1990), however, there is concurrence that cycles of male antler development (Ramesh et al., 2013) and birth frequencies are somewhat seasonal or non-seasonal, consistent with other cervids evolving within 20 degrees of the equator (Lincoln, 1992). Reports regarding captive sambar at increasing distances from the equator indicate that at 1 °S in Malaysia sambar calve during all months with 6 %–12 % of births occurring in each month (Dahlan and Dawend, 2013), at 23 °S in Taiwan most sambar births occurred in the 4 months from March to June (Chan et al., 2009), and in New Zealand at 40 °S 6 %–22 % of calves were born in each of 9 months with the largest numbers being during April and May. Any increased seasonality of birth frequency at greater distances from the equator (Loudon and Brinklow, 1992) is equivocal and indicates only a minor response to photoperiod (Asher, 2011). This is in contrast to cervids of temperate origin which in the case of moose at 63 °N, there is a 95 % concentration of calving within a 16-day period (Bowyer et al., 1998). This evolutionary adaptation of temperate cervids that results in timing of calving and lactation to coincide with periods of optimal nutrition (Lincoln, 1992) applies also within species. Red deer (*Cervus elaphus*) calves born mid-season have greater survival rates than those born several weeks later (Clutton-Brock et al., 1982). The essentially non-seasonal reproduction of equatorial cervids is consistent with the thought that there will be no increase in calf survival associated with seasonal nutrition, but the timing of increase in birth numbers for sambar in their natural temperate habitats is not known.

Throughout their introduced and native ranges, sambar are subject to anthropogenic harvests and sustainable rates of harvesting depend on rates of population increase. Hunting of sambar within their native range is believed to contribute more to the decreases in animal numbers for this species than habitat loss (Leslie, 2011) and harvest numbers from these populations exceeds the capacity for maintenance of the population. In contrast the annual harvest of sambar in Victoria has increased each year for the past decade (Moloney and Powell, 2019) with the belief that the overall population is similarly increasing.

Sambar are the most numerous and rapidly expanding (Moriarty, 2004) of Australia's introduced deer species but there have been no recent studies in which there was evaluation of reproductive biology in the Victoria, Australia region. To more precisely predict and manage sambar populations in Australia it is important to (1) understand their reproductive seasonality and the capacity of sambar to adapt to temperate climates by calving at particular times and (2) estimate the rate of population increase, based on field estimates of demographic measures such as age at first breeding, reproductive lifespan, juvenile survival and fecundity.

## 2. Materials and methods

### 2.1. Location and animals

This study was performed with animal ethics permission granted through the University of Queensland (permit SAFS/ANRFA/080/18) and permission to source animal samples in State Forest and National Parks in Victoria granted by the Department of Environment, Land, Water and Planning (permit number 10,008,679). Animal samples were sourced from a broad area in the approximate centre of the distribution of south-eastern Australian sambar around a latitude of 36.8 °S (Fig. 1). The region comprised the catchments of the Kiewa, Mitta, Ovens and Cobungra rivers with elevations in this region ranging between 250 and 1980 m. Where land is suitable for agriculture, tenure is generally private and on steeper gradients or in areas where there is significant conservation value, tenure is public, either State Forest or National Park. Land types at lower elevations are alluvial river flats utilised for horticulture and dairy farming with some irrigation and at higher elevations undulating land is utilised for cattle grazing. At elevations above those used for agriculture (–450 m) mountain slopes were heavily vegetated with alpine (*Eucalyptus delegatensis*) and mountain ash (*E. regnans*) to a variable altitude of –1400 m. Areas of natural treeless plain with alpine grassland occur at elevations between 1400 and 1980 m and include some 2000 ha of Alpine peatlands, listed as endangered as a result of the Commonwealth Environmental Protection and Biodiversity Conservation Act (1999). Snowfalls occur annually between 800 and 1980 m from May to October with snow remaining for 4–6 months at higher elevations. Temperatures at Mt Beauty (366 m elevation) range from mean February maxima of 29 °C to mean July minima of 2.1 °C and average precipitation of 1263 mm. Falls Creek at 1780 m has a mean January maxima of 18 °C, mean July minima of –2.9 °C and average precipitation of 2242 mm. In both locations approximately 65 % of precipitation occurs between May and October (Australian Bureau of Meteorology, 2019).

The regions sambar inhabit depend on the season of the year, with animals present at lower elevations year-round and some animals present at elevations above 1400 m following snow-melt in late spring and remaining there until the following winter. Timing and rate of plant growth differs with the elevation gradient depending on amount of moisture and the increasing temperatures during spring (Stockdale, 1983). Growth of annual and perennial grasses and forbs is most rapid during September and October and slowest during January and February (<https://www.evergraze.com.au/>).

## 2.2. Sample collection

Samples were taken from 144 sambar that were killed by professionals during culling ( $n = 66$ ), and commercial meat harvests ( $n = 68$ ) and by recreational hunters ( $n = 10$ ) during 2018 and 2019 on private property, state forest and national park lands. Animals were killed during every month except August principally at night by professional shooters on foot using thermal imaging equipment for detection and large calibre suppressed rifles. Animals were mainly solitary or in small groups and were killed on an opportunity basis rather than selectively so as far as possible randomising the samples for the present study. Where females were accompanied by offspring, the offspring were also shot. Animals were confirmed dead, measured (nose tip to tail tip; cm) and girth (body circumference immediately posterior to the front legs; cm), incisor teeth were taken for aging by the cementum annuli method (Hamlin et al., 2000), and where possible whole carcasses (male  $n = 9$ ; female  $n = 9$ ) were weighed by meat harvesters inclusive of gut fill. The relationship between the weight and girth (Millsbaugh and Brundige, 1996) of those animals weighed was used to estimate weights of the other animals evaluated in the present study. For males, the stage of antler development was recorded (stage of velvet growth; < or > half developed, hard antler); for females a lactation score was assigned (1 = nil milk, 2 = moderate milk able to be expressed from teats and 3 = abundant milk readily expressed from engorged teats). Foetal characteristics, where present, were recorded (weight; kg), length crown-rump (cm) (Hamilton et al., 1985), and sex, although determining the sex of foetuses weighing less than approximately 20 g was impossible in the field.

## 2.3. Estimating age of adult sambar

Primary (medial) incisor teeth ( $n = 144$ ; 79 females, 65 males) were submitted to a laboratory (Matsons, Manhattan, Montana) where the staff specialised in the aging of wild animals. Deciduous incisor teeth from animals less than 1 year of age (Leslie, 2011) were aged by inspection and where permanent incisors were present age estimation was conducted by the histological analysis of cementum. Although the physiology which determines cementum layering is not fully understood, it is considered to develop in a seasonal cycle and is more pronounced in temperate than tropical regions (Moore et al., 1995) that are more likely to have variations in seasonal nutritional availability. There are no reports of accuracy of age estimation from sambar of known age, however, in north American cervids, accuracy of age estimation is greater than 85 % in temperate regions to the age of 14 years, which far exceeds the age accuracy estimates based on teeth eruption and wear criteria (Hamlin et al., 2000). Individuals within any cohort, however, may have as much as a 12 month range in actual ages because annuli are deposited during winter whereas sambar may calve during any season of the year. Ages were reported based on the number of annuli present in the teeth to provide an estimate in integers; so to estimate the timing of life history events such as age at first parturition those animals with one annular ring were assumed to be 1.5 years old.

## 2.4. Aging foetuses

The gestational age of foetuses was estimated using two methods based on the weight and length of the developing foetus. The relationship between the cube root of foetal weight and gestational age in mammals (Huggett and Widdas, 1951; Mayor et al., 2019) is linear from conception to parturition and has previously been applied to fallow (*Dama dama*) (Armstrong et al., 1969), white-tailed (*Odocoileus virginianus*) (Short, 1970) and sika deer (*Cervus nippon*) (Suzuki et al., 1996). Gestation length in cervids varies by as much as 7 % in mature and more in younger hinds (Asher, 2007) but is for the most part genetically programmed within a species (Asher, 2011). In the present study, a regression line was formed using an estimated mean gestation length of 258 days (Moore, 1994; Chan et al., 2009), and the cubed foetal weight at term of 8.1 kg, based on the single heaviest foetus from the present study, without differentiating by sex due to the similarity of male and female foetal weights (Leslie, 2011).

The relationship between foetal length (crown to rump) and gestational age is also linear beyond approximately 35 days gestation (Hamilton et al., 1985). A regression line was similarly developed using the length of the closest to full term foetus available for evaluation in the present study (87 cm).

The accuracy of estimating gestational age using foetal weights and lengths has been determined by weighing and measuring white-tailed deer foetuses from females euthanized at known intervals following mating (Hamilton et al., 1985). Gestational age and date of tissue evaluation were used to estimate date of conception and parturition to derive monthly frequency of births.

## 2.5. Determining calving date by stage of lactation

Mean duration of lactation in sambar is 85 days (Chan et al., 2009) and milk production measured in Iberian red deer (*Cervus elaphus hispanicus*) reportedly decreases from approximately 2–4 weeks postpartum (Landete-Castillejos et al., 2000) dependent, in fallow deer (*Dama dama*), on pasture quality (Glatz et al., 2005). In the present study calving dates were estimated for lactating hinds by subtracting 30 and 60 days from necropsy dates for hinds with lactation score 3 (abundant milk,  $n = 21$ ) and 2 (moderate milk,  $n = 6$ ) respectively. The use of lactation scores to assign calving dates was used secondarily to foetal measurements due to the subjectivity of assigning scores, likely variations in lactation between individuals and distorting situations where females may have been sampled after having lost offspring.

## 2.6. Reproductive cycle of stags

The stage of annual antler development (English, 1992; Moore, 1994) was recorded for all stags; either hard antler (231 days), or

velvet antlers (125 days) (Semiadi et al., 1994) estimated to be less or more than half mature size. The estimated hard-antler stage of those stags in velvet, together with stags in the hard antler stage of development, was used to estimate the months in which stags were in the hard antler stage of development and in readiness for the mating season (Ramesh et al., 2013).

## 2.7. Method of calculating rate of increase

The rate of increase of a population has been calculated differently, in the literature, according to available data to derive variations of  $r$  with different meanings and applications. The maximal or intrinsic rate of increase ( $r_m$ ) that assumes optimal nutrition and no predation or disease has been estimated using different means according to the available morphologic or demographic data (Fryxell et al., 2014). This measurement of a population's capacity to expand is both species and site specific (McCallum, 2008). For herbivorous mammals an approximate estimate of  $r_m$  can be derived by scaling adult body weight to an exponent (Caughley and Krebs, 1983) expanded by Duncan et al. (2007) to include the association between weight and  $r_m$  of 69 mammalian species described using the following equation:  $\log_{10} r_m = 0.0533 - 0.27606 \log_{10} W$  (Jim Hone, personal communication 4 June 2020) where  $W$  is mean adult live weight in kg.

Where demographic data are available from animal populations more accurate estimates of  $r$  are derived using variations to the Lotka-Euler equation (McCallum, 2008) including the two stage equation (Hone et al., 2010):

$$\frac{\lambda^\alpha \left(1 - \left(\frac{S}{\lambda}\right)\right)}{1 - \left(\frac{S}{\lambda}\right)^{w-\alpha-1}} = lb$$

Where  $\lambda$  is the rate of population increase  $\lambda = e^r$ . Fecundity ( $b$ ) that has been defined in different ways as either the rate of female calves born (Fryxell et al., 2014) or surviving (McCallum, 2008) was estimated in the present study as the ratio of female to male foetuses. The  $\alpha$  symbol is considered the age of first reproduction from birth (mean age of hinds at first parturition),  $w$  as the age of last reproduction,  $l$  as juvenile survival rate (calculated as the ratio of 2 to 1-year-old animals) and adult survival ( $S$ ) is assumed to approximate one (Hone et al., 2010).

Estimates of  $r$  can be used to estimate the proportion ( $P$ ) of a population increasing at the rate  $r$  required to be removed annually to maintain (or alter) the size of the population (Hone et al., 2010):

$$P = 1 - (1/e^{r^m})$$

## 2.8. Calculating $r_s$ using life tables

Where the ages of individuals are known, and there is random sampling of females, life tables have been used to generate age specific rates of survival and mortality, and estimate the rate of change in a population. The methodology of Caughley (1977) was used in the construction of the life table with log-polynomial smoothing to counter the fact that a sample such as this can result in age classes that are not monotonically decreasing. The number born (age class 0) was calculated using the fertility data. Because females were missing for age classes 10 and 13 or there were few animals in some classes these were estimated by fitting a logistic model to the cumulative fertility and then working backwards to age specific fertility. Calculation of  $r_s$  from a lifetable was achieved by applying the basic Lotka-Euler equation to age specific rates of survival and fecundity (Cole, 1954; Caughley, 1977; Krebs, 2009). Assumptions included a rapid growth rate, consistent fecundity, small death rate and stable age distribution.

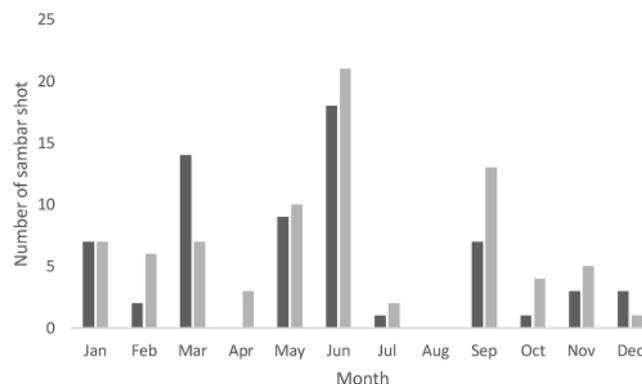


Fig. 2. Timing of monthly sample collection of male (black) and female (grey) sambar.

### 3. Results

#### 3.1. Timing of sample collection

Sambar of both sexes were killed during all seasons (range for males and females combined; summer 26 to Autumn 43; Fig. 2).

#### 3.2. Age structure of the herd

The ages of 22 juvenile sambar were estimated by gross inspection of incisor teeth and the remaining 122 animals by histological examination. Clear and distinct annuli were visible emanating progressively from the cementum-dentine margin of histological specimens. More complex annuli were present at the periphery of the cementum layer in slides from some older animals where interpretation relied on 'scrolling' through focal planes. There were 85 % of specimens assigned the greatest classification of certainty by Matson's laboratory and 15 % assigned a classification of certainty to within 1 year of the estimate.

Cohort sizes of both males and females were largest among younger age groups reducing and stabilizing among prime age animals of 4–7 years (Fig. 3). Females represented 65 % of the sample and as determined in cervid populations elsewhere had longer lifespans than males (Gaillard et al., 2003).

#### 3.3. Weights of male and female sambar

Girth measurements (cm) were strongly associated with body weight inclusive of gut fill (kg; male  $n = 9$ , female  $n = 9$ ) with  $R^2$  values of 0.92 and 0.90 for males and females, respectively. Body weights for the other animals were derived using girth measurements from animal carcasses (male  $n = 65$ , female  $n = 79$ ) and the relevant regression equations (Fig. 4). Weights of sambar hinds ranged from 117 to 184 kg among 2-year-old animals and 119–196 kg among hinds aged 3–7 years old. Weights of 2-year-old sambar stags ranged from 138 to 254 kg and from 171 to 293 kg among those aged from 3–7 years old. The average weight of mature females (>3-year-old) was 68 % of that of mature males indicating some extent of sexual dimorphism consistent with that recorded elsewhere among sambar (Dahlan and Dawend, 2013).

#### 3.4. Incidence of pregnancy and lactation

Of the 12 hinds estimated to be less than 1-year-old, three (25 %) were pregnant whereas fertility increased among hinds aged 1 year and older ( $n = 67$ ), 82 % were either pregnant or lactating or both (Table 1). Among hinds greater than 1 year of age, 55 % ( $n = 37$ ) were pregnant, 30 % ( $n = 20$ ) were assigned lactation score 3, and 9% ( $n = 6$ ) were assigned lactation score 2. Of the 26 lactating females, eight were concurrently pregnant with early stage foetuses. Eleven females 1 year of age and older (16 %) were neither pregnant nor lactating. A total of 40 foetuses were recorded of which the sex could only be determined in 28 at a ratio of 19 males to 9 females. No twins were recorded in the present study, although the rate of twinning reported by venison harvesters that were not involved with the present study was an estimated 0.3 % (personal communication, Ian Scholz 2019).

#### 3.5. Seasonality of parturition

There was a close association between foetal length and the cube root of foetal weight ( $R^2 = 0.99$ , Fig. 5), hence predictions of parturition dates were identical when calculated using either values for foetal length or weight. Birth frequency by month was estimated using foetal measurements ( $n = 40$ ) or lactation ( $n = 18$ ) scores but, where both were available, foetal measurements were used. Sambar births were predicted to occur in each month except December with the greatest frequency of births (69 %) between April and July inclusive (Fig. 6).

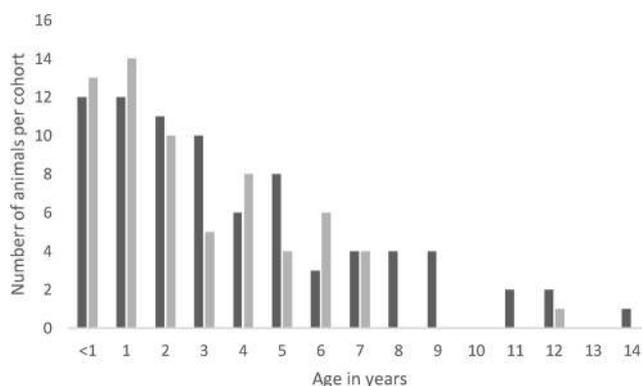


Fig. 3. Cohort sizes of male ( $n = 65$ , grey) and female ( $n = 79$ , black) sambar studied in Victoria.

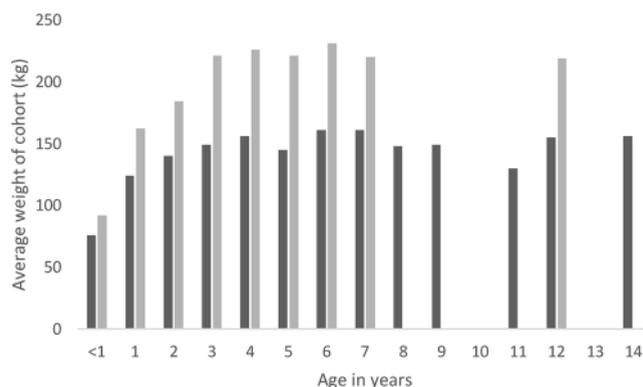


Fig. 4. Average weight of male ( $n = 64$ , grey) and female ( $n = 79$ , black) sambar cohorts in Victoria.

Table 1

Female sambar pregnant, lactating, both pregnant and lactating, and neither pregnant nor lactating in cohorts aged <1 year to 14 years.

Age (years)	Number in Cohort	Pregnant	Lactating only	Pregnant and Lactating	Neither Pregnant nor Lactating
<1	12	3	0	0	9
1	12	6	3	1	3
2	11	6	4	1	1
3	10	5	3	2	2
4	6	5	0	1	1
5	8	6	1	2	1
6	3	2	1	1	0
7	4	2	2	0	0
8	4	3	0	0	1
9	4	0	3	0	1
11	2	0	1	0	1
12	2	2	0	0	0
14	1	0	0	0	1
Total	79	40	18	8	21

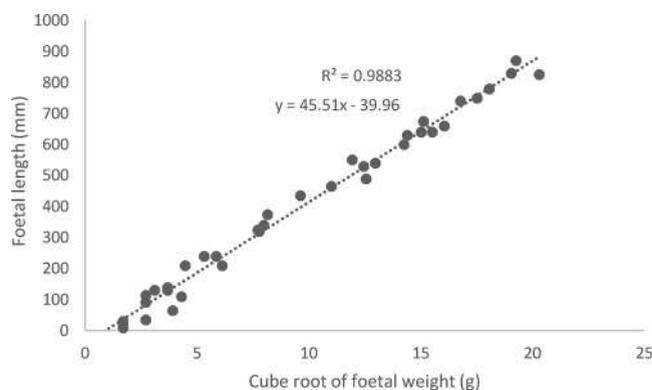


Fig. 5. Linear relationship between cubed root of foetal weight (g) and foetal length (mm),  $n = 38$  from birth to parturition with an estimated gestation length of 258 days.

After adjusting the stage of antler development in stags (velvet antlers < or > half developed and hard antler) to the hard antler stage of development stags were recorded in hard antler developmental stage during all months except April with a peak for this classification in stags 3 years and older between June and November.

### 3.6. Calculating rate of increase using allometric and demographic methods

Allometric estimation of  $r_m$  based on mean weight (189 kg) of adult sambar aged 3 years and older ( $n = 64$ ) was 0.27 inferring an annual rate of increase of 31 % and a requirement to remove 24 % of the population annually to maintain a stable population. Demographic data from the present study ( $\alpha$ ,  $b$ ,  $l$ ,  $w$ ) were used to calculate  $r$ , using the two stage Lotka-Euler equation. Age of first

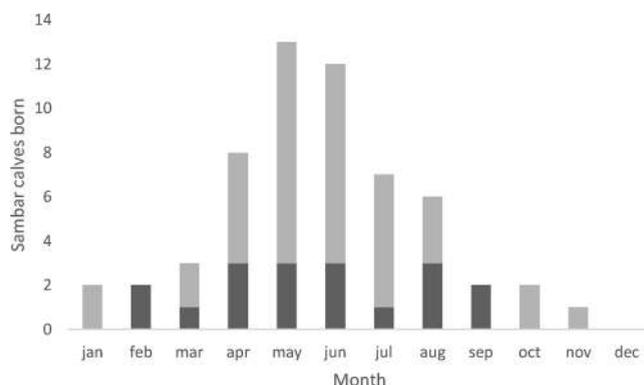


Fig. 6. Frequency distribution of sambar births per month derived using foetal measurements where available ( $n = 40$ , grey), or lactation score ( $n = 18$ , black).

reproduction ( $\alpha$ ) was estimated based as the mean alpha of reproductively active females from the cohort known to be at least 1-year-old but assumed to be 1.5 years. Based on three of the cohort lactating and a mean 121 days to calving for six pregnant hinds the mean age at parturition was 1.8 years and fecundity ( $b$ ) was 0.32 (nine females: 19 males). Juvenile survival ( $l$ ) was estimated to be 0.81 based on the ratio of 2-year-old animals to 1-year-old animals using the procedures of McCallum (2008). The age of last reproduction ( $w$ ) was 12.75 years based on the mean 90 days to calving for two hinds aged as 12-years, and adult survival ( $S$ ) was assumed to be 1 (Hone et al., 2010). Using the two-stage equation  $r = 0.21$ , inferring an annual rate of population growth of 24 % and a required annual removal of 19 % of animals to maintain a stable population. The estimate of  $r_s$  derived from a lifetable (Table 2) was 0.14 inferring an annual growth in the population of 15 % and a required annual harvest of 13 % to maintain a stable population.

## 4. Discussion

### 4.1. Seasonality and survival

Sambar in alpine and sub-alpine Victoria have a seasonal pattern of calving at 36 °S with approximately 80 % of hinds predicted to calve during the 5 months between April and August, however, this seasonal pattern is not as distinct as that of animals of many other species. These findings are consistent with hunter sourced data (Bentley, 1978; Draisma, 1978) in Victoria and represent a more distinct breeding season compared with sambar closer to the equator (Dahlan and Dawend, 2013). Hours of daylight in northern Victoria vary by more than 5 h between summer and winter making it likely that sambar residing in temperate environments do respond to variation in day-length. Seasonality among temperate cervids is principally attributed to photoperiod (Loudon and Brinklow, 1992) although other factors such as nutrition or social cues may affect the timing of reproduction (Lincoln, 1992). Some distortion may also arise when results from short term studies are evaluated which do not account for differences in annual nutritional access that effects the timing of first and subsequent pregnancies among cohorts of temperate cervids (Gaillard et al., 2003). Results from the present study indicate sambar in Victoria generally mate in spring and calve in winter.

As a consequence of seasonal calving in Australian sambar, there is likely to be optimisation of the rate of increase of the

Table 2

Life table of 79 female sambar;  $x$  = age,  $f_x$  = number surviving at each age,  $l_x$  = probability of surviving to a specific age interval,  $d_x$  = probability of dying in each age interval,  $q_x$  = mortality rate and  $p_x$  = survival rate; \*Calculated from fertility data.

$x$	$f_x$	Smoothed $f_x$	$l_x$	$d_x$	$q_x$	$p_x$
0		22*	1.00	0.41	0.410	0.59
1	12	13	0.59	0.04	0.068	0.93
2	12	12	0.55	0.10	0.182	0.82
3	11	10	0.45	0.04	0.089	0.91
4	10	9	0.41	0.09	0.220	0.78
5	6	7	0.32	0.05	0.156	0.84
6	8	6	0.27	0.04	0.148	0.85
7	3	5	0.23	0.05	0.217	0.78
8	4	4	0.18	0	0	1.00
9	4	4	0.18	0.04	0.222	0.78
10	4	3	0.14	0.05	0.357	0.64
11		2	0.09	0	0	1.00
12	2	2	0.09	0	0	1.00
13	2	2	0.09	0.04	0.444	0.56
14		1	0.05	0	0	1.00
15	1	1	0.05			

population. Seasonal timing of reproduction among temperate species is thought to result in maximisation of the survival of juveniles. Malnutrition is considered the largest contributor to juvenile mortalities and survival of the young accounts for most of the variation in growth rates of ungulate populations (Gaillard et al., 2000). Successful lactation (Loudon and Brinklow, 1992) and the quality of forage available to weanlings (Shin et al., 2000) largely determines the viability of offspring (Lincoln, 1992). Considering the majority of sambar births occur during winter, peak lactation periods and weaning coincide with spring when herbivore nutrition in Victoria is usually optimal. Availability and quality of nutrition from annual and perennial grasses as well as forbs in Victoria increases from July and is maximal in October, before there is an annual minimal availability in late summer (January and February) (<https://www.evergraze.com.au/>). Conversely, the survival rate of 14 % of calves born between November and March may be less likely due to malnutrition resulting from reduced plant growth, plant senescence and consequently inferior nutritional quality in the food sources available during this period (Gaillard et al., 2000). The demographic profile of adult sambar indicate differences between male and female rates of survival with 16 % of females living beyond 7 years to a maximal recorded age of 14 years, whereas among males less than 2 % were 7 years of age.

#### 4.2. Population growth

Data from the present study enabled rates of increase to be calculated by several means. The  $r_m$  is an estimation of a species intrinsic capacity to increase population numbers based on measures of maximal rather than mean productivity. Estimates from the present study are affected by variable nutrition and an unknown amount of predation, therefore, making a demographic estimate of  $r_m$  implausible. Life history events among captive sambar; puberty by 7 months (Asher et al., 1997) and reproduction to age 20 (Harrison, 2010) indicate that demographic estimates of  $r_m$  exceed the  $r$  and  $r_s$  values estimated in the present study. The allometric estimation of  $r_m$  (0.27) approximated the estimation of  $r$  derived using the Lotka-Euler equation (0.21) which likely results in an overestimation of the actual rate of increase by assuming adult survival to be one. Estimation of  $r_s$  derived from a life table (0.14) was somewhat less and likely to be more accurate than other estimates by using actual rates of mortality among cohorts.

The current rate of increase ( $r_s$ ) of the Victorian sambar population was estimated as 0.14 inferring a 15 % per annum rate of change in population size based on age specific rates of fecundity and adult survival. This apparent 15 % per annum population increase occurs in Victoria when there is also a -15 % per annum annual increase in sambar harvest by hunters (Moloney and Powell, 2019). In the absence of more precise data this infers there is a resilient population with there being an annual increase (Imperio et al., 2010) in sambar numbers that is greater than the numbers harvested by hunters of -90,000 animals. Sambar hunting at current or moderately greater rates of harvest appears sustainable. Where management is directed toward minimising ecological damage control efforts need to be implemented to reverse the current rate of sambar population growth. If management practices to more precisely control the sambar population cannot be implemented, there should be strategic sambar population control in confined areas where the conservation value is great.

The dispersion of the sambar population into regions where these animals have not previously been resident is speculated to be the result of population density in areas of close proximity to regions in which sambar are dispersing (Harrison, 2010), particularly the distribution into eastern Victoria since 1930 (Forsyth et al., 2015) and the Australian Capital Territory since 2007 (Mulvaney et al., 2017). This dispersion into these regions that have not previously been a habitat for sambar is occurring due to a northward expansion into alpine and sub-alpine habitat that is conducive to sambar survival and reproduction. These areas are largely devoid of large wild generalist herbivores which might compete for food and a large amount of apparently suitable but not occupied habitat exists at the northern margin of the current range for sambar. Results from bioclimatic modelling indicate sambar are most suited to large areas of northern Australia. Presently, however, sambar only occupy areas of southern Australia radiating from sites of original release but in habitat that is less conducive for population growth because of conditions that are not as desirable for animal survival and reproduction as some areas of northern Australia (Moriarty, 2004).

The possibility of medium-term expansion of the sambar population remains in Australia with this expansion in numbers being consistent with the eruptive paradigm when herbivores are introduced into a region (McShea et al., 1997). This scenario contrasts that of native populations where over exploitation and habitat destruction have reduced numbers such that since 2008 sambar have been listed as vulnerable with most endemic populations rapidly decreasing (Timmins et al., 2015).

Abundance and distribution of deer are difficult to determine (Amos et al., 2014), however, efforts to monitor increasing population numbers of sambar in Australia should be maintained so that there can be predictions as to areas in which there should either be actions taken for targeted sambar population control or asset protection measures implemented. The combined recreational and commercial harvest rates of sambar are not limiting growth of the population and any landscape scale control needs to consider the size and trajectory of the current population. Alternatively, or inevitably sambar may become generally accepted in the Australian landscape as a naturalised species to be managed only through agricultural or ecological necessity.

#### 5. Conclusions

The present study is the first to document reproductive seasonality and rate of increase of wild sambar in a new and temperate environment, in Victoria Australia. Sambar reproduction at latitude 36 °S contrasts the reproductive behaviour of sambar at the equator by being seasonal and occurring at rates greater than those of native equatorial populations. Management of sambar for conservation purposes, sustainable use or as a pest species (Sinclair, 1997) requires knowledge of their reproductive potential in specific environments.

## CRediT authorship contribution statement

**K. Watter:** Conceptualization, Methodology, Investigation, Data curation, Writing - original draft. **E. Thomas:** Conceptualization, Methodology, Writing - review & editing. **N. White:** Data curation, Formal analysis, Writing - review & editing. **N. Finch:** Conceptualization, Methodology, Investigation, Data curation, Writing - review & editing. **P.J. Murray:** Conceptualization, Methodology, Investigation, Data curation, Writing - review & editing.

## Declaration of Competing Interest

The authors report no declarations of interest.

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