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Published in:
Austral Ecology

DOI:
[10.1111/aec.13309](https://doi.org/10.1111/aec.13309)

Published: 01/06/2023

Document Version
E-pub ahead of print

[Link to publication](#)

Citation for published version (APA):

Campbell, M. A., Lawton, T., Udyawer, V., Bell-Anderson, K. S., Westcott, D., & Campbell, H. A. (2023). The southern cassowary (*Casuarius casuarius johnsonii*) remains an important disperser of native plants in fragmented rainforest landscapes. *Austral Ecology*, 48(4), 787-802. <https://doi.org/10.1111/aec.13309>

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RESEARCH ARTICLE

The southern cassowary (*Casuarius casuarius johnsonii*) remains an important disperser of native plants in fragmented rainforest landscapes

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Funding information

Birds Queensland; Zoo and Aquarium Association Australasia

Abstract

Large-bodied frugivores are essential to the ecological function of rainforest communities. The southern cassowary (*Casuarius casuarius johnsonii*) is the only large frugivore in the tropical rainforests of Australia. Here, we assessed whether cassowaries remain important to native plant seed dispersal in areas where the rainforest is highly fragmented, and exotic fruits are abundant. To do this, we developed a tri-axial acceleration logger integrated with a motion sensor and VHF radio transmitter. The telemetry device was small enough to be hidden inside a native fruit. The cassowaries ingested it, transported it and defecated it up to 24 h later with the seeds from the fruits they had ingested during the tracking period. The telemetry device was then located by VHF radio and collected with the scat. The distance travelled, activity profile, consumed fruit diversity, and scat energy content were assessed for cassowaries inhabiting regions with different degrees of urbanization. We found that cassowaries inhabiting more urbanized areas consumed the greatest proportion of fruits from exotic plants (~30%) but still incorporated a significant proportion of fruits from native plants in their diet. These individuals existed in higher states of activity and rested less than individuals inhabiting more intact swathes of rainforest, actively moving between urban gardens and the rainforest. The study shows cassowaries have a flexible foraging strategy that has enabled them to persist in rainforest-fragmented landscapes. They remain a significant disperser of seeds from native plants between rainforest patches, and as such, cassowaries remain essential in maintaining native plant diversity within these fragmented patches.

KEYWORDS

accelerometry, Australia, calorimetry, dispersal distance, movement ecology, native seed, Wet Tropics

INTRODUCTION

Large-bodied frugivores play a particularly significant role in dispersing seeds and maintaining rainforest communities (Forget et al., 2007; Janzen & Martin, 1982; Mack, 1993). The modification of contiguous forests

into ever smaller and more widely distributed patches impacts the ecology and survivorship of frugivores by changing the spatial density of food resources (Laurance et al., 2000; Rogan & Lacher, 2018). In turn, the ecological function of these species as propagators of fruiting rainforest plants may be disrupted and their

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fitness reduced, creating a feedback loop that generates chronic degradation of the remnant rainforest community (Buckley et al., 2006; Gosper et al., 2005).

The Australian Wet Tropics bioregion covers an area of 8944 km² (Stork et al., 2008). Over the past 70 years, extensive sections of the low and mid-elevation rainforests have been cleared for sugarcane, tree crops, cattle grazing and urbanization (Stork et al., 2008). These processes have created a patchwork of remnant tropical rainforest patches, contributing to the threatened status of over 50 animals, 200 plants and three ecological communities (EPBC Act, 1999). The southern cassowary (*Casuarius casuarius johnsonii*) is a large flightless ratite that exists throughout this region. This subspecies is endemic to the Australian Wet Tropics and nationally listed as endangered (EPBC Act, 1999).

Cassowaries are the only large-bodied seed disperser in the Australian rainforest (Latch, 2007; Westcott et al., 2008). They significantly contribute to seed dispersal because of their ability to perform long-distance dispersal of large quantities of seeds, particularly of large-seeded species (Bradford et al., 2008). This unique dispersal service suggests that cassowaries make an essential contribution to the structuring and dynamics of Australian rainforests (Bradford et al., 2008; Bradford & Westcott, 2010; Stocker & Irvine, 1983; Westcott et al., 2008), but their significance in influencing the persistence of flora communities in isolated remnant rainforest patches is less clear. Cassowaries are also effective dispersers of the seeds from exotic fruiting plants, and it has been suggested that cassowaries play a significant role in dispersing exotic weeds to locations unattainable by other means (Westcott et al., 2008).

Through the examination of the seeds in cassowary scats, it has been reported that the birds may feed exclusively upon exotic fruits in urbanized and agricultural areas (Crome, 1976; Westcott et al., 2005). This dietary preference may be associated with some exotic fruits having a higher caloric value, higher biomass crop and being more spatially concentrated than the fruit from native plants (Westcott et al., 2008; Wright, 2005). Ultimately, the preference for exotic fruits may negatively impact cassowaries and other native frugivorous species by transforming diverse native vegetation that provides fruit resources throughout the year into a monoculture that only provides abundant fruit in a discrete period (Westcott et al., 2008). This interplay among rainforest patchiness, exotic plants and cassowary foraging behaviour warrants further investigation because it has potential ramifications for the ecological health and functioning of remnant rainforest communities throughout the Australian Wet Tropics, particularly in highly fragmented landscapes. The present study aimed to assess how cassowaries changed their foraging ecology as the rainforest became more fragmented and human density increased under the assumption that it would reveal whether cassowaries remained an important disperser of native plants in these highly fragmented rainforest landscapes that dominate the lowland areas of the Wet Tropics Bioregion in Queensland, Australia.

Despite their size (adult females can weigh up to 76 kg; Campbell et al., 2014), cassowaries are challenging to directly observe in the thick rainforest due to their cryptic colouration and behaviour. To observe foraging behaviour in free-ranging cassowaries, we developed a novel telemetry device that was sufficiently small to fit inside one of the cassowary's favoured fruits. The telemetry device had a tri-axial accelerometer to measure total body activity and a VHF transmitter to determine the distance it was transported by the cassowary and where it was excreted. By locating the telemetry device, we could also collect the scat to determine the diversity of plant species the cassowaries had fed upon, and the relative energy content derived from these fruits. These data were compared from

individuals inhabiting varying levels of urbanization to test the hypothesis: Cassowaries inhabiting urbanized areas would feed predominately on easily accessible exotic fruits from urban gardens to maximize net energy intake and, as a result, would not search for and forage upon native plants within patches of remnant rainforest. Consequently, the role of the southern cassowary (*C. casuarius johnstonii*) as a disperser of native rainforest plants would be diminished within these landscapes.

METHODOLOGY

Study areas

Southern cassowaries (*C. casuarius johnstonii*) were studied at four locations in the Wet Tropics bioregion of Queensland, Australia (Figure 1a,b). The study sites were selected because they possessed a southern cassowary population, and each differed in the degree of rainforest fragmentation and urbanization. Site 1 was classified as a 'remnant rainforest'; located within the Daintree World Heritage Area. This site was chosen because it comprised a large swathe of relatively undisturbed lowland rainforest with very low levels of urbanization. Most of this area is either a national park or other protected rainforest sites. Site 2 was classified as a 'logged mid-elevation rainforest'; located adjacent to the Kuranda township, where urban dwellings tend to be situated on rainforest land tenure blocks of areas between 20 000 and 100 000 m². This area has undergone historical logging and regrowth, with more recent moderate clearing levels around residential dwellings and small horticulture operations. Site 3 was classified as a 'logged lowland rainforest', located on the outer skirts of an urban centre, with a similar level of forest clearing, urbanization and land tenure sizes as Site 2. Site 4 was classified as 'urban fragmented', located by the coastline adjacent to the Innisfail township. The rainforest in this area is highly fragmented into small patches (<4000 m²) interspersed with cleared land and urban dwellings on blocks of ~1000 m².

Human population density and percentage canopy cover of plants >10 m in height were assessed for each study site. Human population data and land tenure block size spatial layers were obtained from the Queensland Government Cadastral Data website (Open Data Portal, 2020), and the woody vegetation cover dataset was downloaded from the TERN/AusCover website (TERN AusCover, 2020). A 500 m radius buffer was created around each of the excreted telemetry devices (plus scat) collection locations, and the various parameters listed above were extracted from the respective layer (R Core Team, 2021). A buffer size of 500 m radius was used because this is roughly the size of the home range (1 km²) of southern cassowary determined from previous studies of tracked individuals from the same area (Campbell et al., 2012).

Animal biotelemetry

Cassowaries are challenging animals to capture and handle. They have a large 'dagger claw' (+12 cm) that they can use to good effect when stressed and any manual restraint or handling requires chemical immobilization (Campbell et al., 2014). Anaesthetics are highly likely to affect foraging activity for the proceeding 24 h, and because we wanted to assess foraging activity, we developed a telemetry device that a cassowary could swallow without requiring physical interference by humans. The telemetry device was concealed inside the seed of a native fruit (Cassowary plum, *Cerbera*

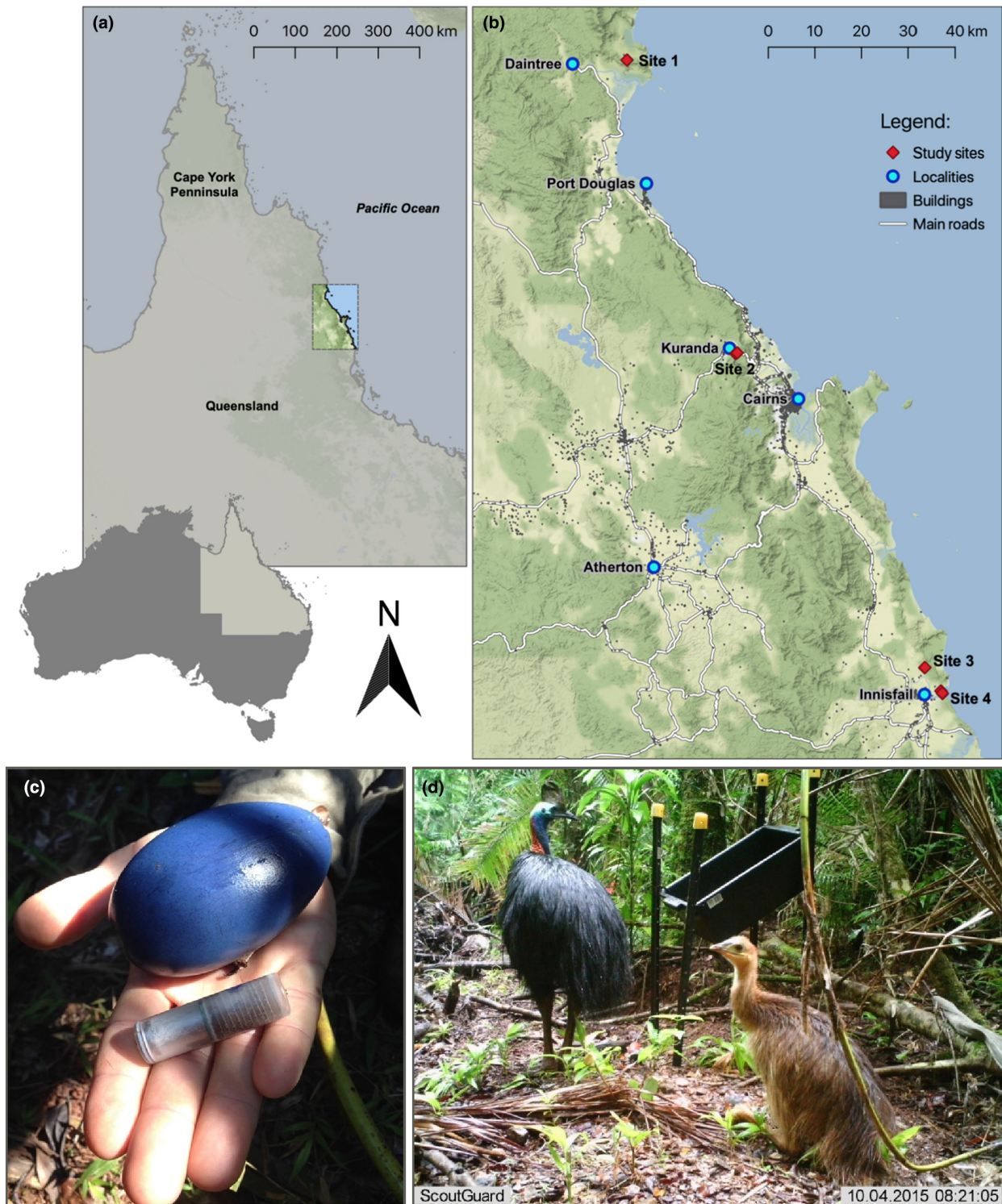


FIGURE 1 (a) Study area within the Wet Tropics bioregion (Queensland, Australia); (b) the locations of four study sites of differing rainforest fragmentation and human density; (c) photograph of an ingestible accelerometry telemetry device alongside an intact cassowary plum (*Cerbera floribunda*); and (d) motion-triggered camera image of an adult and a juvenile southern cassowary (*Casuarius casuarius johnsonii*) beside one of the study stations, where telemetry devices were ingested by foraging cassowaries.

floribunda) to entice the ingestion by the cassowaries. This fruit was chosen because the seed was large enough to conceal the telemetry device (Figure 1c) and is known to be a favoured food of the southern cassowaries (Stocker & Irvine, 1983). The fruit skin and flesh were first carefully sliced using a scalpel. The seed was then opened using a small handsaw

and made partially hollow using a manual bowl gauge grind. The telemetry device was placed inside the internal seed cavity and secured due to the snug fit. The seed was then closed with the fruit flesh and skin still attached. Feeding stations were placed along known cassowary foraging tracks at distances >1 km apart to reduce the potential of the same bird ingesting more than one telemetry device (feeding stations location data are listed in [Table S1](#)). The stations were positioned and designed to effectively present the fruits containing the telemetry devices to the birds and prevent ingestion of fruit containing the telemetry device by other ground-dwelling animals, reducing the risk of interference by non-targeted species. The stations comprised a 40-L black plastic storage container mounted on posts and placed diagonally, with the opening section positioned at an approximately 60° angle to facilitate access. The lower side of the container was suspended ~80 cm off the ground ([Figure 1d](#)). Each telemetry device was hidden inside a piece of native fruit and placed inside the container 30 min before sunrise (2 telemetry devices per feeding station). There were no other food items in the container, only the fruits enclosing the telemetry devices. When telemetry devices were not ingested by 4:00 pm, the fruits containing the telemetry devices were collected and re-set for offering on the next day. Telemetry device deployment occurred for 6 days per study site, with each telemetry device being deployed at different locations on consecutive days.

The purpose-designed ingestible telemetry devices (Telonics) comprised a 3-axis accelerometer data logger, a thermal data logger and a VHF radio. The accelerometer was activated when the cassowary picked up the fruit. This motion caused the VHF beacon to decrease pulse frequency from 60 to 40 pulses per minute. This change in the radio frequency alerted the research team, who monitored all telemetry devices' VHF frequencies using a five-prong Yagi antenna and hand-held VHF receiver unit (Titley), that a cassowary had picked up a telemetry device. These cylindrical ingestible telemetry devices (4.5 cm length × 1 cm diameter) were coated in inert PVC and weighed 20 g. These dimensions and weight were comparable to the seeds of fruits routinely ingested and egested by cassowaries and were smaller and lighter than some of these (Bradford et al., 2008). The bird's measure of total body activity was calculated as an average root mean squared value ($RMS = \sqrt{A_x^2 + A_y^2 + A_z^2}$) representing the vectorial dynamic body acceleration (VeDBA, unit = g; Qasem et al., 2012). The telemetry device recorded VeDBA measures at 500 Hz, averaged over 1-min intervals and stored onboard. The temperature was also recorded and logged on board at 5 min intervals. The telemetry device then passed through the cassowary gut and was egested effortlessly. Once the bird egested the telemetry device and remained motionless for 15 min, the VHF radio pulse rate increased to 60 bpm to enable telemetry device retrieval. Egested telemetry devices were located using a directional Yagi antenna and a VHF receiver (Titley), and latitude and longitude were recorded upon retrieval. The telemetry device displacement distance (DD; m) was defined as the linear distance between the feeding station where the telemetry device was ingested and the location where the telemetry device plus scats were found. The habitat type and canopy cover of the location where the scats were found was also recorded. The present study was conducted over two periods: pre (October 2015) and post (April 2016) wet monsoonal seasons. Those periods were selected because of the fruiting seasonality of several native plants and the cassowary mating season occurring towards the end of the dry season (Crome, 1976).

The states of activity for each bird during their full tracked periods were determined from the VeDBA data using K-means clustering analysis from the package 'cluster' (Maechler et al., 2019) in R (R Core Team, 2021). The

'elbow method' was used to identify the optimal number of clusters ($k = 3$). These clusters were ranked as 'low' (resting), 'medium' and 'high' states of activity (Figure 2a). The proportion of time each bird spent within each of these states of activity was then determined.

Scat analysis

Upon telemetry device retrieval, the whole cassowary scat was collected. Total scat weight was recorded, and a 5 g sub-sample of soft faecal matter was separated and frozen for further calorimetry analysis. The scat was rinsed with water using a sieve to remove soft faecal matter. The remaining undigested seeds were weighed and counted, and the plant species were visually identified (CPD = consumed plant diversity). The organic subsample from the scat was freeze-dried at -40°C (Dynavac Freeze Dryer) and then assessed for calorific content (SEC = scat energy content) by bomb calorimetry (PARR 6200; John Morris Scientific Pty Limited). An effort was also made to collect fresh fruit from all the identified seed varieties found in the scats from the study sites. However, some seed species could not be identified, nor the fruiting plant located in the forest. All fruit and scat samples were weighed, freeze-dried and then weighed again to obtain the extracted moisture content. Dried fruit and scat samples were then subjected to duplicate combustion within an oxygen vessel (PARR 1108) to determine energy content (kJ/g dry weight). The energy equivalence of the vessel and calorimeter (kJ/ $^{\circ}\text{C}$) was determined with a benzoic acid standard (26.44 kJ/g). The moisture content data were used to calculate the energy content for wet weight.

Statistical analysis

Model selection framework was used to investigate the effects of season, site, attributes of diet and telemetry device retention time (RT; min) on the total body activity (VeDBA; g) and on telemetry device displacement distance (DD = linear distance between feeding station and the location where scat and telemetry device were egested; m). Season (pre- and post-wet) was included in the models because it would likely have affected the abundance and distribution of rainforest fruits (Table 2). A generalized linear model (GLM) was used to identify key factors that explained the variability in telemetry device displacement distance (DD; m), whereas a linear mixed-effects model (LMM) was used to analyse the measure of VeDBA (g) as the response variable. Due to heteroscedasticity in values of VeDBA (g), this variable was square-root transformed to normalize the data, and models were built using the package '*lme4*' (Bates et al., 2014) in R (R Core Team, 2021). Bird trace ID was included in LMMs as a random term to account for the repeated measures nature of the activity data (VeDBA). The 'dredge' function in the '*MuMIn*' R package (Bartoń, 2020) was used to build all candidate models that were used to identify the best combination of explanatory factors for each response variable (Table 2; the complete list of all tested models can be found in Table S2). The best model selection was assessed based on the goodness of fit and parsimony of models using Akaike's information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). Additional models were built to assess the effect of site, season and telemetry device retention time (RT) on the properties of the scat collected from each tracked bird (CPD and SEC).

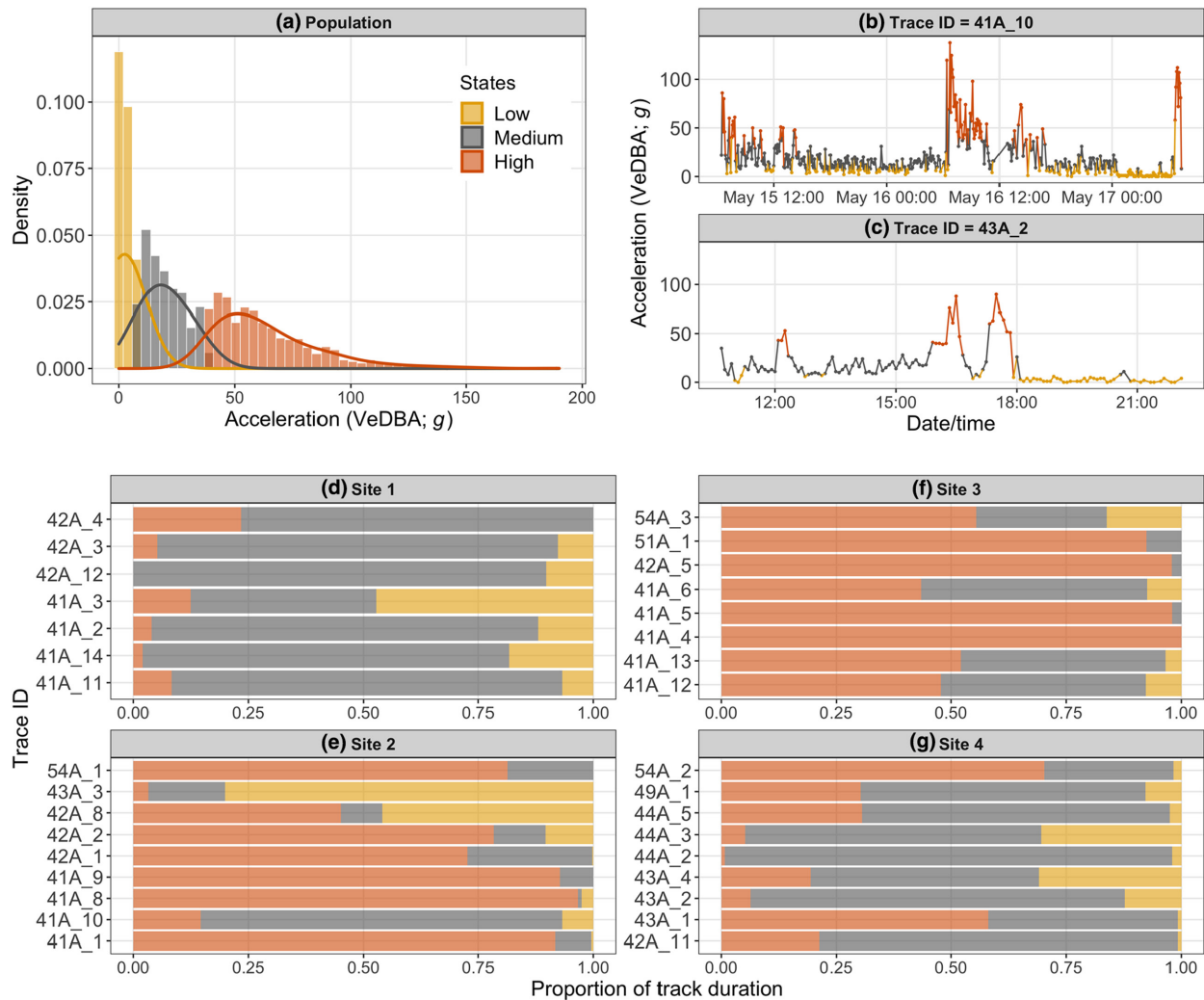


FIGURE 2 K-means cluster behavioural classification. (a) Frequency distribution (Density) of the three states of activity from sampled birds ($n = 33$). (b, c) Two accelerometry sample traces (Trace ID: 41A_10 and 43A_2). (d–g) Proportion of time (track duration) the birds spent at each state of activity per study site. The traces from all birds recorded in the present study ($n = 33$) are shown in [Figure S1](#).

RESULTS

Across the four study sites, the telemetry devices were ingested and egested by southern cassowaries (*C. casuarius johnstonii*) and then successfully recovered 33 times ([Table 1](#)). On four occasions, the same individual ingested two telemetry devices simultaneously, in which case, the data from only one of those telemetry devices were used in the analysis. The photographs from the camera trapping showed that a mix of males and females were sampled, but it was challenging to confidently determine the cassowary ID, sex and age from the photographs. Therefore, we cannot confirm or deny that the same individual was not tracked more than once in each location. Some adults had juvenile cassowaries with them during feeding, but the telemetry device-embedded fruit was too large for juveniles to feed upon.

The cassowaries ingested the telemetry devices during morning foraging, with the earliest recorded at 05:35 am and the latest at 11:00 am. Only two of the 33 deployments were ingested in the afternoon (01:50 and 3:15 pm). All cassowaries egested the telemetry devices throughout the afternoons and evenings, with the earliest defecation occurring at 02:15 pm and the latest at 10:05 pm. Most cassowaries defecated the telemetry device under the

TABLE 1 Summary data on southern cassowary (*Casuarius casuarius johnsonii*) foraging ecology across four study sites of varying rainforest fragmentation and human population density.

Study site	1	2	3	4
Total telemetry device deployments (pre post-wet)	7 (4 3)	8 (3 5)	8 (3 5)	10 (4 6)
Human population density/km ² (mean±SD)	2.66±3.68	9.66±1.04	2.55±0.90	28.14±34.20
% Canopy cover trees >10m tall (mean±SD)	43.11±0.57	43.82±0.52	37.24±5.70	26.98±0.75
Diurnal VeDBA (g; mean±SD)	24.7±18.7	40.7±32.8	45.8±31.2	29.9±23.5
Proportion time high state activity (mean±SD)	0.13±0.11	0.55±0.27	0.67±0.27	0.30±0.17
Telemetry device displacement distance (m; mean±SD)	228.91±117.52	289.84±192.39	237.85±293.64	472.27±324.59
Telemetry device retention time (min; mean±SD)	261.43±92.14	312.50±146.60	218.89±69.54	438.00±200.27
Proportion of natives/scat (mean±SD)	1.00	0.68±0.44	0.78±0.32	0.80±0.25
Diversity seed species in scat (mean±SD)	1.71±1.5	2.38±1.41	3.0±1.51	3.7±2.58
Scat energy content (kJ/g; mean±SD)	2.45±0.58	3.18±1.25	2.90±0.47	2.68±0.69
Weight of collected scat (g; mean±SD)	607.14±266.49	256.25±161.42	353.00±100.77	366.00±212.74
Proportion of scats deposited in rainforest	1	0.78	1	1

rainforest canopy, and only twice (both at Site 2) was the telemetry device deposited outside a remnant rainforest patch (Table 1). The telemetry devices recorded the birds' internal temperature as $\bar{x} \pm \text{SD}$: $38.5 \pm 1.13^\circ\text{C}$.

Foraging activity and seed dispersal

Cassowaries foraging at Sites 1 and 4 exhibited significantly lower mean diurnal VeDBA (vectorial dynamic body acceleration; g) than birds monitored at Sites 2 and 3 (Table 1; Figure 2). Accordingly, individuals in study Sites 2 and 3 spent the largest proportion of time in high states of activity (Table 1). Birds from Site 4 (most fragmented) showed an ~1.7-fold greater telemetry device retention time (RT; $\bar{x} \pm \text{SD}$: 438.0 ± 200.27 min; Table 1; Figure 3b) than birds at Site 1 (least fragmented). Cassowaries foraging at Site 1 spent the least proportion of time in high states of activity ($\bar{x} \pm \text{SD}$: 0.13 ± 0.11 ; Table 1 and Figure 2) throughout both pre- and post-wet seasons (Figure 3a) and the second-lowest telemetry device retention time ($\bar{x} \pm \text{SD}$: 261.43 ± 92.14 min; Table 1), following those recorded for Site 3 ($\bar{x} \pm \text{SD}$: 218.89 ± 69.64 min; Table 1). The mean VeDBA recorded across all individuals in the pre-wet season ($\bar{x} \pm \text{SD}$: 36.9 ± 0.87 g) was ~1.5-fold greater than that recorded from individuals during the post-wet season ($\bar{x} \pm \text{SD}$: 25.1 ± 0.66 g). Accordingly, the top-ranked model for VeDBA included study site, season and telemetry device retention time (Table 2).

Cassowaries monitored at Site 4 had a greater mean telemetry device displacement distance (DD; $\bar{x} \pm \text{SD}$: 472.27 ± 324.59 m), and Site 1 had the lowest mean DD ($\bar{x} \pm \text{SD}$: 228.91 ± 117.52 m; Figure 3b; Table 1). Despite this difference in the mean DD values between the study sites, and likely due to large individual variability, the top-ranked model for DD included only season (Table 2). Birds studied in the post-wet season showed a threefold greater DD (m) than birds monitored in the pre-wet at the same site (Figure 3c). There was no significant effect of study site, proportion of native seeds in scats (prop_nat), telemetry device retention time (RT) or scat energy content (SEC) on DD (Table 2).

Diet and energetics

The cassowaries monitored in this study fed primarily on native fruits, even those recorded within highly fragmented areas (Table 1).

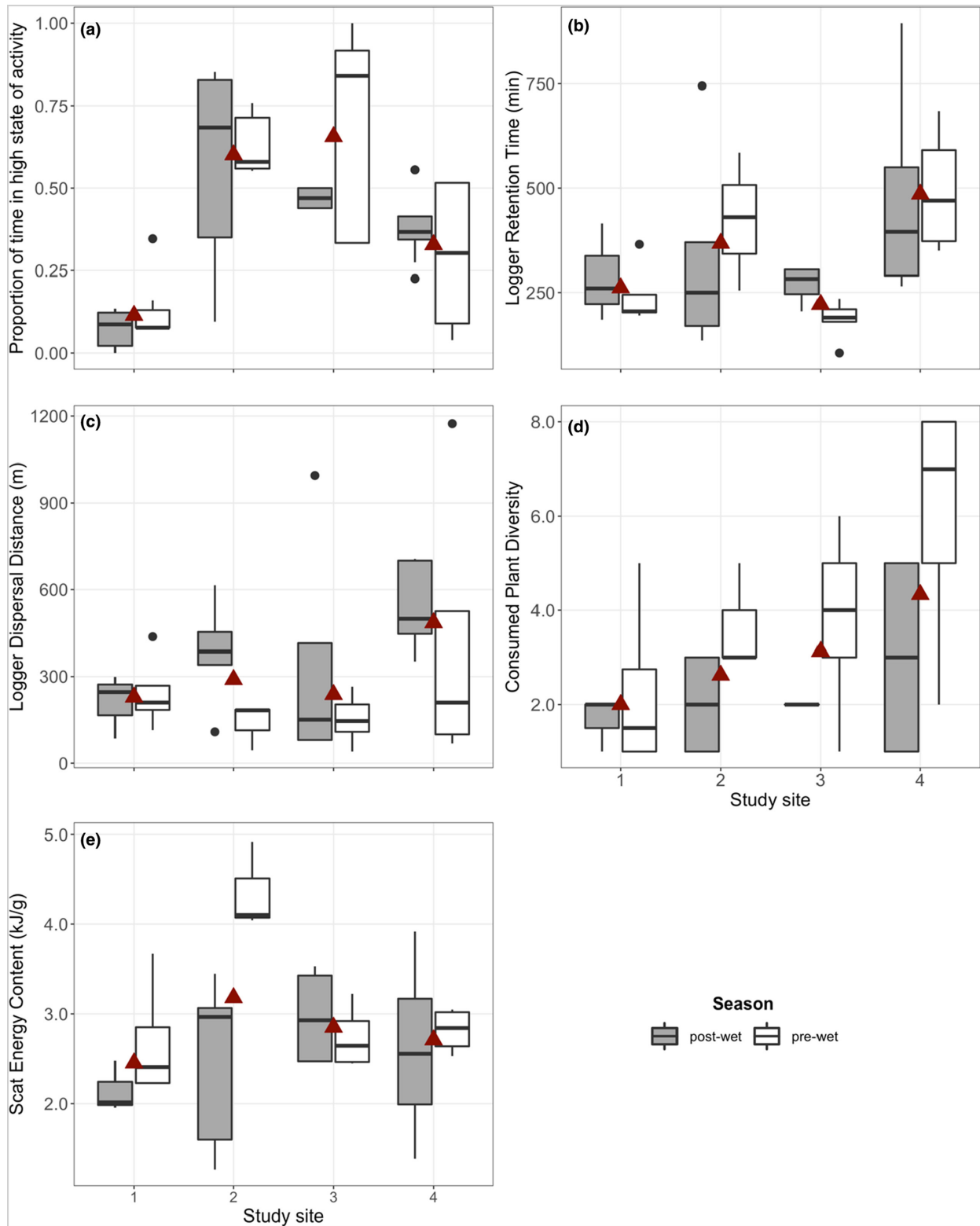


FIGURE 3 Data recorded by telemetry devices ingested by southern cassowaries (*Casuarius casuarius johnsonii*) per study site and season (grey fill = post-wet; white fill = pre-wet): (a) Proportion of time in high state of activity; (b) telemetry device retention time (RT; min); (c) telemetry device displacement distance (DD; km); (d) consumed plant diversity (CPD; number of species); and (e) scat energy content (SEC; kJ/g). Red triangles represent the mean.

Cassowaries foraging at Site 2 (low fragmentation and high population density), Site 3 (partially fragmented with low population density) and Site 4 (most urbanized) had a greater proportion of exotic seeds in their

scats (Table 1) compared with individuals inhabiting Site 1 (large rainforest swathes). The overall diversity of seed species in the birds' diet was different across all study sites. The birds monitored in the dense remnant rainforest (Site 1) showed a preference for only a few plant species (CPD = consumed plant diversity), and all of those were identified as natives (Table 1). Contrarily, the birds foraging in the most fragmented and urbanized habitat (Site 4) had a greater overall mean diversity of seed species (CPD) in their scats, which was twofold greater than Site 1 (Table 1). The CPD was also ~twofold greater pre-wet season ($\bar{x} \pm \text{SD}$: 4.5 ± 2.24 species) than in the post-wet season ($\bar{x} \pm \text{SD}$: 2.43 ± 1.34 species) for Sites 2–4 (Figure 3d), reflecting a wider diversity of available fruits at this time of the year. Conversely, cassowaries foraging in Site 1 displayed the opposite pattern, with a decrease of ~35% in CPD between pre- ($\bar{x} \pm \text{SD}$: 2.25 ± 1.89 species) and post-wet season ($\bar{x} \pm \text{SD}$: 1.67 ± 0.6 species). As expected, there was a positive linear trend between the time birds spent foraging (time from ingesting to egesting the telemetry device; RT = telemetry device retention time) and the CPD ($R^2 = 0.34$, $p = 0.058$). Accordingly, the top-ranked model for consumed plant diversity included only season and telemetry device retention time (RT; Table 2).

Fruits ingested by the cassowaries varied greatly in energy content (Figure 4), with no significant differences in energy content per gram of flesh between the native and exotic fruits examined in the present study ($n = 17$). However, the native cassowary plum (*C. floribunda*) had a two- to threefold higher energy content per gram of flesh than all the other fruits consumed by cassowaries (Figure 4). The exact amount of energy ingested by each bird could not be estimated because we could not obtain fresh fruit samples from several plant species found in the cassowaries' scats in time for the calorimetry component. Hence, we have used the scat energy content as a proxy for energy intake. Our data analysis showed that the overall mean energy content found in the cassowary scats (SEC = scat energy content; kJ/g) was not influenced by CPD. Season, however, was shown to have a significant effect on SEC. Birds from Site 2 showed a significant difference in both CPD and SEC between the seasons (Figure 3e). The birds' proportion of time in high state of activity (PTHSA) had an impact on SEC, as there was a positive trend between SEC and the proportion of time at high states of activity during the pre-wet season ($R^2 = 0.23$, $p = 0.026$) and a negatively skewed trend in the post-wet season ($R^2 = -0.27$, $p = 0.073$). Across all sites and for both seasons, the length of time the cassowaries took to pass the telemetry devices through their digestive system (RT = telemetry device retention time; min) had a positive linear trend to the SEC ($R^2 = 0.36$, $p < 0.001$). Accordingly, the top-ranked model for SEC included season, study site, RT and PTHSA (Table 2).

DISCUSSION

Our study supported previous observations that cassowaries inhabiting more urbanized landscapes ingest a larger variety of exotic fruits than cassowaries inhabiting rainforest landscapes (Crome, 1976; Westcott et al., 2005). However, we reject the hypothesis that the role of the southern cassowary (*C. casuarius johnstonii*) as a disperser of native plants decreased as the degree of rainforest fragmentation and human density increased. On the contrary, the tagged cassowaries inhabiting urbanized landscapes retained a high diversity of seeds from native plants within their scats. These individuals rested less and exhibited significantly higher total body activity (VeDBA) than cassowaries inhabiting more intact rainforest

TABLE 2 Ranked generalized linear models used to investigate the effects of forest fragmentation on the foraging activity of southern cassowaries (*Casuaris casuaris johnsonii*).

Response	Model	df	logLik	AICc	Δ AICc	wAICc	
√VeDBA	season + site + RT	8	-4798.76	9613.58	0.00	0.13	
	prop_nat + season + site + SEC	9	-4797.92	9613.92	0.34	0.11	
	season + site + SEC	8	-4799.07	9614.21	0.63	0.10	
	site + RT	7	-4800.13	9614.31	0.73	0.09	
	Null	3	-4807.86	9621.74	8.15	0.00	
Full model	prop_nat + season + site + RT + SEC	10	-4798.28	9616.67	3.09	0.03	
DD	season	3	-185.48	377.91	0.00	0.34	
	prop_nat + season	4	-184.93	379.53	1.62	0.15	
	season + RT	4	-185.15	379.97	2.05	0.12	
	season + SEC	4	-185.47	380.60	2.69	0.09	
	Null	2	-189.36	383.18	5.27	0.02	
Full model	prop_nat + season + site + RT + SEC	9	-182.61	392.70	14.79	0.00	
CPD	season + RT	4	-63.02	135.47	0.00	0.57	
	season + site	6	-61.20	137.63	2.17	0.19	
	Full model	season + site + RT	7	-60.29	139.05	3.58	0.10
	season	3	-66.15	139.13	3.66	0.09	
	RT	3	-67.59	142.02	6.55	0.02	
Null	2	-69.28	142.97	7.50	0.01		
SEC	PTHSA + season + site + RT	8	-122.88	262.84	0.00	0.43	
	season + site + RT	7	-124.33	263.49	0.65	0.31	
	Full model	PTHSA + season + CPD + site + RT	9	-122.82	264.99	2.15	0.15
	season + CPD + site + RT	8	-124.25	265.58	2.74	0.11	
	PTHSA + season + CPD + RT	6	-132.16	276.93	14.09	0.00	
Null	2	-169.51	343.10	80.25	0.00		

Note: The values in bold indicate the top-ranked model. Degrees of freedom (df), log-likelihood (logLik), sample corrected Akaike's information criterion (AICc), change in AICc relative to the model with the lowest AICc value (Δ AICc) and the relative AICc weight (wAICc) are shown for each model. The variables are: $\sqrt{\text{VeDBA}}$ = vectorial dynamic body acceleration (g; square-root transformed), season = pre- and post-wet seasons; site = study sites; SEC = scat energy content (kJ/g); prop_nat = proportion of native seeds in scat; DD = telemetry device displacement distance (m); RT = telemetry device retention time (min); CPD = consumed plant diversity (number of species); PTHSA = proportion of time in high state of activity. The table below contains the top 4 ranked, full, and null models. The complete list of models can be found in [Table S2](#).

landscapes. This activity pattern was a consequence of them frequently moving between remnant rainforest patches to forage on native fruits, and whilst doing so, the birds deposited seeds from native plants they had acquired in other rainforest patches.

Consequently, the Southern cassowary remains an important disperser of native plants between remnant rainforest patches within the highly fragmented and urbanized landscapes that dominate the lowland regions of the Wet Tropics Bioregion in Australia. As far as we know, this is the first application of an ingestible accelerometry telemetry device to measure individual-based foraging activity. The technique offers great potential in studying animal–plant interactions in environments where the sky is precluded from satellites (e.g. dense canopy cover).

The biotelemetry methodology used in the present study could not determine fine-scale individual-based movement metrics. Measurement of an individual's activity space, habitat selection and movement rates between preferred sites would have enabled a fuller picture of the impact of rainforest patchiness on cassowary foraging activity. However, these data are challenging to collect for cassowaries in the rainforest. Manual handling of cassowaries is not recommended because they can cause significant injury to humans from their large dagger-like claws (Campbell et al., 2012,

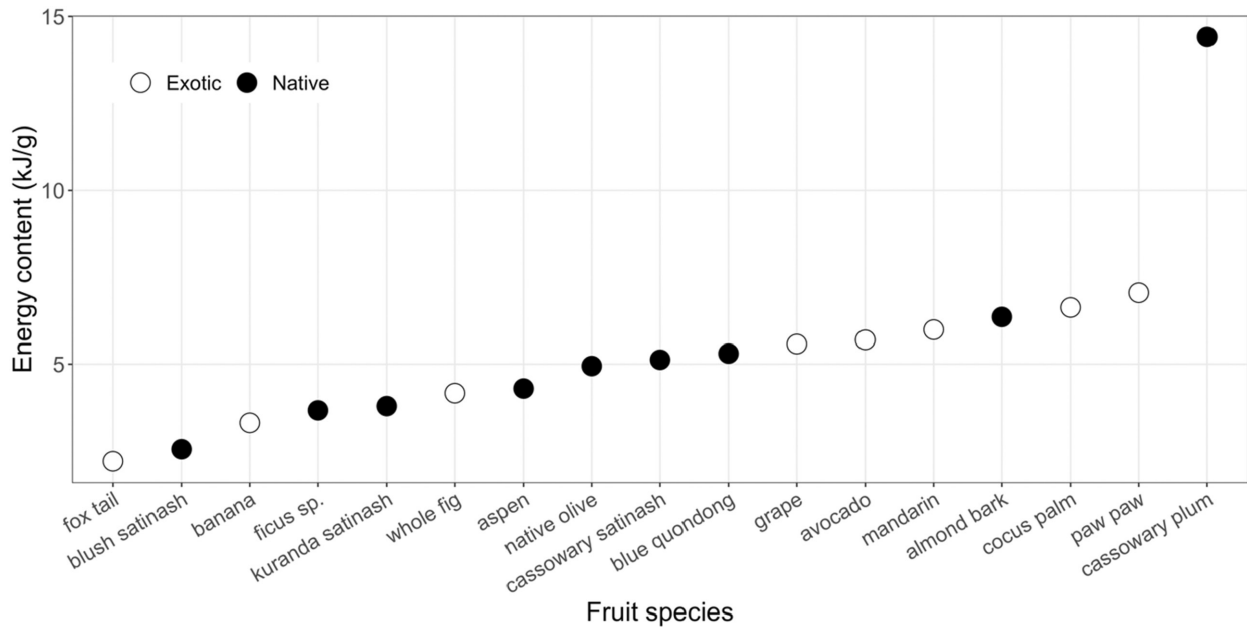


FIGURE 4 Energy content of fruit samples (kJ/g) obtained by bomb calorimetry analysis ($n = 17$). The black circles represent plant species native to the Wet Tropics region of Queensland (Australia), and the white circles represent the plant species introduced to the region from other parts of Australia or overseas.

2014). Sedation is possible, but recovery times vary greatly between individuals (Campbell et al., 2014). Moreover, biotelemetry in the rainforest is problematic as satellite connectivity is intermittent and active tracking challenging, even for the experienced (Campbell et al., 2012). Instead, we used a tri-axial accelerometer to measure rates of activity, and by integrating a VHF radio transmitter and having the cassowaries swallow the device, we were able to track the seed dispersal.

Cassowaries confine their daily movements within a defined home range of $<1 \text{ km}^2$ (Campbell et al., 2014). They appear to have a good cognitive map of the resources within their home range and move along defined pathways between roost sites and fruiting trees (Crome & Moore, 1990). The females tend to have a more extensive home range than the males and encompass the ranges of 2–3 males (Campbell et al., 2014). Although there is overlap in the home ranges of cassowaries, they are territorial, and the home range size appears to be primarily determined by social factors (Campbell et al., 2012; Crome & Moore, 1990). This aspect of the bird's biology may explain why the direct distance telemetry devices were transported (i.e. the distance the ingested telemetry devices were transported between ingestion and egestion) by the cassowaries was not statistically different, irrespective of the landscape type. However, season significantly affected telemetry device displacement distance at all sites, with cassowaries transporting the telemetry devices further during the post-wet season than the pre-wet season. The seasonality of the fruiting plants is likely to have played a role in the observed seasonal changes in cassowary spatial movement because the maximum abundance of fruits in the Wet Tropics rainforest occurs during the pre-wet season (Crome, 1976).

Previous studies examining seeds in scats have reported that cassowaries prefer to feed on exotic species over native fruits if available (Crome, 1976; Westcott et al., 2005; Wright, 2005). On the contrary, all cassowaries in this study fed predominately on native fruits even when exotic fruits were available in abundance. This result was not entirely surprising, as the calorimetry component of the present study showed that the

energy content per gram of fruit from exotic and native species fed upon by cassowaries was comparable. Hence, providing no energetic advantage for the cassowary to forage exclusively on exotic species if native fruit were also available. Exotic fruits tend to have a much greater flesh-to-seed ratio than native rainforest fruits, which may play a role in digestion. In this study, cassowaries inhabiting fragmented landscapes had a higher proportion of seeds from exotic fruits in their diet compared with cassowaries in more intact rainforests, and the telemetry device retention time was significantly greater in these birds. However, the longer telemetry device retention time by cassowaries in urbanized areas did not significantly affect the distance that the telemetry device was transported between ingestion and excretion.

Interestingly, the native cassowary plum (*C. floribunda*) had an energy content per gram that was ~threefold greater than any other exotic and native fruits consumed by the cassowaries during this study. This fruit has presumably been given the name because the tree's presence is associated with cassowary visitation. The high energy content of the fruit likely explains its attractiveness to cassowaries, and the cassowary is the only animal large enough to eat the fruit from the cassowary plum tree and disperse its seeds (Forster, 1992; Stocker & Irvine, 1983). In the present study, the cassowary plum was the only fruit species found in the scats of birds from Site 1 (intact rainforest) during the post-wet season, and the observation highlights the plant's significance as an important cassowary food resource.

The southern cassowary is found throughout the Wet Tropics Bioregion in both pristine and highly disturbed habitats. It is very challenging to assess cassowary population density due to their rainforest habitat, but the analysis of DNA from within the scats has been used to provide fine-scale population estimates (Westcott et al., 2014). This previous study reported that one of the highest southern cassowary densities throughout the Wet Tropics Bioregion was around our Site 1. This area comprised the largest swathes of unbroken rainforest and a very low level of urbanization. The present study found cassowaries in this habitat to have the lowest daily rates of activity, the least diverse diet, the highest proportion of native fruit consumption, the lowest energy content within the scat, and the shortest telemetry device retention times. Therefore, it seems these birds undertake a less energy-demanding lifestyle compared with individuals in more fragmented and urbanized landscapes. However, we do not know whether this influences survivorship and reproductive success, and further investigation is required.

The population of cassowaries in the area where our study Site 2 was located (Kuranda range) was estimated by DNA analysis to be 75% less than the cassowary density at Site 1 (Latch, 2007; Westcott et al., 2014). Both these sites have low levels of rainforest fragmentation, but, Site 2 had a threefold greater human population density than Site 1. This would likely have resulted in increased threats to cassowaries from dogs and road traffic (Campbell et al., 2012). The present study found that cassowaries in Site 2 fed on a greater density of exotic fruits (a reflection of the higher human population) and showed higher total body activity (perhaps to evade dogs and traffic) compared with cassowaries inhabiting Site 1.

Cassowary density around our study Sites 3 and 4 were reported to be around 50% less than at Site 1 (Latch, 2007; Westcott et al., 2014). The human population density at these sites is high, and the cassowaries foraged on a greater abundance of exotic fruits than at Sites 1 and 2. The cassowaries at Site 3 spent a greater proportion of time in higher states of activity (PTHTSA) than at Site 4. A key difference between these two sites was the size of the land tenure plots. At Site 4, most properties are around 1000 m², with only a few >4000 m², whilst the plots at

Site 3 are between 10 000 and 40 000 m² and generally comprise an urban dwelling with small gardens surrounded by rainforest. Therefore, the cassowaries at Site 3 would have been required to travel greater distances to move between urbanized gardens, which may explain the observed accelerometry data.

In conclusion, as the human population increases within an area, the type and distribution of cassowary food resources change. Cassowaries seem very able to adapt their foraging repertoire and survive in these modified landscapes. However, the increased human population is also associated with decreased local cassowary abundance, which may be for reasons other than energy budgets.

The findings from the present study suggest that cassowaries remain an effective disperser of seeds from native plants in highly fragmented landscapes throughout the Wet Tropics Bioregion in Australia. However, cassowaries will equally feed upon the fruits from exotic plants and deposit the seeds from those plants within remnant rainforest patches. To help promote the persistence and ecological function of remnant rainforest patches, we suggest an effort be made to limit cassowary access to exotic fruiting plants and supplement urban gardens with native fruiting plants, such as cassowary plum.

AUTHOR CONTRIBUTIONS

Mariana A. Campbell: Conceptualization (supporting); data curation (lead); formal analysis (equal); investigation (equal); project administration (equal); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Tom Lawton:** Conceptualization (equal); methodology (equal); project administration (equal); resources (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Vinay Udyawer:** Data curation (equal); formal analysis (equal); methodology (equal); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (equal). **Kim S. Bell-Anderson:** Formal analysis (supporting); methodology (equal); resources (equal); writing – review and editing (supporting). **David Westcott:** Formal analysis (supporting); validation (equal); writing – review and editing (equal). **Hamish A. Campbell:** Conceptualization (lead); funding acquisition (lead); investigation (lead); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (supporting); writing – original draft (equal); writing – review and editing (lead).

ACKNOWLEDGEMENTS

The team would like to thank the many volunteers who worked long hours in the rainforest and Adrian Hogg for assisting with identifying rainforest plants from seeds. Open access publishing facilitated by Charles Darwin University, as part of the Wiley - Charles Darwin University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

The funding for this study was supplemented by small grants awarded to HAC by Birds Queensland and Zoo Aquarium Association Australia.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

ETHICAL APPROVAL

All animal research was completed under the University of New England Animal Ethics Permit (AEC15-062) and Queensland Government Scientific Purposes Permit (WISP16173915).

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How to cite this article:

Campbell, M.A., Lawton, T., Udyawer, V., Bell-Anderson, K.S., Westcott, D. & Campbell, H.A. (2023) The southern cassowary (*Casuarius casuarius johnsonii*) remains an important disperser of native plants in fragmented rainforest landscapes. *Austral Ecology*, 00, 1–16. Available from: <https://doi.org/10.1111/aec.13309>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.