Seasonal diet preferences of chital deer in the northern Queensland dry tropics, Australia

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Abstract. Chital deer (*Axis axis*) were introduced to the Burdekin dry tropics of north Queensland, Australia, in the late 1800s. Here rainfall and plant growth are highly seasonal and a nutritional bottleneck for grazing animals occurs annually before the wet season. This study describes the seasonal changes in diet and diet preference of chital in this seasonally-variable environment. Rumen samples were taken from 162 deer from two sites over the wet and dry seasons of two consecutive years and sorted macroscopically for identification. Relative seasonal availability of plant groups was estimated using step point sampling of areas grazed by chital. Chital alter their diet seasonally according to availability and plant phenology. Chital utilised 42 plant genera including grasses, forbs, subshrubs, shrubs, trees and litter. Grass consumption ranged from 53% of biomass intake during the dry season to 95% during the wet season. The predominance of grass in the wet season diet exceeded relative availability, indicating a strong preference. Although grass contributed more than half of the dry season diet it was the least preferred plant group, given availability, and the least actively growing. Shrubs were the preferred plant type in the dry season, and least subject to seasonal senescence. Composition and quantity of seasonal pastures vary markedly in north Queensland, and chital alter their diet by consuming those plants most actively growing. The increased dry season intake of non-grass forage appears to be a strategy to limit the detriment resulting from the progressive deterioration in the quality of grass.

Additional keywords: *Axis axis*, diet, forage, grasses, introduced species, seasonality.

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Introduction

On the Indian subcontinent, chital or Indian spotted deer (*Axis axis*) are an important keystone species supporting wild carnivore populations (Dave 2008), and are considered an indicator of ecosystem health (Sankar and Acharya 2004). In contrast, they have, at times, become a pest wherever they have been introduced outside their native range (Congdon and Harrison 2008). Their adaptability to habitat, climate and diet (Sankar and Acharya 2004) have allowed them to become widespread and abundant in their native and introduced ranges (Waring 1996), and modelling suggests large areas of Australia currently without chital represent suitable habitat (Davis *et al.* 2016).

Chital were introduced to Maryvale Station in north Queensland in 1886 (Roff 1960), and by 2014 had increased to an estimated population of 32 000 and spread ~100 km from their initial point of release (Brennan and Pople 2016). This slow rate of increase and overall low density suggests an ability to persist rather than be a major invasive species. However, some areas support chital at densities exceeding 170 deer/km² (Brennan and Pople 2016). The reasons for variation in abundance might

include the availability of plants that comprise chital diet, distribution of minerals in the environment (Watter *et al.* 2019*b*), proximity to water and homesteads (Forsyth *et al.* 2019) and predation – all of which may be predictors to their future distribution and abundance. Management implications for landholders may include the likelihood that pasture improvements could expand the current range and create high density source populations of chital.

Seasonal fluctuations in forage quantity and quality in the Burdekin dry tropics region of north Queensland where chital are found regulate the abundance of both domestic (Ash *et al.* 2000) and presumably wild herbivores. Rainfall and pasture growth occur principally during the five-month wet season followed by a dry season when pastures senesce creating a nutritional bottleneck. For herbivore populations to persist and expand, individuals must obtain above-maintenance nutrition over the course of a year to enable breeding and recruitment. This seasonal variation will be exacerbated by annual variation in rainfall (Stone *et al.* 2019). In order to survive, chital must maintain a dietary intake that meets minimum thresholds for

maintenance throughout the year (O'Reagain and Schwartz 1995). Grazing animals employ various strategies to buffer themselves against seasonal declines in forage quality. Animals may alter their spatial and temporal utilisation of the environment by increasing or altering their foraging range (O'Reagain and Schwartz 1995), time spent grazing, bite rate (Spalinger *et al.* 1988; Shrader *et al.* 2006) or by altering the range and proportion of forage species consumed (Owen-Smith 1994).

The diet of grazing animals can be assessed through direct observation of feeding animals (Dave 2008), measuring plant offtake (McInnis *et al.* 1983) or by taking samples of ingested material from various points along the animal's alimentary canal (Medin 1970; Alipayo *et al.* 1992). These methods return similar results in terms of plant species identified, but all have biases estimating different relative proportions of plants in the diet (Holecheck *et al.* 1982; Forsyth and Davis 2011). Care must therefore be taken when interpreting results and making comparisons across studies. The advantage of samples sourced from the animal (including faecal material collected from the ground) is that the sample has been selected by the animal and thus reflects actual intake. Ingested food can be analysed using various techniques (Osborn *et al.* 1997), but due to the variation among individual animals the method used is less important than sample size in order to produce results of sufficient accuracy (Puglisi *et al.* 1978). Among those herbivores that are morphologically adapted to utilising more than one plant type (Hofmann 1985), any preference for a particular plant can be measured as the proportion of that plant in the diet according to its relative availability in the environment (Petrides 1975; Norbury and Sanson 1992; Manly *et al.* 2007), on a seasonal basis.

The objective of the present study was to determine the seasonal diet and food preferences of chital in an environment characterised by fluctuations in forage quality and quantity (Poppi and McLennan 1995). Where nutritional quality and relative availability of food plants change seasonally, the composition of chital diet may alter accordingly. As intermediate feeders (Hofmann 1985) chital can consume grasses, forbs and shrubs (Dinerstein 1979; Khan 1994; Dave 2008) which have different seasonal patterns of growth and maturation. If chital diet reflected availability of plant types, then no change in preference would occur between seasons. However, if chital discriminate seasonally between plant types and diet preferences do change, we would expect a nutritional basis for this change. Seasonal changes in diet in response to relative growth stages and diet quality of food plants may allow chital to meet annual nutritional thresholds for maintenance.

Materials and methods

Study area

The study area is situated within the Burdekin dry tropics ~150 km north of Charters Towers (20°06.0S, 146°16.0E) in Queensland, Australia. The district is naturally wooded with some areas cleared to allow for improved grazing conditions but with forage of generally low quality (Burrows *et al.* 1990). In this report we followed the botanical nomenclature of the International Plant Names Index (IPNI 2020). Average annual rainfall in Charters Towers is 648 mm, with 79% falling in the five months from November, average maximum temperature for

December is 34.5°C and minimum temperature for July is 11.5°C (Bureau of Meteorology, Australian Government; www.bom.gov.au). The predominant land use is extensive cattle ranching with average property sizes of 30 000 ha supporting cattle densities of 5–25/km^2 (McIvor 2012).

Rumen samples were obtained from chital on Niall and Spyglass stations, and pasture composition was measured on Spyglass which was representative of both properties. Both sites are cattle properties separated by ~40 km with similar rainfall patterns and soil types, but different in terms of chital density and history.

Niall Station comprises 43200 ha and is 170 km north of Charters Towers (19°25.14S, 145°18.37E). Niall has a mixture of red and black basalt soils with the predominant tree species being ironbark (*Eucalyptus crebra*), box (*Eucalyptus persistens*) and black gidyea (*Acacia argyrodendron*). Pasture comprises mainly native grasses (e.g. *Dactyloctenium radulans*) and, in years of average rainfall the property has a carrying capacity of 4500 adult cattle (O'Reagain *et al.* 2009) based on sustainable utilisation of pasture (McKeon *et al.* 1990). Spyglass is 38 200 ha in extent and located 110 km north of Charters Towers (19°29.35S, 145°41.11E) with frontage to the Burdekin River. The carrying capacity is ~4000 adult cattle (O'Reagain *et al.* 2009). Vegetation is dominated by narrow-leaved ironbark and yellowjacket (*Eucalyptus similis*) with a mixture of both native (*D. radulans*, *Cyperus* sp.) and introduced (*Cenchrus ciliaris*, *Echinochloa mosambicensis*) graminoids.

Niall Station is located ~10 km north-east of the original release point of chital at Maryvale Station, whereas Spyglass is ~35 km east of Maryvale. In March 2015 the density of chital was estimated by vehicle spotlight transects along property tracks at 40 deer/km^2 and 10 deer/km^2 on Niall and Spyglass respectively (Brennan and Pople 2016).

Collection of chital rumen samples

Chital were sampled from both properties during successive wet seasons in March 2015 and 2016, and dry seasons in October 2014 and 2015. These discrete sampling periods represented times of seasonally high and low pasture biomass when hunters operated for periods not exceeding five days to minimise potential temporal variation in diet. Chital were shot by marksmen from vehicles situated on farm tracks, as well as by hunters on foot during times when chital fed; early morning, late afternoon and at night. Shooting occurred over specific areas occupied by chital comprising less than 10% of the total area on both properties. Anecdotal information from landholders suggested this restricted distribution is long standing (>20 years) and does not change seasonally.

At each of the four sampling events, on average ~20 adult animals were shot and necropsied on each property; 73 males and 89 females, (*n* = 162). Approximately 750 mL rumen samples were collected through an incision on the dorsal surface of the rumen. These samples were bagged, individually identified and frozen for laboratory analyses. In addition, the location of shooting (GPS point) (Fig. 1), pregnancy and lactation status were recorded, and jawbone extracted for aging by eruption and wear of molar teeth as for fallow deer (Brown and Chapman 1990). This method of aging allows rapid and accurate age
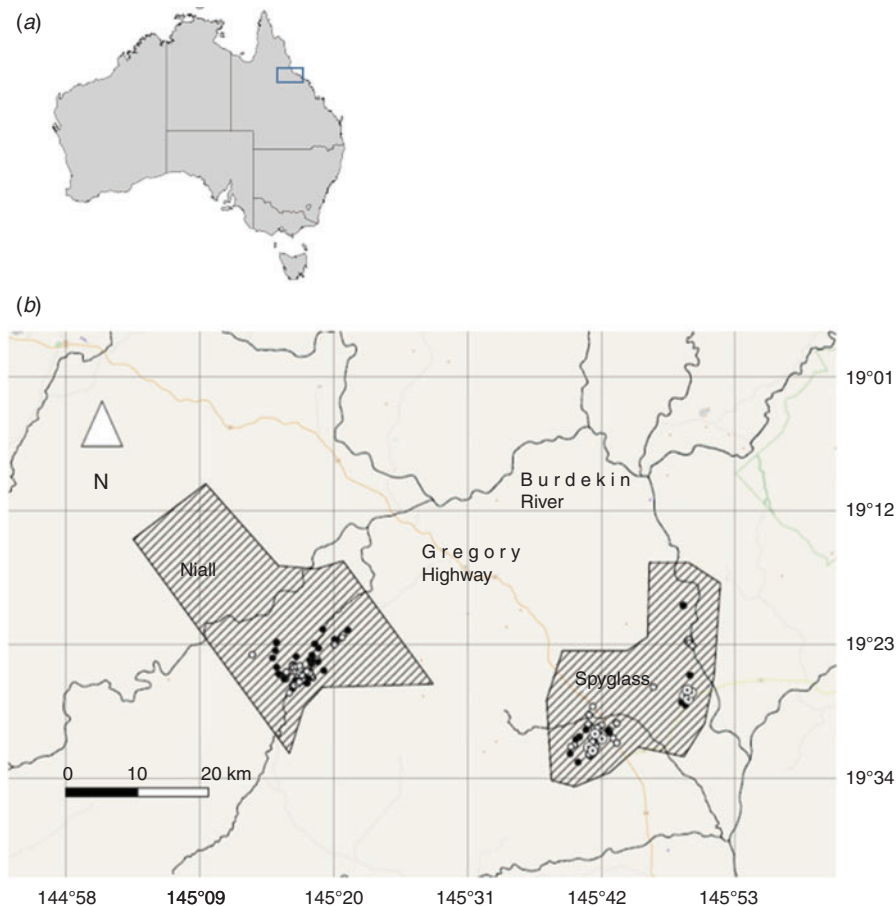
Fig. 1. (*a*) Map of Australia with inset showing study region and (*b*) Burdekin River district showing Spyglass and Niall stations with dry season chital sample locations (●), wet season chital sample locations (¡) and transect locations (¤).

estimation in deer less than three years old, but in white-tailed deer (*Odocoileus virginianus*) accuracy declined in animals over three years old to <50% (Hamlin *et al.* 2000).

A reference collection of plant samples were taken from a broad area during both wet and dry seasons based on preliminary observations of animals feeding (Ward 1970). Plants included grasses, forbs, shrubs, subshrubs and trees. These samples comprised leaves, fruits, flowers and stems to be compared with partially masticated samples from chital rumens.

Laboratory assessment of rumen contents

Rumen contents were sorted and components of the diet were identified macroscopically (Nugent 1983). Each of the rumen samples were thawed, mixed and reduced to 500 mL for uniformity and washed through a 5.3-mm pore steel sieve. Material collected within the sieve was sorted grossly and where necessary under ×10 magnification, and separated into portions taxonomically as close as possible to species level. Identification of plant material was made by gross leaf and stem recognition, leaf hair patterns, leaf venation and leaf margin characteristics. Separation of plant fragments was sometimes difficult when the vegetative portion of forb leaves was digested and absent at the time of sorting, leaving the veined structure of the forb leaf

entangled with coarser grasses. In these instances, subsamples were disentangled, reweighed and a ratio applied to the whole sample. Where necessary, sample identification was verified by the Queensland Herbarium. Samples that were not identifiable due to size, degree of digestion or mastication, or lack of recognisable plant structure, were recorded as unidentified material or unidentified dicotyledon. Samples were then dried at 80°C for 48 h and weighed in order to record dietary components on a dry weight basis.

Analyses of diet data

Factors that might influence the degree of selectivity might include animal size (ability to access higher plant material) (Bugalho *et al.* 2001), metabolic requirements related to growth stage and reproduction (Bobek *et al.* 1990) and availability of alternative food. The relationship between mean percentage grass intake according to season, site, age, sex and reproductive status was analysed using two-way ANOVAs. The seven chital estimated to be one year old and the 32 estimated to be 1.5 years old were combined and their diets compared with the 123 animals estimated to be 2.5 years old or older. Data were adjusted by angular transformation (arcsine) before analysis and checked using a residual plot to ensure normality and homogeneity of variances.

Pasture composition and cover

Vegetation cover and composition on Spyglass was estimated using eight step point transects (Mentis 1981) during the dry season (October) of 2015 and the wet season (March) of 2016 (Fig. 1). The length (400 m) and location of these transects were designed to reflect the size and location of grazing sites, and on each sampling occasion the same transect lines and two observers were used to ensure comparability.

Vegetation data were recorded at a fixed point on the observer's boot at one step intervals. Information included the presence of vegetation, plant class (grass, forb, subshrub, shrub, regrowth), height (measured in 10 cm increments), and growth stage. Forbs were classified as herbaceous understory plants, subshrubs were plants with woody stems less than 0.9 m high, shrubs were woody stemmed between 0.9 and 1.8 m, and regrowth were trees re-shooting following agricultural land clearing with leaves at a height to which chital could reach. Growth stage was recorded by assigning a greenness score (0 = nil green, 1 = trace green, 2 = predominantly green), which was a subjective assessment based on colour alone to reflect the degree to which plants were actively growing. Mature trees were not recorded as seasonal growth could not easily be measured. Each of the transects comprised 400 steps originating from a preselected GPS location and followed a predetermined compass bearing. Mean plant cover was compared across seasons using a two-tailed *t*-test assuming unequal variance.

Diet preference

Preference, which is the likelihood that a herbivore will select (choose) one plant over another, has been measured by several means according to usage as a proportion of availability at a particular time (Manly *et al.* 2007). A plant that is a principal food or eaten in large quantities may not be a preferred food according to its availability and similarly, a plant which comprises only a small part of the diet may be a preferred food if its availability is low (Petrides 1975). Algorithms used to estimate preference differ principally in magnitude of preference rather than rank order of electivity (Lechowicz 1982) and we used a modified version of Ivlev's electivity index (Loehle and Rittenhouse 1982) used previously to estimate diet preference in red (*Cervus elaphus*) (Forsyth *et al.* 2005) and white-tailed deer (Nugent and Challies 1988). This equation was:

$$I_i = U_i - \dot{O}_i / U_i + \dot{O}_i$$

where I_i denotes the electivity index for plant type i, U_i is the proportion of the plant in the diet and $\dot{O}_i$ is the proportion of the plant i available to chital. The index has an even scale that ranges from –1 for plants totally avoided to a maximum preference of +1 and a neutral or random value of 0. Relative availability of plant types was estimated using the product of plant percentage cover and plant height which served as a surrogate for aerial biomass.

Results

Rainfall

The sampling period from October 2014 to March 2016 was ~30% drier than average for both properties, although the seasonality and timing of rainfall approximated the 30-year mean (https://www.longpaddock.qld.gov.au/silo/point-data/, accessed 23 July 2020).

Diet composition

We identified 42 different plants to genus including 31 to species from the rumen samples of chital (Table 1). The predominant functional group found in samples was grass within which four species were identified. Due to the difficulty in identifying and sorting grass species, no attempt was made to quantify relative species proportions. A total of 38 dicotyledon genera were identified, of which 10 contributed 94% of the total identified dicotyledon by dry weight. Of the remaining 28 dicotyledon genera, no single genus comprised more than 0.4%. Unidentified dicotyledons represented 3.9% of the total sample and 12.4% of the dicotyledon component.

The dominance of grass in the diet was consistent across all sampling periods and both study sites. Three species of grass and one sedge were identified, *C. ciliaris* (buffel grass), *E. mosambicensis* (urochloa) and *D. radulans* (button grass), and one sedge *Cyperus* sp. (nut grass) were identified. The first two grass species are introduced pasture species, whereas *D. radulans* is a native grass and *Cyperus* is a sedge found along watercourses. The proportion of the diet that was grass differed between sites (2–33% range) and between seasons (15–42% range) (Fig. 2).

Mean proportions of grass in the rumens varied more at Spyglass (53–96%) than at Niall (80–95%), but the interaction between season and location was significant ($P < 0.001$, $F_{154} = 11.9$). Differences in forage proportions between locations depended on season. The mean percentage of grass in the diet of chital at both sites was lower in the dry season (mean = 0.69, $n = 80$, se = 0.02) than the wet season (mean = 0.92, $n = 82$, se = 0.01). Mean proportions of grass intake were higher on Niall (mean = 0.89, $n = 80$, se = 0.1) than Spyglass (mean = 0.72, $n = 82$, se = 0.02). However, there was considerable overall variability between individual animals where the grass component ranged from 16 to 99%.

Animal factors influencing browse intake

Mean percentage grass intake did not differ between cohorts of animals older and younger than two years ($F_{1, 151} = 0.21$, $P = 0.89$), male and female animals ($F_{1, 153} = 0.01$, $P = 0.92$), pregnant females and non-pregnant females ($F_{1, 152} = 0.99$, $P = 0.32$), and lactating females and non-lactating females ($F_{1, 152} = 0.067$, $P = 0.79$).

The average non-grass component was 17.7% of the diet across all samples. This comprised 38 plant species or plant genera for those items where identification to species level was not possible. Most of these plants made only minor contributions to the diet based on dry weight. The 10 most common dicotyledons by percentage dry weight contributed 13.3% of the total diet or 75% of the dicotyledon portion (Table 2). The unidentified dicotyledon component contributed 3.1% to the total diet and the remaining 28 dicotyledons 1.3% to the total diet.

The dry season diet comprised a greater range of non-grass species than during the wet season, including small trees for which chital would have to reach upwards and litter from the

Table 1. Percentage contribution by dry weight and frequency occurrence (percentage of rumens containing the plant) of plant species and functional groups identified from chital rumen samples on Spyglass and Niall Station

Plant group	Scientific name	Common name	Spyglass				Niall			
			Contribution weight		Frequency		Contribution weight		Frequency	
			Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Grasses (Poaceae)	*Cenchrus ciliaris*	Buffel grass								
	Echinochloa mosambicensis	–								
	Dactyloctenium radulans	Button grass								
	Cyperus sp.	Nut grass								
Total grasses			53	91	10	100	84	95	100	100
Forbs	*Chamaecrista rotundafolia*	Wynn cassia	11	1	59	46	1	0	13	20
	Portulaca sp.	Pigweed	0	1	0	29	0	1	0	35
	Stylosanthes humilis	Townsville stylo	0	0	0	2	0	0	0	0
	Neptunia oleracea	Water mimosa	0	0	2	0	0	0	3	0
Total forbs			11	2	61	77	1	1	16	55
Subshrubs	*Stylosanthes scabra*	Shrubby stylo	4	3	22	76	0	1	0	5
	Cucumis sp.		1	0	2	5	0	0	0	0
	Carissa ovata	Currant bush	0	0	1	0	0	0	5	13
	Hybanthus stellarioides	Spade flower	0	0	0	5	0	0	0	0
	Phyllanthus sp.		0	0	0	2	0	0	0	5
	Indigofera linnaei	Birdsville indigo	0	0	0	0	0	0	0	3
	Galactia sp.	Wild pea	0	0	0	0	0	0	3	0
	Sida sp.		0	0	0	0	0	0	0	3
Total subshrub			5	3	25	88	0	1	8	29
Shrubs	*Petalostigma pubescens*	Quinine bush	12	1	54	34	1	0	8	0
	Carissa lanceolate	Conckerberry	1	0	24	5	2	1	75	48
	Vachellia farnesiana	Mimosa bush	1	0	7	0	0	0	3	3
	Duranta sp.		0	0	0	0	0	0	1	0
	Chamaesyce sp.		0	0	2	0	0	0	3	0
	Pittosporum spinescens	Wallaby apple	0	0	5	0	0	0	3	0
	Acacia leptostachya	Wattle	0	0	2	0	0	0	0	0
	Flueggia virosa	White currant	0	0	0	5	0	0	0	0
	Denhamia sp.		0	0	2	2	0	0	0	0
	Capparis canescens		0	0	2	0	0	0	0	0
	Senna sp.		0	0	2	0	0	0	0	0
	Crotalaria novaehollandiae	Rattlepod	0	0	2	2	0	0	0	0
	Melaleuca bracteate	Tea tree	0	0	0	0	0	0	3	0
	Eremophila mitchellii	Sandalwood	0	0	0	0	0	0	3	0
	Calotropis procera	Rubber tree	0	0	0	0	0	0	0	3
Total shrubs			14	1	102	48	3	1	99	54
Trees	*Acacia shirleyi*	Lancewood	7	0	7	0	0	0	0	0
	Acacia sp.	Wattle	5	0	41	5	0	0	2	3
	Mangifera indica	Mango	3	1	2	2	0	0	0	0
	Pleiogynium timorense	Burdekin plum	0	1	0	2	1	0	5	0
	Atalaya hemiglauca	Whitewood	0	0	7	0	0	0	8	0
	Casuarina cunninghammi	Sheoak	0	0	2	0	0	0	15	0
	Flindersia dissosperma	Leopardwood	0	0	2	0	0	0	8	3
	Archidendropsis basaltica	Red lancewood	0	0	2	0	0	0	0	0
	Melaleuca nervosa	Fibrebark	0	0	5	0	0	0	0	3
	Geijera parviflora	Wilga	0	0	2	0	0	0	3	3
	Eucalyptus sp.		0	0	0	0	4	1	43	25
Total trees			15	2	70	9	5	1	84	37
Unidentified dicot			3	1	51	39	5	2	58	65

ground. *Eucalyptus* species in this region are small to medium size trees, common to both sites but found only in the samples from Niall Station. *Eucalyptus* leaves were found in the diet of 63% of Niall Station animals during the dry season and were notably often bleached and desiccated. The presence of bleached leaves ($n = 8$), bark ($n = 4$), sticks ($n = 3$) and possum scats ($n = 1$) in the rumens of chital sampled during the dry season on Niall indicate chital were consuming leaf litter. Four samples contained ticks (*Haemaphysalis longicornis*), presumably ingested during grooming.
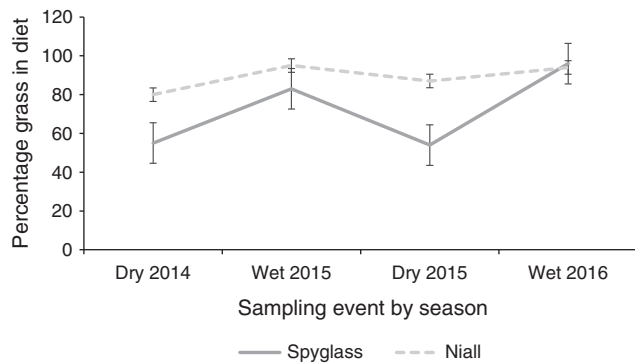
Fig. 2. Mean percentage (± s.e.) of grass in the rumen of chital for each sampling time (dry season 2014, wet season 2015, dry season 2015, and wet season 2016).

Table 2. Mean percentage occurrence of the most common plant species or groups during both seasons combined in rumens of chital on Spyglass (*n* = 82) and Niall Station (*n* = 80)

Percentage contribution by dry weight (DW) is also shown for both properties combined. Plant species or groups are listed in order of dry weight contribution

Plant	Spyglass (%)	Niall (%)	DW (%)
Poaceae	100	100	82.3
Unidentified dicot.	46	61	3.1
Petalostigma pubescens	44	4	2.8
Chamaecrista rotundafolia	51	16	2.5
Stylosanthes scabra	49	4	1.9
Eucalyptus species	0	34	1.4
Acacia shirleyi	4	0	1.2
Acacia species	23	11	1.0
Mangifera indica	2	0	0.8
Carissa lanceolata	15	61	0.8
Pleiogynium timorense	1	3	0.6
Portulaca species	15	17	0.3

Pasture analyses

There were seasonal changes in the presence of vegetation classes (grass, forb, subshrub, shrub, regrowth) and average height (cm) of plant classes measured on Spyglass (Table 3).

In October 2015 (dry season) cover (mean = 17%, *n* = 8) was significantly less (*P* < 0.001, *t* = 5.19) than in March 2016 (wet season) (mean = 55%, *n* = 8). Percentage cover of all plant types except shrubs increased during the wet season (Fig. 3).

Increases in vegetation cover on Spyglass were mainly attributable to greater abundance of grass, forbs and subshrubs. Grasses were the predominant plant class in both seasons, recorded at a percentage cover of 11 and 27% for dry and wet seasons respectively. Although the cover of subshrubs increased from 3 to 8%, the largest increase in cover was recorded among forbs. Forbs were present on only two dry season transects at a negligible frequency whereas they were present on all wet season transects at an average wet season cover of 19%.

The predominant forb observed during the wet season was *Chamaecrista rotundaifolia* and, although not abundant as a standing plant during the dry season, comprised a large proportion of the leaf litter. *C. rotundifolia* is categorised as either a short-lived perennial or annual species which did not persist in the pasture during the dry season of 2015. The most common subshrub was *Stylosanthes scabra* (shrubby stylo), a perennial plant with a tendency to develop a woody stem. This species was found in wet and dry seasons, although was approximately twice as common during the wet season.

Changes in aerial cover over time were attributable to both the presence and absence of plants as well as changes in plant size. The average height of grass swards was 14 cm during the dry season, which increased by more than 140% to 34 cm during the wet season. Other plant categories showed similar increases, the exception being the greater proportional increase of ~500% in forb height from 4 to 22 cm. The mean 'greenness' score of all plant classes during the wet season was 2.0, indicating active growth. The seasonal contrast in the in the mean 'greenness' score was greatest for dry season grass (0.2) and least for shrubs (~1.0).

Diet preference of chital on Spyglass

Ivlev's electivity index for grass, forbs and shrubs (shrubs, subshrubs, and regrowth) altered in rank between the dry season in October 2015 and wet season March 2016 (Table 4).

All vegetation types were abundant during the wet season of 2016 when chital showed strong preference for grass. In contrast, in the dry season chital demonstrated a preference for shrubs and avoided grass. Grass consumption was only 53% of the diet by dry matter on Spyglass despite remaining the predominant plant available in the pasture at 78% biomass index.

Discussion

In the savannah woodlands of north Queensland chital deer are primarily grazers with an ability to alter forage intake with changing pasture composition. At least 42 plant species contributed to the diet including grasses, forbs, shrubs, trees and litter. In both the wet and dry seasons grass comprised most of the diet, and where surveyed also contributed most to the available standing crop. We had only eight transects where we measured plant availability, but they showed that during the wet season all classes of food plants were more available, larger in size and growing more actively. Chital diet during the wet season was almost exclusively grass; grass was preferred and non-grass forages were avoided. In contrast, dry season food plants were less prevalent, smaller, growing less actively and, although grass then comprised a greater proportion of available forage, it was eaten at a rate below that of its relative availability. Chital showed a clear dry season preference for shrubs which were available in the environment at an estimated proportion of 21% of biomass but comprised 41% of the diet.

Several dry season rumen samples from Niall station contained material including bark, bleached leaves (due to time spent on the ground), and possum scats. Six rumens contained the seeds of *Mangifera indica* and *Pleiogynium timorense*, which were possibly also eaten from the ground. This ingestion of fallen vegetation might suggest an indiscriminate vacuum

Average	Vegetation		Grass		Forb		Subshrub		Shrub		Regrowth	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Cover	17	55	11	27	<0.5	19	3	8	2	<0.5	<0.5	<0.5
Height of vegetation	–	–	14	34	4	22	17	38	28	37	22	29
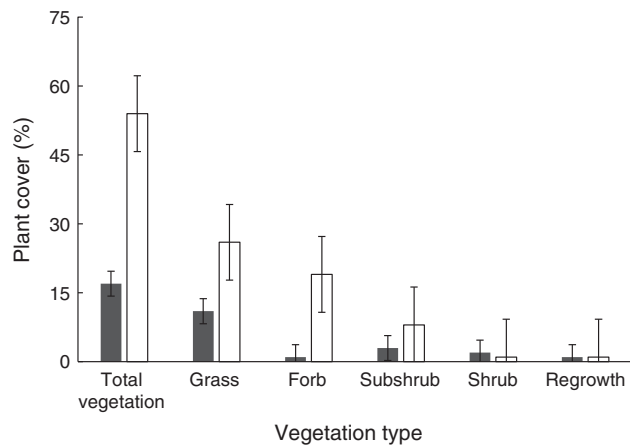
Fig. 3. Average plant cover (%, ± s.e.) recorded on step point transects for all vegetation classes (total vegetation, grass, forb, subshrub, shrub, regrowth), dry season 2015 (black) and wet season 2016 (grey) at Spyglass.

approach to feeding made necessary when forage was in short supply, although ungulates eating fallen browse material from the forest floor has been observed elsewhere. For example, chital in Guindy National Park in India were observed to commonly consume fallen fruits and leaves (Raman 1997), and in Corbett National Park chital were observed to eat items dislodged from the canopy by monkeys (Dinerstein 1979). The use of litterfall by white-tailed deer has been recorded in New Zealand (Nugent and Challies 1988) and North America (Ditchkoff and Servello 1998) where the nutritional value of litterfall may exceed that of browse.

The possibility that some classes of animals might utilise browse at a higher rate because of increased metabolic demand (e.g. growth, lactation) or sex or age was not supported. Consumption of browse related principally to season although individual animals varied in the percentage of grass eaten and breadth of species utilised. Although individual variation in diet has been noted in other deer species in Australia (Forsyth and Davis 2011), the variation in diet of individual animals over time is not known (Prache *et al.* 1998). However, it demonstrates the importance of adequate sample size as emphasised by (Puglisi *et al.* 1978) to characterise the average diet.

The most limiting component of most rangeland diets for herbivores is energy, followed by protein (Mlay *et al.* 2006). In the Burdekin district the differences between wet season and dry season concentrations of protein (N), phosphorus (P) and percentage dry matter digestibility (DMD) in grasses relate principally to stage of growth rather than plant component (leaf, stem) or species (McIvor 1981). Declines for grasses in mean wet season N, P and DMD of green leaf to dry season leaf range from 50 to 75%. (McIvor 1981) The dry season preference of chital for shrubs rather than grass showed a bias for food plants in a more active stage of growth, which aligns with diet quality that is highest in the actively growing stage of plant development and least in senescence (Albon and Langvatn 1992). Our greenness index on Spyglass varied greatly between seasons suggesting forage quality (growth stage) also varied. Changes in greenness were most apparent in grasses, which were essentially dried stem during the dry season whereas browse items maintained some signs of active growth. The nutritional value of browse varies according to species, and although generally inferior to actively growing grass, the levels of protein and digestible energy are retained for longer following periods of growth (Le Houérou 1980). Some forb and browse plants are known to accumulate specific micronutrients; *Portulaca* sp. is an annual forb endemic to northern Australia found in more than half of the wet season rumens from both sites in 2016 and which contains sodium at more than 30 times the concentration of grasses from the same area (Watter *et al.* 2019b). During the dry season when the nutritive value of senescent grass was likely to be very low, browse species presumably offered a relative benefit. In a concurrent study of body condition (kidney fat indices and bone marrow fat) undertaken on the same animals (Watter *et al.* 2019a), measures of condition (and by association the recent plane of nutrition) were consistently higher in the wet season than the dry season. From this we assume that, although chital alter their dry season diet by consuming plants that are more actively growing, the dry season diet is demonstrably inferior to the wet season diet.

The seasonal change in chital diet in north Queensland might be best explained in terms of their ability to choose food plants according to nutritional value rather than plant type or species. Chital utilise a range of plants which are broadly selected according to phenology and especially during the dry season better approximate food quality than food availability. The ability of chital to selectively utilise a range of forage types allows them to exploit different plants during their active growth stage. Grasses that respond rapidly to rain, and have a short growing season before starting to dry are attractive to grazers for a shorter period than browse that continue to produce new growth for longer following rainfall.

The manner in which chital utilise food plants in north Queensland is consistent with the models of Hofmann (1989) and Hanley (1982) using predictors of animal size, rumeno-reticular volume and mouth size. The extent to which ruminants

Table 4.   Ivlev's modified electivity index (Loehle and Rittenhouse 1982) with 95% confidence intervals for grass, forbs and shrubs (shrubs, subshrubs and regrowth considered together), on Spyglass dry season October 2015 and wet season March 2016

Season	Forage type	% Dry weight contribution	Plant biomass index (cover × height)	Ivlev's Electivity Index	95% Confidence interval
Wet season	Grass	91	884	0.21	0.20 – 0.21
	Forb	2	418	−0.93)	−0.98 to −0.88
	Shrub	6	101	−0.45)	−0.59 to −0.32
Dry season	Grass	53	154	−0.18)	−0.26 to −0.11
	Forb	11	1	−0.39)	−0.82 to −0.02
	Shrub	34	42	0.16	−0.02 to 0.34

can utilise different forage types is influenced by their morpho-physiology. Hofmann (1989, p. 444) related differences in the alimentary tract to behaviours of diet selection, and categorised ruminants according to a 'flexible system of overlapping ruminant feeding types'. This determination classifies chital as intermediate feeders that choose a varied diet which might change seasonally. The basis of this categorisation is food selectivity rather than animal size, and is related to morphological adaptations of the alimentary tract. Chital, with smaller mouths, are better able to selectively take leaf material from shrubs than cattle (*Bos indicus*) in north Queensland for instance. The morphology of cattle requires that they consume larger relative quantities of food but have the ability to utilise more lignified forage of poorer quality.

Chital diet and food preferences change markedly between wet and dry seasons which we speculate to be a strategy to limit the detriment of declining forage quality. Chital are affected by dry season nutritional bottlenecks (Watter *et al.* 2019a), and broader studies of dry season diet quality and body condition are needed to further assess the effect on chital abundance (Watter 2020). Further study of nutrition combined with other limiting factors (e.g. predation, soil micronutrients, year-to-year variation in rainfall) are required to predict the extent to which wild chital herds might expand in the future.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

References

Albon, S., and Langvatn, R. (1992). Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* **65**, 502–513. doi:10.2307/3545568

Alipayo, D., Valdez, R., Holechek, J. L., and Cardenas, M. (1992). Evaluation of microhistological analysis for determining ruminant diet botanical composition. *Journal of Range Management* **45**, 148–152. doi:10.2307/4002773

Ash, A., O'Reagain, P., Mckeon, G., and Smith, M. S. (2000). Managing climate variability in grazing enterprises: a case study of Dalrymple Shire, North-eastern Australia. *In:* 'Applications of Seasonal Climate Forecasting in Agricultural and Natural Ecosystems'. pp. 253–270. (Springer: Dordrecht, Netherlands.)

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, A. (2016). Chital Deer – An Expanding Problem in North Queensland. *In:* '2016 Pest Animal Symposium'. Queensland.

Brown, W., and Chapman, N. G. (1990). The dentition of fallow deer (*Dama dama*): a scoring scheme to assess age from wear of the permanent molariform teeth. *Journal of Zoology* **221**, 659–682.

Bugalho, M., Milne, J., and Racey, P. (2001). The foraging ecology of red deer (*Cervus elaphus*) in a Mediterranean environment: is a larger body size advantageous? *Journal of Zoology* **255**, 285–289. doi:10.1017/S0952836901001376

Burrows, W., Carter, J., Scanlan, J., and Anderson, E. (1990). Management of savannas for livestock production in north-east Australia: contrasts across the tree-grass continuum. *Journal of Biogeography* **17**, 503–512. doi:10.2307/2845383

Congdon, B. C., and Harrison, D.A. (2008). 'Vertebrate Pests of the Wet Tropics Bioregion: Current Status and Future Trends.' pp. 322–333. (Blackwell Publishing: Oxford, UK.)

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. (1979). An ecological survey of the Royal Karnali-Bardia wildlife reserve, Nepal. Part II: Habitat/animal interactions. *Biological Conservation* **16**, 265–300. doi:10.1016/0006-3207(79)90055-7

Ditchkoff, S. S., and Servello, F. A. (1998). Litterfall: an overlooked food source for wintering white-tailed deer. *The Journal of Wildlife Management* **62**, 250–255. doi:10.2307/3802285

Forsyth, D. M., and Davis, N. E. (2011). Diets of non-native deer in Australia estimated by macroscopic versus microhistological rumen analysis. *The Journal of Wildlife Management* **75**, 1488–1497. doi:10.1002/jwmg.179

Forsyth, D., Richardson, S., and Menchenton, K. (2005). Foliar fibre predicts diet selection by invasive red deer *Cervus elaphus scoticus* in a temperate New Zealand forest. *Functional Ecology* **19**, 495–504. doi:10.1111/j.1365-2435.2005.00991.x

Forsyth, D. M., Pople, A., Woodford, L., Brennan, M., Amos, M., Moloney, P. D., Fanson, B., and Story, G. (2019). Landscape-scale effects of homesteads, water, and dingoes on invading chital deer in Australia's dry tropics. *Journal of Mammalogy* **100**, 1954–1965. doi:10.1093/jmammal/gyz139

Hamlin, K. L., Pac, D. F., Sime, C. A., DeSimone, R. M., and Dusek, G. L. (2000). Evaluating the accuracy of ages obtained by two methods for Montana ungulates. *The Journal of Wildlife Management* **64**, 441–449. doi:10.2307/3803242

Hanley, T. A. (1982). The nutritional basis for food selection by ungulates. *Journal of Range Management* **35**, 146–151.

Hofmann, R. (1985). Digestive physiology of the deer-their morphophysiological specialisation and adaptation. *In*: 'Biology of deer production. Proceedings of an International Conference'. Dunedin, New Zealand, 13–18 February 1983. pp. 393–407.

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* **78**, 443–457. doi:10.1007/BF00378733

Holecheck, J. L., Vavra, M., and Pieper, R. D. (1982). Methods for determining the nutritive quality of range ruminant diets – a review. *Journal of Animal Science* **54**, 363–376. doi:10.2527/jas1982.542363x

IPNI (2020). International Plant Names Index. The Royal Botanic Gardens, Kew, Harvard University Herbaria and Libraries and Australian National Botanic Gardens. Available at: http://www.ipni.org (accessed 7 June 2020).

Khan, J. (1994). Food habits of ungulates in dry tropical forests of Gir Lion Sanctuary, Gujarat, India. *Acta Theriologica* **39**, 185–193. doi:10.4098/AT.arch.94-21

Le Houérou, H. (1980). Chemical composition and nutritive value of browse in tropical West Africa. *In:* 'Browse in Africa; The Current State of Knowledge'. (Ed. H. N. Le Houerou.) pp. 261–289. (International Livestock Centre for Africa: Addis Ababa, Ethiopia.)

Lechowicz, M. J. (1982). The sampling characteristics of electivity indices. *Oecologia* **52**, 22–30. doi:10.1007/BF00349007

Loehle, C., and Rittenhouse, L. R. (1982). An analysis of forage preference indices diets of cattle, sheep. *Rangeland Ecology & Management/Journal of Range Management Archives* **35**, 316–319.

Manly, B., McDonald, L., Thomas, D. L., McDonald, T. L., and Erickson, W. P. (2007). 'Resource Selection by Animals: Statistical Design and Analysis for Field Studies,' 2nd edn. (Springer Science & Business Media: Berlin, Germany.)

McInnis, M. L., Vavra, M., and Krueger, W. C. (1983). A comparison of four methods used to determine the diets of large herbivores. *Journal of Range Management* **36**, 302–306. doi:10.2307/3898474

McIvor, J. (1981). Seasonal changes in the growth, dry matter distribution and herbage quality of three native grasses in northern Queensland. *Australian Journal of Experimental Agriculture* **21**, 600–609. doi:10.1071/EA9810600

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. Department of Agriculture, Fisheries and Forestry, Government of Queensland, Brisbane, Qld, Australia. Available at: https://futurebeef.com.au/wp-content/uploads/BurdekinGrazing_final-04a.pdf (accessed 21 July 2020).

McKeon, G., Day, K., Howden, S., Mott, J., Orr, D., Scattini, W., and Weston, E. (1990). Northern Australian savannas: management for pastoral production. *Journal of Biogeography* **17**, 355–372. doi:10.2307/2845365

Medin, D. E. (1970). Stomach content analyses: collections from wild herbivores and birds. *In*: 'Range and Wildlife Habitat Evaluation – A Research Symposium'. Flagstaff, AZ, USA, May 1968. pp. 133–145. (University of Minnesota: MN, USA.)

Mentis, M. (1981). Evaluation of the wheel-point and step-point methods of veld condition assessment. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa* **16**, 89–94. doi:10.1080/00725560.1981.9648927

Mlay, P. S., Pereka, A., Chikula Phiri, E., Balthazary, S., Igusti, J., Hvelplund, T., Riis Weisbjerg, M., and Madsen, J. (2006). Feed value of selected tropical grasses, legumes and concentrates. *Veterinarski Arhiv* **76**, 53–63.

Norbury, G., and Sanson, G. (1992). Problems with measuring diet selection of terrestrial, mammalian herbivores. *Australian Journal of Ecology* **17**, 1–7. doi:10.1111/j.1442-9993.1992.tb00774.x

Nugent, G. (1983). 'Deer Diet Estimation by Rumen or Faecal Analysis: An Evaluation of Available Techniques.' (Protection Forestry Division, Forest Research Institute: Rotorua, New Zealand.)

Nugent, G., and Challies, C. (1988). Diet and food preferences of white-tailed deer in north-eastern Stewart Island. *New Zealand Journal of Ecology* **11**, 61–71.

O'Reagain, P. J., and Schwartz, J. (1995). Dietary selection and foraging strategies of animals on rangeland. Coping with spatial and temporal variability. *In:* 'Recent Developments in the Nutrition of Herbivores'. (Eds M. Journet, E. Grenet, M. H. Farce, M. Theriez and C. Demarquilly.) pp. 407–423. (INRA: Paris.)

O'Reagain, P., Bushell, J., Holloway, C., and Reid, A. (2009). Managing for rainfall variability: effect of grazing strategy on cattle production in a dry tropical savanna. *Animal Production Science* **49**, 85–99. doi:10.1071/EA07187

Osborn, R. G., Jenks, J. A., and Jensen, W. F. (1997). Diet of North Dakota elk determined from rumen and fecal analyses. *Prairie Naturalist* **29**, 237–248.

Owen-Smith, N. (1994). Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology* **75**, 1050–1062. doi:10.2307/1939429

Petrides, G. A. (1975). Principal foods versus preferred foods and their relations to stocking rate and range condition. *Biological Conservation* **7**, 161–169. doi:10.1016/0006-3207(75)90012-9

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

Prache, S., Gordon, I. J., and Rook, A. J. (1998). Foraging behaviour and diet selection in domestic herbivores. *Annales de Zootechnie* **47**, 335–345. doi:10.1051/animres:19980502

Puglisi, M. J., Liscinsky, S. A., and Harlow, R. F. (1978). An improved methodology of rumen content analysis for white-tailed deer. *Journal of Wildlife Management* **42**, 397–403. doi:10.2307/3800276

Raman, T. S. (1997). Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India. *Journal of Biosciences* **22**, 203–218. doi:10.1007/BF02704733

Roff, C. (1960). Deer in Queensland. *Queensland Journal of Agricultural Science* **17**, 43–58.

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

Shrader, A., Owen-Smith, N., and Ogutu, J. (2006). How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. *Functional Ecology* **20**, 376–384. doi:10.1111/j.1365-2435.2006.01107.x

Spalinger, D., Hanley, T., and Robbins, C. (1988). Analysis of the functional response in foraging in the Sitka black-tailed deer. *Ecology* **69**, 1166–1175. doi:10.2307/1941271

Stone, G., Dalla Pozza, R., Carter, J., and McKeon, G. (2019). Long paddock: climate risk and grazing information for Australian rangelands and grazing communities. *The Rangeland Journal* **41**, 225–232. doi:10.1071/RJ18036

Ward, A. L. (1970). Stomach content and fecal analysis: methods of forage identification. Range and Wildlife Habitat Evaluation. US Forest Service Miscellaneous Publications 1147, Washington, DC, USA. p. 146.

Waring, G. H. (1996) Preliminary study of the behavior and ecology of axis deer on Maui, Hawaii. Department of Zoology, Southern Illinois University, Carbondale, IL, USA. Available at: http://www.hear.org/AlienSpecies InHawaii/waringreports/axisdeer.htm (accessed 20 December 2006).

Watter, K. A. (2020). How nutrition influences the distribution and abundance of chital deer (*Axis axis*) in northern Queensland. PhD Thesis, School of Agriculture and Food Sciences, The University of Queensland, Qld, Australia. . doi:doi:10.14264/uql.2020.147

Watter, K., Baxter, G., Brennan, M., Pople, T., and Murray, P. (2019*a*). Decline in body condition and high drought mortality limit the spread of wild chital deer in north-east Queensland, Australia. *The Rangeland Journal* **41**, 293–299. doi:10.1071/RJ18113

Watter, K., Baxter, G. S., Pople, T., and Murray, P. J. (2019*b*). Effects of wet season mineral nutrition on chital deer distribution in northern Queensland. *Wildlife Research* **46**, 499–508. doi:10.1071/WR19039