CSIRO PUBLISHING

The Rangeland Journal, 2019, **41**, 293–299
https://doi.org/10.1071/RJ18113

Decline in body condition and high drought mortality limit the spread of wild chital deer in north-east Queensland, Australia

Kurt Watter[A,C], *Greg Baxter*[A], *Michael Brennan*[B], *Anthony Pople*[B] and *Peter Murray*[A]

[A]School of Agriculture and Food Sciences, The University of Queensland, Gatton Campus, Qld 4343, Australia.
[B]Biosecurity Queensland, Queensland Department of Agriculture and Fisheries, 41 Boggo Rd, Dutton Park, Qld 4102, Australia.
[C]Corresponding author. Email: watter@bigpond.net.au

Abstract. Chital deer (*Axis axis*) were introduced to the Burdekin district of northern Queensland, Australia in 1886. Compared with most successful ungulate introductions they have been slow to expand their distribution and increase in abundance (Moriarty 2004). In this study we consider the possibility that forage shortages caused by periodic droughts have caused sufficient mortalities to limit the increase and spread of chital in the region. The Burdekin district experiences fluctuations in forage according to seasonal rainfall as well as multi-year droughts. This study recorded the decline in body condition, measured as kidney fat index (KFI) and bone marrow fat (BMF), over the wet and dry seasons of two successive years in two chital deer populations during a period when annual rainfall was ~40% below average. We relate the falls in mean KFI from ~45–15%, and mean BMF from ~80–50% to the surveyed decline in chital populations of ~80%. The extent of the decline implies increased mortalities in all age classes as well as reduced reproductive output. We propose that it is likely that chital populations have experienced several such drought mortality events since the 1890s which have contributed to their limited spread.

Additional keywords: *Axis axis*, bone marrow fat, kidney fat index.

Received 26 November 2018, accepted 17 June 2019, published online 10 August 2019

Introduction

Chital or Indian spotted deer (*Axis axis*) are endemic to south Asia including India, Bangladesh, Sri Lanka and Nepal and have been successfully introduced to several countries including the USA, Brazil, Argentina and Australia (Sankar and Acharya 2004). Despite an ability to inhabit a range of forest types in their native range (Dave 2008) the species has had variable success in new habitats. Some introduced populations have failed to persist and others have expanded at low rates suggesting the species and its new environment are poorly suited (Bentley 1978). Success of a species in a new environment is influenced by founder population size, food, water, shelter availability, and a relative lack of competitors for these resources, low rates of predation (Pimm 1989), and factors influencing the health of individuals including disease and parasites. Identifying those factors that limit population size enable predictions as to the extent to which a species may spread. In Australia there is increasing recognition of the potential for deer species to expand their range and increase in abundance (Davis *et al*. 2016).

Chital released in the Burdekin district of northern Queensland in 1886 established free-living populations, but those released on the Darling Downs of southern Queensland around the same time did not. By 2014 (128 years after release) chital had spread some 100 km from the point of release in northern Queensland. Within this invaded range chital distribution is not uniform with localised high-density populations but low overall densities recorded by aerial survey (Brennan and Pople 2016). There is little published information on chital numbers in northern Queensland but (Brennan and Pople 2016) estimated a population of 32 000 animals in 2014. Over the subsequent two years, chital populations surveyed on two different cattle grazing properties declined by more than 80% during a period when the two-year rainfall total was ~40% below the long-term average. Between February 2014 and April 2016 chital densities on Spyglass station declined from >10/km^2 to <2/km^2. Between December 2014 and April 2016 chital densities on nearby Niall station declined from >60/km^2 to <4/km^2 with the most substantial declines during 2015 (Brennan and Pople 2016). In this paper we aim to provide an explanation for this decline by making the temporal link between subnormal rainfall, historically low forage availability, and poor body condition of adult chital. We suggest that drought reduced forage resources sufficiently to cause nutritional stress in chital and that declines in body condition were significant enough to cause sufficient mortalities to affect population size.

The nutritional status of wild animals has been assessed using estimates of fat deposits at various locations in an animal's body (Nieminen and Laitinen 1986). Total fat percentages in the bodies of white-tailed deer (*Odocoileus virginianus*) correlate with kidney fat indices (KFI; Finger *et al*. 1981), which correlate strongly with bone marrow fat (BMF; Nieminen and Laitinen 1986). Fat is not deposited uniformly throughout the body but when nutrition allows fat is deposited first in the bone marrow, then around the kidney, and lastly in subcutaneous tissues (Riney 1955). During times of condition loss fat is first utilised from the subcutis and lastly from the marrow.

When energy intake is limited fat stores are utilised for the maintenance of physiological functions as well as the additional cost of functions such as growth and reproduction. The adequacy of fat reserves for individuals vary accordingly. Growing deer require approximately twice the energy of adult hinds, which in turn, have an increasing energy demand during pregnancy and approximately twice maintenance requirement during lactation (Mulley and Flesch 2001). Increased energy requirements for reproduction in deer applies to both males and females and in the case of red deer (*Cervus elaphus*) in approximately equal measure (Bobek *et al*. 1990). Although the metabolic demand for antler growth in male red deer is ~1% of the annual energy budget the energy expended during the 30-day rut period is ~25% of the annual energy budget (Bobek *et al*. 1990). A similar energy cost would be expected to apply to chital, but they do not follow a synchronised breeding season but are known to mate and give birth in any month (Bentley 1978). Birth frequency in Queensland is highest in the wet season, and rutting activity is most common during the dry season (A. Pople, unpubl. data).

Models of ungulate dynamics suggest that species weighing more than 30 kg are almost always extrinsically regulated (Caughley and Krebs 1983) through dynamics created by interactions between animals and their environment. Under conditions of high population density should growth rates of large mammal populations decline animal classes are affected in a predictable order. Initially juvenile survival is reduced followed by increased age at first reproduction, reduced reproductive output in mature females and finally increased adult mortality (Eberhardt 2002). The resulting fluctuations in animal density vary according to the extent of the environmental change with sudden sharp changes in numbers representing an extreme case of population restructuring.

Fat stores in herbivores reflect the health of the population but oscillate around a long-term and potentially variable equilibrium (Caughley 1970*b*). As indices of body condition both KFI and BMF are useful at different stages of fat depletion with KFI reflecting short-term food availability and requirements and BMF reflecting longer-term nutritional conditions (Takatsuki 2000). If food is limiting, then this should be reflected in an animals' body condition. If acute and prolonged the food shortage may in turn affect a population's rate of increase through increasing the mortality rate, decreasing the birth rate or both.

Our objective in this study was to investigate drought mortality as a possible regulator of chital populations in northern Queensland. We hypothesise that where population regulation takes the form of a dynamic oscillation, primarily the result of altered juvenile survival, impacts on adult fat storage would be minimal. However, in the event of a prolonged or catastrophic food shortage reduced fat storage in adults would be measurable in both kidney and bone marrow stores. If this were the case body condition may be a reliable predictor of population growth. In this study we monitored the body condition of adult chital during the period from 2014 to 2016 when food was limited and the population declined by ~80%.

Using modelled historical records of forage availability, we also relate rainfall patterns to previously observed declines in the chital population in the Queensland dry tropics. In the Burdekin district the modest spread of chital since 1886 is considered in the light of these seasonal and drought-induced forage shortages, as is their potential to spread further across northern Australia.

Methods

Study area

The study sites were located ~130 km north of Charters Towers in the greater catchment area of the Burdekin River, northern Queensland, Australia. Both Spyglass (19°29.35S, 145°41.11E) and Niall (19°25.14S, 145°18.37E) stations are cattle properties separated by ~40 km, ~40 000 ha in size with carrying capacities of around 4000 adult cattle in years with average rainfall. The district is naturally wooded on soils of low fertility (McIvor 2012), with some cleared areas sown to pasture grasses and legumes with artificial water sources built to complement natural watercourses. The average December maximum temperature is 34.5°C, and average July minimum temperature is 11.5°C (http://www.bom.gov.au, accessed 26 May 2019). Average annual rainfall for Spyglass station is 598 mm, and Niall station 637 mm, with ~80% falling in the five months from November (https://www.longpaddock.qld.gov.au, accessed 26 May 2019) producing a dry season shortage of forage in terms of both availability and quality (Poppi and McLennan 1995). Herbivores other than chital include cattle present at densities of 5–25/km^2, and three principal species of macropod, eastern grey kangaroo (*Macropus giganteus*), red kangaroo (*Macropus rufus*), and common wallaroo (*Macropus robustus*) present in 2014 at a combined average density of 4.4/km^2). (https://www.qld.gov.au/environment/plants-animals/wildlife-permits/macropods, accessed 26 May 2019).

Forage availability

The software 'FORAGE' (http://www.longpaddock.qld.gov.au/forage, accessed 26 May 2019) was used to predict available vegetation on Niall station (which experienced similar rainfall and climate to Spyglass) for the months from January 1970 to September 2018. FORAGE was used to estimate monthly total standing dry matter (TSDM, kg/ha) and growth (new growth of vegetation, kg/ha).

Sample collection from chital

Samples from 162 chital were taken at necropsy during four sampling events conducted on Spyglass and Niall stations, where during the same years surveys were conducted by (Brennan and Pople 2016). Samples included the lower jaw for aging by patterns of molar eruption and wear (Hall *et al*. 2012), kidneys for kidney fat measurement, and a femur for measuring bone marrow fat. The sex and reproductive status (e.g. lactating, pregnant) of each animal was also recorded. Animals were sampled during discrete five-day periods in October 2014 and 2015, and March 2015 and 2016, coinciding with dry and wet seasons respectively. On each occasion a minimum of 20 adult animals (10 males and 10 females) were shot on each property at either dawn, dusk, or at night while animals were feeding, with Department of Agriculture and Fisheries Animal Ethics approval (AEC SA2014/07/475).

Laboratory analyses of kidney and bone marrow fat

Both kidneys were transported frozen to the laboratory, thawed, and trimmed of fat beyond both the caudal and cranial poles (Finger *et al*. 1981). The remaining fat was separated and the relative weight of the fat to the kidneys expressed as a percentage (KFI).

Femurs were transported frozen to the laboratory for analysis as outlined by (Neiland 1970). Femur marrow samples were weighed before and after drying for three days at 60°C. The weight difference was attributed to water content and the remaining substrate expressed as percentage fat (BMF).

Statistical analyses

KFI indices were log-transformed to normalise distribution. A generalised linear model was used to examine the influence of season, location, sex, age, pregnancy and lactation status on KFI. BMF percentages were analysed using both Welch two sample *t*-tests and Wilcoxon rank sum tests with continuity correction using the same variables. Body condition was compared between animals according to age (>2 years and <2 years), which was the age at which survival increased and cohort (age group) sizes stabilised (K. Watter, unpubl. data).

Pearson's correlations were used to test the relationship between two response variables (KFI and BMF), and environmental predictors including TSDM kg/ha for the months when condition scores were measured, mean monthly TSDM (kg/ha) for the six months before sampling (six-month trailing average), and previous six-month total rainfall.

Results

Rainfall and forage availability

Annual rainfall on Spyglass station for 2013 to 2016 inclusive ranged from 221 to 480 mm, 40% below the long-term average (Fig. 1). Similarly, on Niall station annual rainfall ranged from 217 to 498 mm, or 41% below the long-term annual average. Both sites received 66% less rainfall than the long-term average in 2015.

Monthly estimations of total standing dry matter (TSDM kg/ha) from Niall station since 1970 as generated by FORAGE showed large variations around a monthly mean of 1519 kg/ha (Fig. 2).

From October 2013 TSDM (kg/ha) and mean monthly new growth (kg/ha) declined and were below average (Fig. 3). Mean monthly TSDM in 2015 was 147 kg/ha (average = 1519 kg/ha), and mean monthly growth 12 kg/ha (long-term monthly growth = 152 kg/ha). Both TSDM and 'growth' increased from November 2015 along with rainfall for the previous six months.

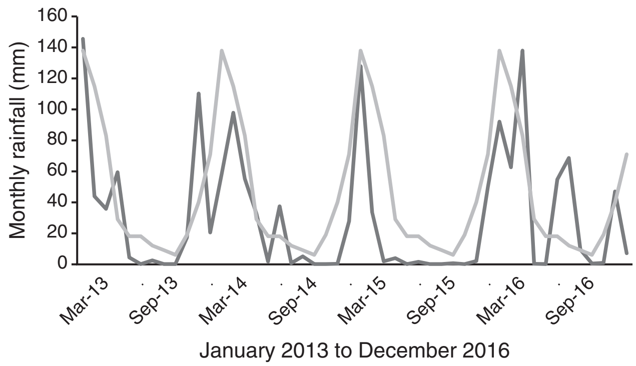

Fig. 1. Monthly rainfall at Spyglass station (black), which was similar to Niall station, and average monthly rainfall since 1900 recorded at Bureau of Meteorology (BOM) weather station Hillgrove (grey). Hillgrove is situated close to both properties.

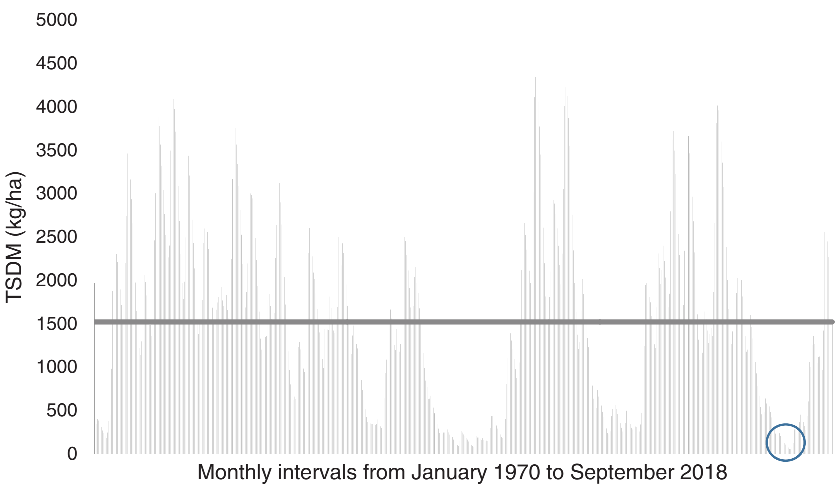

Fig. 2. Monthly total standing dry matter (kg/ha) for the period from January 1970 to September 2018 with the horizontal line denoting the monthly mean TSDM (1519 kg/ha) since January 1970, symbol centred on the sampling period from October 2014 to March 2016.

Body condition of chital assessed using KFI

Mean KFI of chital from both study sites varied seasonally, being less than 25% fat during the dry seasons to above 45% during the wet seasons. Highest mean KFI was recorded during the 2016 wet season on Niall station, and the lowest mean value during the dry season in 2015 on Spyglass station (Fig. 4*a*).

The primary effect on KFI was season, with a minor effect of location during the dry season. KFI differed significantly between seasons ($F_{1,147} = 103.2$, $P < 0.001$), and between seasons according to location ($F_{1,147} = 4.03$, $P = 0.046$). No significant differences were found between animals less than or older than 2 years of age ($F_{1,146} = 0.88$, $P = 0.35$). Neither sex ($F_{1,146} = 0.012$, $P = 0.91$), pregnancy ($F_{1,83} = 1.08$, $P = 0.30$), nor lactation ($F_{1,83} = 0.03$, $P = 0.86$) were significant.

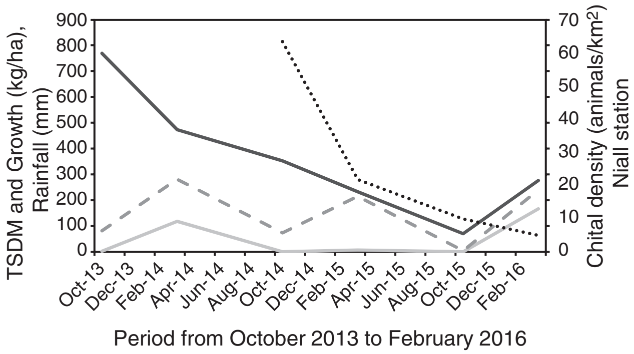

Fig. 3. Total standing dry matter (kg/ha) (black line), forage growth (kg/ha) (grey line) and rainfall (mm for the previous six months) (dashed line) for the period October 2013 to March 2016. Chital density Niall station from December 2014 to April 2016 (animals/km^2) (dotted line) (Brennan and Pople 2016).

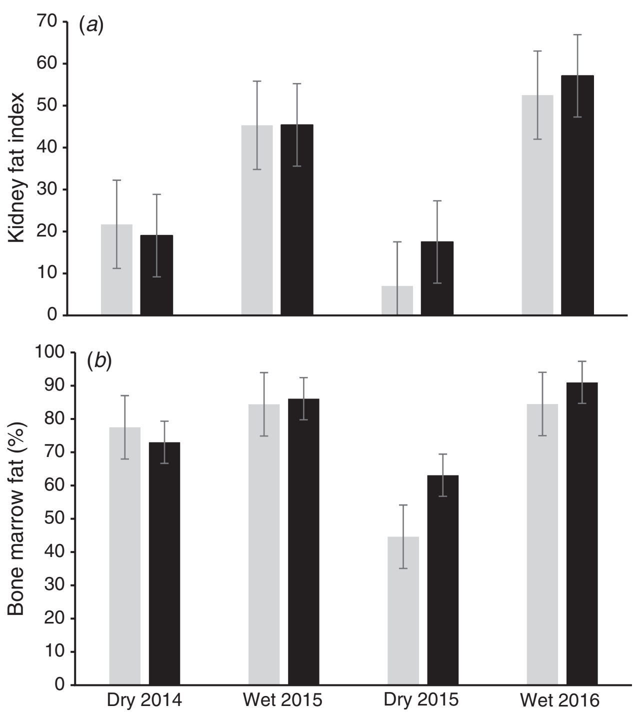

Fig. 4. (*a*) Mean kidney fat index (KFI) by season, Spyglass (grey), Niall (black) with s.e. shown, n = 162, each column represents ~20 animals. (*b*) Mean bone marrow fat (BMF) by season, Spyglass (grey), Niall (black).

Body condition of chital assessed using BMF

Mean BMF displayed a similar pattern at both study sites with lowest values recorded in dry season 2015 (Fig. 4*b*). BMF differed significantly between seasons ($P < 0.001$) (dry season mean = 65.7 ± 3.4%, n = 76; wet season mean = 87.2 ± 1.9%, n = 80), using both a Welch two sample *t*-test ($t_{119} = 5.47$) and a non-parametric Wilcoxon rank sum test (W = 1382). Standard errors varied greatly between seasons (Fig. 4*b*).

After partitioning the databased according to season, further testing using Welch two sample *t*-tests showed no significant effects of location (dry season $t_{72} = 0.65$, $P = 0.52$; wet season $t_{78} = 0.80$, $P = 0.42$), sex (dry season $t_{62} = 0.04$, $P = 0.96$; wet season $t_{55} = 1.31$, $P = 0.20$), or age (dry season $t_{16} = 1.06$, $P = 0.30$; wet season $t_{30} = 0.07$, $P = 0.94$) on BMF. Similar results were obtained using Wilcoxon rank sum tests.

Neither pregnancy (dry season $t_{21} = 1.33$, $P = 0.20$; wet season $t_{35} = 1.24$, $P = 0.22$) nor lactation status (dry season $t_8 = 0.35$, $P = 0.73$; wet season $t_{11} = 0.10$, $P = 0.92$) had any significant effect on BMF using a Welch two-sample *t*-test. Comparable results were obtained with the Wilcoxon test.

Relationship between KFI and BMF

The (convex) relationship between KFI and BMF in chital reflects the relative cascade of fat utilisation from peri-renal depots to bone marrow depots as body condition declined (Fig. 5.). Kidney fat in chital was utilised to around 30% before large amounts of fat from femoral bone marrow was used. KFI was a more sensitive measure of condition for animals with KFI above 30% than those with KFI below 30%. Below ~30% KFI, the BMF became the more sensitive measure.

Correlation of body condition with environmental variables

Pearson's correlations showed KFI and BMF were more closely related to rainfall than either a sampling date or six-month trailing TSDM average. Correlation of BMF with rainfall over the previous six months was 0.83 (t = 2.09, d.f. = 2, P = 0.17),

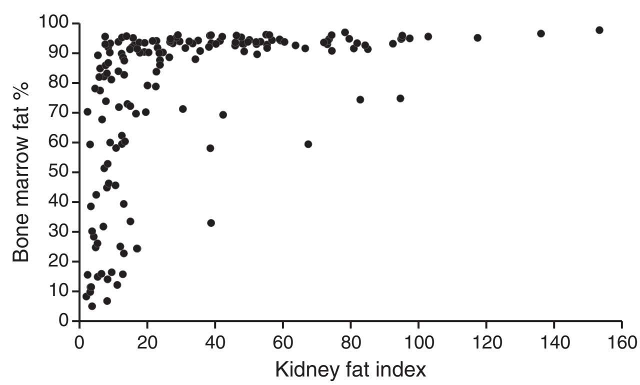

Fig. 5. Bone marrow fat (BMF) and kidney fat index (KFI) of individual animals, Spyglass and Niall, n = 162.

whereas that of KFI with rainfall was significant ($P < 0.05$) at 0.97, ($t = 6.28$, d.f. = 2, $P = 0.02$).

Discussion

Effects of body condition decline on the population

Annual fluctuations in body condition of deer are common and have been observed in white-tailed deer (Finger *et al*. 1981), mule deer (*Odocoileus hemionus*) (Anderson *et al*. 1972) and red deer (Riney 1955). The extent of the fall in mean condition of chital during 2015 however, was beyond the normal seasonal fluctuations reported in north America (Anderson *et al*. 1972), and those observed in this study during 2014. BMF measurements consistent with starvation in other deer species (Ratcliffe 1980) were recorded in dry season 2015, coincident with the observed decline in chital numbers. Although animals most vulnerable to nutritional stress were juveniles still suckling and reliant on their mothers (Eberhardt 2002), the scale of the population declines reported by (Brennan and Pople 2016) during 2015 indicate mortalities beyond that of the young and recently weaned.

Kidney fat measurements are considered most useful for animals in moderate to good condition (Takatsuki 2000) but show considerable variation (Caughley 1970*a*; Anderson *et al*. 1972). The extent of variation in KFI is dependent on region and the extent of seasonal differences with north American white-tailed deer storing more fat before winter in northern latitudes than those in the subtropical south (Johns *et al*. 1984). Interpretations of KFI require consideration of species, region and season.

Kidney fat was not utilised to exhaustion by chital before other fat stores were used, with marrow fat used increasingly when KFI fell below ~30%. The simultaneous use of both fat depots during periods of severe condition loss has been recorded in red deer (Suttie 1983) with some fat remaining around the kidney even during starvation events. Generally, however, fat mobilisation was sequential from kidneys to bone marrow below a KFI of ~30%, recorded also in Sika deer (*Cervus nippon*) in Japan (Takatsuki 2000) and in white-tailed deer in Manitoba (Ransom 1965). In red deer, BMF was utilised at kidney fat indices below ~50% (Suttie 1983). Fat measurements from kidney depots are accordingly most appropriate for well-conditioned animals whereas BMF is more appropriate for less well conditioned animals. For those animals in a transitional stage, when utilising fat stores from both sources, both measures should be used (Riney 1955; Anderson *et al*. 1972; Takatsuki 2000). At both study sites, mean KFI during the dry seasons was below 25% making BMF a more sensitive measure of condition.

Interpretation of BMF to predict the health of individual chital, or consequences for the population, can be made subjectively by correlating data with visual appraisals of body condition, by comparing chital BMF with published data from another species, or by relating BMF to population rates of increase. BMF below 8% was associated with starvation in reindeer (*Rangifer tarandus*) in Scandinavia (Nieminen and Laitinen 1986), whereas roe deer (*Capreolus capreolus*) with less than 50% BMF in Scotland were considered in poor condition with 11% diagnostic of starvation (Ratcliffe 1980). In a study of white-tailed deer in New York (Cheatum 1949) severe malnutrition was manifest where BMF dropped below 25%, although individuals still standing recorded less than 2% BMF but were considered unlikely to survive. Chital in the 2015 dry season had a BMF of ~50% (range 6–93%), with 23% of individuals recording <20% BMF during the period of marked population decline. Although broadly consistent with BMF recorded in other species under nutritional stress, the threshold below which a population declines is most likely species specific.

How declining body condition impacts individuals

The significance of fat stores for survival of individual animals can be related to their energy requirements. Cohorts of chital with increased metabolic demands due to growth and lactation (Mulley and Flesch 2001) had mean BMF measurements below that of the mean of the remainder of the sampled population although the trend was not statistically significant. Several factors might explain this finding. Regardless of condition fat deposition either around the kidneys or in marrow cavities in younger (growing) animals only occurs to a limited degree. Kidney fat measurements in impala (*Aepyceros melampus*) were not considered reliable indicators of condition in animals under three years (Hanks *et al*. 1976), whereas those of bone marrow were not considered reliable in juvenile impala or deer of various species (Ratcliffe 1980). Anderson *et al*. (1972) found BMF to be higher in older and female mule deer in Colorado describing a strongly seasonal cycle in BMF associated with reproduction. The lack of a relationship between condition and reproductive status in chital might be explained by their aseasonal pattern of reproduction in an environment where pasture growth and food availability are highly seasonal (Poppi and McLennan 1995). The peak period of energy demand for most chital females (lactation) coincides with the wet season when feed is most abundant and feed quality highest. But for the ~30% of females lactating during the dry season energy deficits might be expected to occur. Overwhelmingly body condition was related to season and this factor potentially swamped the expected effects of age and reproductive state.

The 11 individual chital recorded in poorest condition (lowest BMF) were all dry season samples having less than 17% BMF and represented 13.7% of all animals sampled during the dry seasons. Of these, all at risk of death by starvation, all but two had increased metabolic demands for energy. Two female animals were lactating, one young (<1 year) male weighed only 27 kg, three females <1.5 years old were pregnant, and three adult males were in hard antler, presumed rutting.

Identifying those cohorts most susceptible to death by starvation allows some conclusions on the composition and resilience (Hanks 1981) of the remaining population. The survival of dependent young can be expected to be lowest (Eberhardt 2002) associated with poor condition of lactating females, especially those born during the dry season. Similarly, adult females lactating during the dry season are at an increased risk of starvation. The resultant population would be comprised of individuals with an age distribution skewed towards mature animals and a sex ratio skewed towards females (Clutton-Brock and Coulson 2002).

Mortalities undoubtedly occurred as a direct result of starvation, so it follows that animals with less fat are also more vulnerable to death by other means. Secondary risk factors associated with reduced body condition include the need to travel further for food and the reduced ability of individuals to escape predation. Chital in northern Queensland represent a food source for wild dogs with more than 40% of wild dog scats collected at Spyglass and Niall stations during 2016 containing chital hair (D. M. Forsyth, A. Pople, L. Woodford, M. Brennan, M. Amos, P. D. Moloney, B. Fanson, and G. Story, unpubl.). Contracting water sources likely exacerbated the nutritional shortfall for chital which rely on drinking at least daily (Dinerstein 1980). This likely increased the energy required to travel to more distant grazing areas. The ability of chital to alter their diet, increase their feeding area, or increase time spent feeding in response to food shortage was insufficient to meet nutritional requirements during 2014–2016.

Population dynamics of the Burdekin chital herd

Fat reserves in other animal populations have served as a barometer of herd health and sustainability. Juvenile survival and fecundity of Himalayan thar (*Hemitragus jemlahicus*) in New Zealand were related to body condition where high density populations closer to the point of release displayed lower rates of increase than those at lower densities away from the site of release (Caughley 1970*a*). As Caughley suggested, female fat reserves in summer is an index relating to rate of increase for thar, so BMF taken in the dry season seems a similarly informative index for chital.

If the years before 2013 represent an eruption in chital numbers, subsequent years (2014–2015) may represent a crash caused by forage depletion subsequent to drought. Caughley (1970*a*; p.53) defined an irruptive fluctuation as 'an increase in numbers over at least two generations, followed by a marked decline'. This eruptive (Riney 1955), or irruptive (Leopold 1943; Gross *et al*. 2010) pattern of herbivore population dynamics where numbers overshoot sustainable levels has been documented in red deer (Riney 1955), thar (Caughley 1970*a*), and reindeer (Klein 1968). Caughley (1979) noted eruptive dynamics as being normal for herbivores with the present example displaying characteristics of eruptions observed elsewhere in which sustained increases in populations were reversed by severe weather (Klein 1968) and resource depletion (Caughley 1970*a*). Riney (1964; p. 261) states 'introduced populations of large herbivores, if undisturbed usually follow a period of adjustment to the new environment which consists of a single eruptive oscillation', which implies populations find a new and more sustainable, but variable equilibrium. The possibility that the variability of rainfall in northern Queensland determines a semi-regular series of eruptive events is a testable hypothesis requiring larger scale and longer-term population records.

The multi-year cycles of forage availability in the Burdekin region show great variation with low points in 1995 and 2004 (Fig. 2) according to FORAGE model predictions. These predictions of TSDM and 'Growth' are supported by vegetation studies conducted on Spyglass station in October 2015 (dry season) and March 2016 (wet season) (K. Watter, G. Baxter, M. Brennan, T. Pople, and P. Murray, 2018, unpubl.) which measured presence and height of grasses, forbs and shrubs contributing to chital diet. The product of plant percentage cover and plant height produced a total increase in the biomass index of ~600% from the dry to the wet season with similar increases in 'greenness', a good correlate with diet quality. Chital body condition (KFI) during 2014–2016 showed significant correlation with rainfall over the previous six-month period although the predictive value of this relationship should be treated with caution as the effective data points are limited to four. Estimates of total standing dry matter generated by FORAGE suggest that pasture conditions similar to those observed in 2015 might have occurred many times since the 1890s. Jesser (2005) reported a population decline in the Charters Towers chital herd attributable to drought conditions of 2003–2004. The sensitivity of chital to periodic droughts in northern Queensland and the possibility that chital might have experienced a succession of eruptive events, may explain the modest rate of expansion of the species since 1886.

Future spread of chital

Climatch (http://data.daff.gov.au:8080/Climatch/climatch.jsp, accessed 26 May 2019), which uses bioclimatic comparisons between the native and introduced ranges of animals to predict suitability of the introduced range, suggests chital have the potential to expand across large areas of northern Australia. Moriarty (2004); however, acknowledges area and animal specific limitations to making such predictions. One such limitation for chital appears to be an inability to cope with the forage shortages which characterise much of northern Australia. The frequency at which chital drink and the distance they travel from water may also limit their distribution. Dinerstein (1980) found chital in Nepal were rarely found more than 2 km from water, whereas Amos (M. Amos, unpubl. data) found radio-collared chital in our study area mostly remained within 3 km of water. Areas of northern Australia more distant from permanent water are unlikely to support chital populations despite climatic similarities with their countries of origin.

Conclusion

Although limited to two years, our results suggest that under drought conditions chital deer in northern Queensland do experience a marked decline in body condition. Hence, poor nutrition and inadequate fat reserves could explain the collapse of chital populations. We hypothesise that historic forage supply shortfalls may have been substantial enough to cause major population declines and may have reduced the capacity of chital herds to expand and spread. This apparently irruptive dynamic might be confirmed through studies of longer duration including multi-year periods when the rate of increase of the population was not food limited. Models of irruptive dynamics applied to animal populations require datasets over a longer period of time (typically 20 years) than are available for chital (Forsyth and Caley 2006). The potential for chital to become invasive in northern Queensland appears to be limited by drought mortality, and the rate of increase of the population is reflected in both the KFI and BMF. BMF taken during the dry season is the most useful gauge of the nutritional status of wild chital, and indicates the likely trajectory of the population.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

This research was partially supported by funding from Biosecurity Queensland, Queensland Department of Agriculture and Fisheries. The authors thank Allan Lisle for his assistance with the statistical analysis of the data.

References

Anderson, A. E., Medin, E., and Bowden, D. C. (1972). Indices of carcass fat in a Colorado mule deer population. *The Journal of Wildlife Management* **36**, 579–594. doi:10.2307/3799091

Bentley, A. (1978) 'An introduction to the deer of Australia: with special reference to Victoria.' (R. Manning for the Koetong Trust Service Fund, Forests Commission, Victoria)

Bobek, B., Perzanowski, K., and Weiner, J. (1990). Energy expenditure for reproduction in male red deer. *Journal of Mammalogy* **71**, 230–232. doi:10.2307/1382171

Brennan, M., and Pople, T. (2016). Chital Deer – an expanding problem in north Queensland. In '2016 Pest Animal Symposium'. Queensland.

Caughley, G. (1970*a*). Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology* **51**, 53–72. doi:10.2307/1933599

Caughley, G. (1970*b*). Fat reserves of Himalayan thar in New Zealand by season, sex, area and age. *New Zealand Journal of Science* **13**, 209–219.

Caughley, G. (1979) What is this thing called carrying capacity? *In*: 'North American Elk: Ecology, Behavior, and Management'. pp. 2–8. (University of Wyoming Press: WY.)

Caughley, G., and Krebs, C. J. (1983). Are big mammals simply little mammals writ large? *Oecologia* **59**, 7–17. doi:10.1007/BF00388066

Cheatum, E. (1949). Bone marrow as an index of malnutrition in deer. *New York State Conservation* **3**, 19–22.

Clutton–Brock, T., and Coulson, T. (2002). Comparative ungulate dynamics: the devil is in the detail. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **357**, 1285–1298. doi:10.1098/rstb.2002.1128

Dave, C. V. (2008). Ecology of chital (*Axis axis*) in Gir. PhD Thesis, Saurashtra University, India.

Davis, N. E., Bennett, A., Forsyth, D. M., Bowman, D. M., Lefroy, E. C., Wood, S. W., Woolnough, A. P., West, P., Hampton, J. O., and Johnson, C. N. (2016). A systematic review of the impacts and management of introduced deer (family Cervidae) in Australia. *Wildlife Research* **43**, 515–532. doi:10.1071/WR16148

Dinerstein, E. (1980). An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal: Part III: Ungulate populations. *Biological Conservation* **18**, 5–37. doi:10.1016/0006-3207(80)90063-4

Eberhardt, L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology* **83**, 2841–2854. doi:10.1890/0012-9658(2002)083[2841:APFPAO]2.0.CO;2

Finger, S. E., Brisbin, I. L., Smith, M. H., and Urbston, D. F. (1981). Kidney Fat as a predictor of body condition in white-tailed deer. *The Journal of Wildlife Management* **45**, 964–968. doi:10.2307/3808104

Forsyth, D. M., and Caley, P. (2006). Testing the irruptive paradigm of large-herbivore dynamics. *Ecology* **87**, 297–303. doi:10.1890/05-0709

Gross, J. E., Gordon, I. J., and Owen-Smith, N. (2010). Dynamics of large herbivore populations in changing environments: *In*: 'Towards Appropriate Models'. pp. 117–140. (Wiley-Blackwell: Oxford, UK)

Hall, G. P., Murray, P. J., Byrne, M. J., and Lisle, A. T. (2012). Is tooth wear a reliable means of aging wild European fallow deer in Tasmania, Australia? *Wildlife Society Bulletin* **36**, 124–129. doi:10.1002/wsb.89

Hanks, J. (1981). Characterization of population condition. *In*: 'Dynamics of Large Mammal Populations'. (Eds C. Fowler and T. Smith.) pp. 47–73. (John Wiley: New York.)

Hanks, J., Cumming, D. H. M., Orpen, J. L., Parry, D. F., and Warren, H. B. (1976). Growth, condition and reproduction in the impala ram (*Aepyceros melampus*). *Journal of Zoology* **179**, 421–435.

Jesser, P. (2005). 'Deer in Queensland.' (State of Queensland (Department of Natural Resources and Mines))

Johns, P. E., Smith, M. H., and Chesser, R. K. (1984). Annual cycles of the kidney fat index in a southeastern white-tailed deer herd. *The Journal of Wildlife Management* **48**, 969–973. doi:10.2307/3801449

Klein, D. R. (1968). The introduction, increase, and crash of reindeer on St. Matthew Island. *The Journal of Wildlife Management* **32**, 350–367. doi:10.2307/3798981

Leopold, A. (1943). Deer irruptions. *Wisconsin Conservation Bulletin* **8**, 3–11.

McIvor, J. (2012). Sustainable management of the Burdekin grazing lands–A technical guide of options for stocking rate management, pasture spelling, infrastructure development and prescribed burning to optimise animal production, profitability, land condition and water quality outcomes.

Moriarty, A. (2004). The liberation, distribution, abundance and management of wild deer in Australia. *Wildlife Research* **31**, 291–299. doi:10.1071/WR02100

Mulley, R. C., and Flesch, J. (2001). Nutritional requirements for pregnant and lactating red and fallow deer: A report for the rural industries research and development corporation. RIRDC Project No. UWS-16A. (RIRDC)

Neiland, K. A. (1970). Weight of dried marrow as indicator of fat in caribou femurs. *The Journal of Wildlife Management* **34**, 904–907. doi:10.2307/3799158

Nieminen, M., and Laitinen, M. (1986). Bone marrow and kidney fat as indicators of condition in reindeer. *Rangifer* **6**, 219–226. doi:10.7557/2.6.2.649

Pimm, S. L. (1989). Theories of predicting success and impact of introduced species. *In*: 'Biological Invasions: A Global Perspective'. (Ed. J. A. Drake.) pp. 351–367. (John Wiley and Sons Ltd.: New York, Chichester.)

Poppi, D. P., and McLennan, S. R. (1995). Protein and energy utilization by ruminants at pasture. *Journal of Animal Science* **73**, 278–290. doi:10.2527/1995.731278x

Ransom, A. B. (1965). Kidney and marrow fat as indicators of white-tailed deer. *The Journal of Wildlife Management* **29**, 397–398. doi:10.2307/3798449

Ratcliffe, P. R. (1980). Bone marrow fat as an indicator of condition in roe deer. *Acta Theriologica* **25**, 333–340. doi:10.4098/AT.arch.80-30

Riney, T. (1955) 'Evaluating Condition of Free-ranging Red Deer (*Cervus elaphus*), with Special Reference to New Zealand.' (Council of Scientific and Industrial Research: Wellington, NZ.)

Riney, T. (1964). The impact of introductions of large herbivores on the tropical environment. *IUCN Publication New Series* **4**, 261–273.

Sankar, K., and Acharya, B. (2004). 'Spotted Deer or Chital (*Axis axis* Erxleben, 1777).' pp. 171–180. (Wildlife Institute of India: Dehradun, India)

Suttie, J. (1983). The relationship between kidney fat index and marrow fat percentage as indicators of condition in red deer stags (*Cervus eluphus*). *Journal of Zoology* **201**, 563–565. doi:10.1111/j.1469-7998.1983.tb05078.x

Takatsuki, S. (2000). Kidney fat and marrow fat indices of the sika deer population at Mount Goyo, northern Japan. *Ecological Research* **15**, 453–457. doi:10.1046/j.1440-1703.2000.00365.x