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Diet and Dietary Preferences of the Southern Cassowary (*Casuarius casuarius*) in North Queensland, Australia

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ABSTRACT

We investigated the diet of the southern cassowary (*Casuarius casuarius*) by identifying the seeds and fruits in fecal droppings encountered on a set of transects over 2 yr in upland rain forest in the wet tropics of North Queensland. A total of 198 droppings containing 56 plant species were found. We surveyed fleshy fruit availability over the subsequent 68 mo on transects in the same area to ascertain fruiting patterns in the study area. The number of droppings found each month did not correspond to the pattern of available fruit biomass. There was no relationship between the fruit traits of moisture content, flesh to seed mass ratio, color, or crop size to contribution of a species to the diet. During the lean fruiting season (May–July) cassowaries relied more on species that fruited continuously throughout the year as they were significantly over-represented in droppings, while annual fruiting species were under-represented. During months of high fruit availability (October–December), continuously fruiting species were still over-represented in the diet but became less important while annual and biennial species became more important. Significantly more species with large fruit and large seeds appeared in the diet than expected and we confirm that the cassowary contributes to the continued dispersal of these species over long distances and in large quantities.

Key words: frugivory; fruit phenology; seed dispersal; wet tropics.

Tropical forests worldwide are increasingly under threat. In Australia's wet tropics, 19 percent of closed, tropical forest has been deforested since European settlement (Winter *et al.* 1987) and human-induced climate change is predicted to dramatically affect forest dynamics and species distributions (Hilbert *et al.* 2001). These changes have and will continue to have an impact on the ecosystem services provided by vertebrate dispersers. As the majority of plants (up to 95%) in Australia's wet tropical forests are fleshy fruited species adapted for dispersal by vertebrate frugivores (Webb & Tracey 1981, Hyland *et al.* 2003), diet choice and the dispersal services provided by these animals underlie both the present and future forest composition and structure.

Knowledge of the way plants and frugivorous animals interact in tropical forests is essential to understand ecological processes such as seed dispersal, niche, and dietary partitioning between species and the potential consequences of species loss from ecosystems. Fruit choice is a fundamental component of plant–animal interactions. Studies of fruit choice by frugivores have examined aspects of the fruit such as spatial and temporal patterns of fruit availability (Levey 1988) the nutritional and energy components of particular fruit (*e.g.*, Laska *et al.* 2003), color (Willson *et al.* 1989), fruit and seed traits (*e.g.*, Wheelwright 1993, Jordano 1995), and presentation of the fruit to frugivores (Shanahan *et al.* 2001). Each of these factors can be important in the choice of dietary items for particular or broad groups of frugivores (Gautier-Hion *et al.* 1985) or at particular times of the year. However, these complexes of fruit attributes do not act in isolation and all choices may vary with the availability of other resources or the age and experience of the animal doing the choosing (Schmidt & Schaefer 2004).

The largest and probably the most important frugivore in the closed forests of north Queensland is the southern cassowary, *Casuarius casuarius.* Cassowaries make an important contribution to dispersal services in that they disperse a variety of plant species long distances and in large quantities, including large-fruited and seeded species (Westcott *et al.* 2005a). No other individual animal in Australia's tropical forests is capable of seed dispersal of this magnitude. The large majority of the cassowary's diet consists of fleshy fruit (Pratt 1982, Stocker & Irvine 1983, Wright 2005) and it therefore potentially consumes and disperses more than 1500 plant species within its Australian range (Hyland *et al.* 2003).

Cassowary diet has been intensively studied previously in upland and highland forest in Papua New Guinea (Pratt 1982, Wright 2005) and lowland rain forest in Australia (Crome 1976, Stocker & Irvine 1983, Bentrupperbäumer 1998). Due to extensive clearing of these lowland forests, there are few continuous, lowland forested areas remaining in Australia's wet tropics (Winter *et al.* 1987) and often large distances occur between these areas. In contrast, much of the upland and highland forest has remained relatively undisturbed. Hence, these areas provide increasingly important habitat for supporting significant populations of the endangered cassowary (Crome & Moore 1990, Westcott 1999). In turn, the long-distance dispersal service provided by cassowaries in these areas undoubtedly contributes to the increase or maintenance of species richness, forest regeneration, and gene flow across the landscape. In this study, we report on the diet of the southern cassowary from 1998 to 2000 in upland rain forest. To examine whether cassowary utilization of fruits reflects the phenological patterns of the site and to explore the role of fruit traits in diet choice, we then compared this diet data with the fruit characteristics at the site and fruiting phenology over the subsequent 68 mo.

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METHODS

STUDY AREA.—We conducted the study on the western edge of Wooroonooran National Park, which lies on the eastern edge of the Atherton Tablelands, North Queensland (17°22′ S, 145°45′ E). Most of the area lies within Australia's Wet Tropics World Heritage Area. The study area covers approximately 14 km^2 and is contiguous with the much larger Queensland Wet Tropics forested area. The vegetation is complex mesophyll vine forest, ranging from 500 m to nearly 900 m asl, which was selectively logged > 30 yr prior to this study. We feel that the low logging intensity and amount of time passed since logging ceased have resulted in the study site being structurally sound with most fleshy fruited species recovering to a pre-logging state. Annual rainfall exceeds 3000 mm, most of which falls in the summer months (December–April).

STUDY SPECIES.—Southern cassowaries (*C. casuarius*) are large, flightless, highly frugivorous birds that occur in northern Queensland, Australia, and southern Papua New Guinea (Davies 2002). Large specimens can stand 2 m, weigh 76 kg, and have a gape width of 62 mm. Cassowaries are generally solitary birds occurring in densities as high as 0.08/ha in lowland forests (Bentrupperbäumer 1998). Cassowaries forage mainly on the forest floor, which limits their choice to the availability of fallen fruits and fruits presented below 2 m. The population in the Wet Tropics of Queensland is listed as endangered due to habitat loss under both the Environmental Protection and Biodiversity Conservation Act (Environment Australia 1999) and the Queensland Nature Conservation Act (Queensland Government Environment Protection Agency 1992).

MONITORING CASSOWARY DIET.—Between March 1998 and July 2000, a census of cassowary fecal droppings was conducted each month (excluding October 1998) along 9 km of unsealed tracks and 12 km of infrequently used walking trails. The unsealed tracks were driven slowly while the trails were walked, scanning *ca* 2 m each side. We recorded the species of fruit or seeds in the droppings. Those that could not be immediately identified were sown in a glasshouse and identified upon germination. Droppings with small seeds were spread onto a soil tray and species were identified as they germinated. We visually estimated the volume that the seed plus fruit of each species contributed to the dropping (nearest 5%). No attempt was made to count the number of fruit or seeds.

PHENOLOGY.—We recorded fruiting patterns within the study area by conducting monthly phenology surveys from July 2000 to February 2006. Four 250 × 5 m transects (totaling 0.5 ha) were established and then censused monthly. The transects were all located in the study area and were chosen to represent the variations in geology, topography, altitude, and vegetation. Along these transects, all trees, shrubs, palms, vines, and large epiphytes were identified. All fleshy fruits encountered on the ground and to a height of 2 m within the transects were counted and converted into a biomass estimate. Biomass was calculated using a mean mass per fruit for each species. This was calculated from measurements conducted on a sample of 2–70 fruits for most species present along transects (mean = 12.5 ± 0.6 SE). For all other species, we estimated the mass of the fruit from volume calculations taken from dimensions sourced from the literature. We combined the biomass estimate and the phenological data for each fruit species to provide a monthly estimate of fleshy fruited biomass in the study area. Because the fruit phenology survey was not concurrent with the survey for droppings, we used the phenological data to determine patterns of available fruit only. Consequently, we compared diet characteristics and fruiting patterns using mean monthly values determined from 68 mo of fruit phenology records.

CASSOWARY DIET RELATIVE TO FRUIT TRAITS.—We compiled a list of fruit characteristics for 250 fleshy-fruited species found in the study area using data from this study and from A. Ford (pers. comm.). We obtained data on fruit dimensions from direct measurements of a sample of 2–70 fruits ($N = 143$ species), usually from two or more individual plants. Measurements taken include mass, length, width, and depth (nearest 1 mm) of entire fruit and seed; the number of seeds per fruit; and the wet and dry mass of the flesh and seed components separately. For the remaining 107 species, similar data were gleaned from the literature (Hyland *et al.* 2003, Cooper & Cooper 2004). In these cases, fruit dimensions and seed number were taken as the mid point of the reported range for each species. We also recorded the dominant ripe fruit color using the classification of Willson *et al.* (1989), omitting the temporal bicolor class, (where mature and pre-ripe colors are present concurrently), and the morphological bicolor class, (where the fruit has two or three colors), as we were only searching for strong patterns as cassowaries may perceive colors differently to humans. We examined these fruit characteristic data in relation to fruit choice by cassowaries.

The 250 species from the study site for which we collected fruit characteristic data were grouped into phenological classes based upon annual, biennial, or continuous (both synchronous and asynchronous) fruiting. Species were assigned to these classes on the basis of phenological data collected during the 68 mo of this study, Westcott *et al.* (2005b), and M. Bradford, unpublished data). Species classified as 'annual' are those which fruit for a short period (1–8 mo) every year at a similar time of year; 'biennial' species fruit for a short period at intervals greater than one year but at a similar time of the year; and 'continuous' species fruit constantly throughout the year (≥ 9 mo of the year).

RESULTS

CASSOWARY DIET IN THE STUDY AREA.—Over the 28 mo of dropping surveys, a total of 198 droppings containing the fruits of 56 species of plant from 28 families were collected. All droppings encountered contained fruit or seeds of at least one species. Due to nongerminations and the possible oversight of some small seeds we cannot confidently say we identified and recorded all seeds in the droppings; however, we estimate that we accounted for at least 95 percent of the total seeds. In addition to fruits, fungus, hair and bones, leaves of various plants, and the flowers of *Syzygium cormiflorum* occurred in the droppings. Dietary items other than fruit

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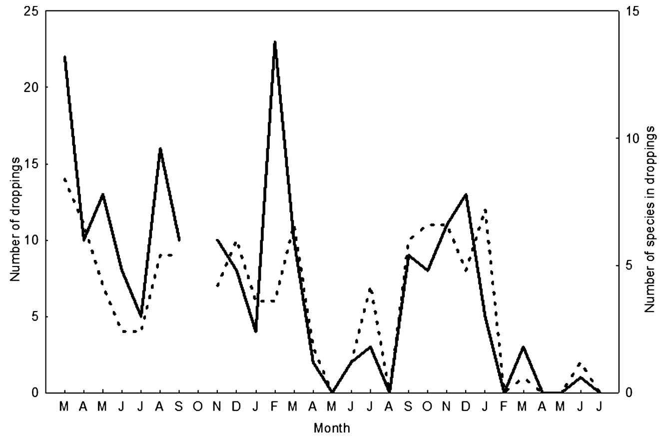

FIGURE 1. Frequency distribution of the number of droppings (solid line) and number of species in all droppings (dotted line) for each month of the study.

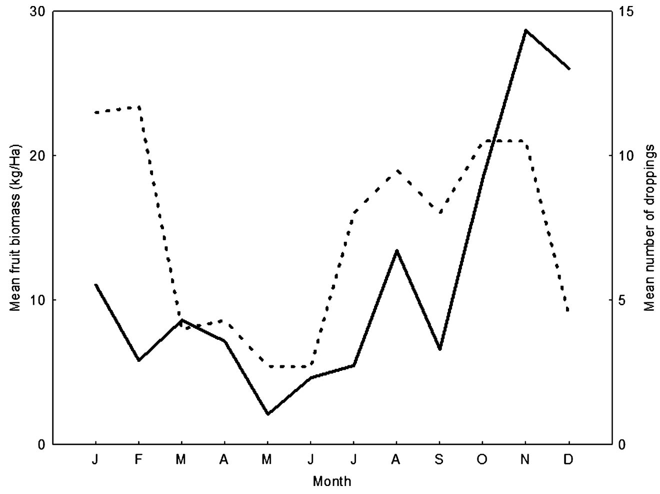

FIGURE 2. Estimated mean monthly fleshy fruit biomass available to cassowaries (solid line), and mean monthly dropping numbers lagged by one month (dotted line), *i.e.*, January's fruit is found in February's droppings. All droppings contained fruit or seed of at least one species.

made up less than 1 percent of total volume of the droppings. The mean number of species per month in the droppings was 5.1 ± 4.5 SD, (range: 0–14) (Fig. 1). The most abundant species in the droppings were *Aceratium doggrellii* (16% of total volume) and *Acmena divaricata* (14.5%) (Table S1).

The families most frequently recorded in the droppings were Elaeocarpaceae (105 droppings; 32.7% total volume), Lauraceae (66; 15.5%), Myrtaceae (42; 14.6%), and Rutaceae (37; 8.8%). Trees species contributed the most fruits and seeds to the droppings with 45 (80%) followed by vines with 5 (9%), shrubs/herbs with 4 (7%), and palms with 2 (4%). All species recorded were fleshy or had a fleshy aril or receptacle. Fruits widths recorded in the droppings ranged from 9.6 mm (*Cordyline cannifolia* and *Halfordia kendack*) to 50.1 mm (*Faradaya splendida*), with a mean of 24.6 (± 1.8 SE). Seed widths ranged from 0.5 mm for *Ficus congesta* var. *congesta* to 38.1 mm for *Elaeocarpus stellaris*, with a mean of 16.3 (± 1.5). A mean of 2.16 (± 1.23 SD) species occurred in each fecal dropping (range: 1–6). Most droppings were dominated by a single species with 68 droppings (34.3%) composed of only one species and 113 (57.1%) droppings containing ≥ 90 percent of one species by volume.

Over the period of the study, the number of droppings each month was significantly correlated with the number of species in the droppings for that month (Fig. 1; $R^2 = 0.51$, df = 1,26, $P < 0.01$). The mean number of droppings encountered each month was not correlated with the annual pattern of available fruit biomass in the subsequent phenology survey ($R^2 = 0.25$, df = 1,10, $P = 0.10$). More realistically, if the number of droppings is lagged by one month, *i.e.*, January's fruit is found in February's droppings, there is again no significant correlation with the pattern of available fruit biomass (Fig. 2; $R^2 = 0.10$, df = 1,10, $P = 0.32$). Lagging the mean number of species found in the droppings by 1 mo results in no correlation with the mean number of species available to the cassowaries for the previous month ($R^2 = 0.21$, df = 1,10, $P = 0.13$). The highest fruit availability was present from October to December while a distinct lean season was apparent from May to July, with similarly low biomass recorded in February and September (Fig. 2).

CASSOWARY DIET RELATIVE TO FRUIT TRAITS.—Large-fruited and seeded species are more likely to be included in the diet than smaller-fruited species. Both mean fruit width and mean seed width of species in cassowary diets were significantly higher than those of species recorded at the study area and not in the diet ($t = -4.13$, df = 239, $P < 0.001$; $t = -3.80$, df = 220, $P < 0.001$, respectively). Of the 56 fruit species we recorded from cassowary droppings, 15 (26.8%) were large seeded as defined by Westcott *et al.* (2005b), (>20 ml) and 27 (48%) were large seeded as defined by Stocker and Irvine (1983), (> 8 ml). Using Westcott *et al.*'s (2005b) conservative definition, a significantly greater proportion of large-seeded species occurred in the diet than occurs at the study area generally, ($\chi^2 = 7.41$, df = 1, $P < 0.01$).

There was no significant difference between the colors of fruits in the diet and those in the study area generally (χ^2, df = 1, $P > 0.1$ for all colors). Fruits in the diet did not have a significantly different flesh moisture content ($t = 1.21$, df = 133, $P = 0.23$) or flesh to seed mass ratio ($t = -0.73$, df = 141, $P = 0.47$) to fruits recorded in the study area but not in the diet. Estimated available fruit crop size (kg/ha/yr) for species in the diet was the same as the overall estimated available fruit crop size for all species in the study area that did not appear in the diet ($t = -0.83$, df = 141, $P = 0.40$).

During the peak fruiting months (October–December), 35 species (62% of total species in the diet) were found in droppings. A small proportion of these were continuously fruiting species (17.1%), with 42.8 percent fruiting biennially and 40.1 percent being annual fruiting species. In these months of fruit abundance, cassowaries consumed annual, biennial, and continuous fruiting

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species in significantly different proportions than they occur in the study area ($\chi^2 = 7.7$, df = 2, $P = 0.02$). Continuous fruiting species were consumed in slightly higher proportions than expected.

During the months of low fruit availability (May–July), 17 species (30%) were found in the diet. A large proportion of these were continuously fruiting species (41.2%) with 29.4 percent fruiting biennially and 29.4 percent being annual fruiting species. In these lean months, cassowaries also consumed annual, biennial, and continuous fruiting species in different proportions than they occur in the study area ($\chi^2 = 115.4$, df = 2, $P < 0.001$); continuous fruiting species were consumed at much higher proportions and annual species were consumed in significantly lower proportions than expected.

DISCUSSION

Our work confirms that cassowaries are significant seed dispersers in Australia because not only do they travel and disperse fruits over large distances (Westcott *et al.* 2005a), but they also eat the fruit of a large diversity of plant species of all sizes and colors. Despite this, cassowaries included a greater than expected proportion of large fruit and large-seeded fruit species. This broad dietary range and, in particular, their preference for large species, which are dispersed by fewer disperser functional groups and individuals (Dennis & Westcott 2006, Westcott *et al.* 2007), highlights the unique role played by cassowaries in dispersal processes in Australia's wet tropical forests.

The number of species found in the droppings closely parallels the number of droppings encountered each month (Fig. 1), the exceptions being March, May, and August 1998, and February 1999. These anomalous months each correspond to the droppings being dominated by a small number of species, consistently including *A. doggrellii* and *A. divaricata*. Our phenology data cannot show how prolifically these two species fruited during the dropping collection period but they are not common in the study area suggesting that these particular species are targeted by cassowaries. Other studies in Australia show diet preference toward some species including *A. divaricata*, *Ficus crassipes* and *Melastoma* sp. (Stocker & Irvine 1983), or families including Lauraceae (Crome 1976) and Myrtaceae (Stocker & Irvine 1983). Studies on the dwarf cassowary in Papua New Guinea showed no particular families dominated the studied diets although *Galbulimima baccata* was common in droppings (Pratt 1982) and fruits of the Lauraceae were commonly found in droppings when they were fruiting heavily (Wright 2005). In our study, the four most common families found in the droppings (Elaeocarpaceae, Lauraceae, Myrtaceae, and Rutaceae) contributed over 70 percent of the total volume and occurred in 156 of 198 droppings.

When the dropping numbers are lagged by 1 mo behind the estimated fruit biomass each month, the dropping numbers generally follow the pattern of available fruit except during November and December when fruit is plentiful (Fig. 2). It seems that, in the periods of high fruit availability when there is potentially an excess of fruit available, there is a point where the number of droppings encountered reaches a limit. This is not surprising as a limited number of cassowaries in an area can consume a finite amount of fruit. On the other hand, the small number of droppings encountered during periods of low fruit availability may be due to a number of factors. First, resident cassowaries may be forced to subsist on less food and consequently defecate less. Cassowaries may also leave the area for places with a higher fruit availability (Crome 1976), as has been recorded for the dwarf cassowary in New Guinea (Wright 2005), and for other large, frugivorous birds in other systems (Holbrook *et al.* 2002). A reduction in the number of foraging individuals within the study area might also occur during this period through the initiation of nesting by males. Males do not feed during nesting, which lasts for as long as 50 d (Marchant & Higgins 1990). This may result in a potential reduction in the number of foraging individuals by as much as 25 percent (Bentrupperbäumer 1998). Cassowaries may also be changing the spatial distribution of their activity in response to the scarcity of food. When resources are abundant, they travel along predictable paths between fruiting trees (Crome & Moore 1990) or on gentle slopes (Mack 1995) resulting in a more clumped distribution of droppings. When resources are scarce, they travel more widely through the forest or remain at fruiting trees (Bentrupperbäumer 1998). This results in a changed distribution of droppings, which will be encountered less frequently on surveyed tracks and trails.

Our study has shown that cassowaries include a disproportionate number of large-fruited and large-seeded species in their diet, agreeing with the findings of Pratt (1982) and Stocker and Irvine (1983). Other fruit and seed characteristics tested in this study and found to be important in diet selection for other frugivores *i.e.*, flesh moisture (Li *et al.* 1999), flesh/aril to seed ratio (Stevenson 2004), and crop size (Russo 2003, Ortiz-Pulido *et al.* 2007), did not influence diet selection. As large arboreal frugivores are absent in Australian closed forests, a large proportion of the crop of large and large-seeded fruit is likely to become available to cassowaries on the ground, providing them with a wide choice of these fruit. In addition, larger fruits are favored by avian frugivores because the net pulp mass increases with fruit diameter (Wheelwright 1993); therefore, a large frugivore with a large gape width (62 mm) such as the cassowary can potentially increase foraging efficiency by targeting large fruits. Cassowaries are one of a few species of animal in North Queensland's rain forests capable of dispersing large-seeded fruits and the only species that can disperse large numbers of such seeds over long distances; > 2 km (Westcott *et al.* 2005a). As cassowaries eat a wide diversity of fruits, it is highly unlikely that any one plant species is essential for the cassowary's survival. However, without the cassowary in Australia's closed forests, effective uphill and across catchment dispersal of a number of large-fruited species would be limited. Mack (1995) predicts such a scenario for a large-seeded species dispersed by the dwarf cassowary in Papua New Guinea.

During the plentiful fruiting months of October to December, cassowaries have greater choice of food. In lean months, their options are more limited and necessity may force them to consume what is available, often species with a continuous fruiting pattern. Species that have a continuous fruiting pattern were also consumed

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during abundant fruit months in this study area, but became relatively more important as a food source during the leaner months. Similarly, the dwarf cassowary in Papua New Guinea (Wright 2005) was found to rely on continuous fruiting species in months of low fruiting although continuous fruiting species made up a much larger proportion of the total species both in the study area and in the droppings in that study. In our study area, continuous fruiting species are not common and are often dominated by a few species each year. Nearly half of the lean season diet in our study consisted of three continuously fruiting species: *Elaeocarpus ruminatus*, *Ficus pleurocarpa* and *Halfordia kendack*. *Ficus pleurocarpa* has an asynchronous fruiting pattern, *E. ruminatus* has an unpredictable synchronous pattern, and *H. kendack* has a predictable biennial pattern; but all have fruit for most months throughout the year and, in our experience, present a continuous supply of fruit during those months.

The 56 plant species found in cassowary droppings in this study is fewer than that of previous studies in Australia by Stocker and Irvine (1983); 78 species over 25 mo, Bentrupperbäumer (1998); 107 species over 30 mo, and Crome (1976); 75 species over 24 mo. The three previous studies were conducted in lowland forest of north Queensland where the abundance of cassowaries is considered to be higher than in upland and highland areas (Crome & Moore 1990) and the plant diversity is also considered greater (A. Ford, pers. comm. 2006). The difference in sampling technique and effort could account for some of the difference in the number of species in cassowary diets between the two altitudes; however, it is likely that cassowaries are consuming a broader range of fruit species in Australian lowland forests. Studies in Papua New Guinea on the dwarf cassowary report varying fruit diversity in diets, Pratt (1982); 34 species over 32 mo, and Wright (2005); 192 species over 36 mo. While it is probable that the dwarf cassowary in Papua New Guinea is consuming a much higher diversity of fruits than the southern cassowary in Australia, it is difficult to compare the two cassowary species and the consequences of the different forest communities on the diets. New Guinea highlands are generally more floristically diverse than the forests of the Wet Tropics of Queensland so there is more potential for a higher diversity of fruit in the dwarf cassowary's diet, but it is clear in both forests that the cassowary is eating and dispersing a wide range of fruit sizes and types.

Knowledge of cassowary diet and preferences can be incorporated into practical applications. Like many frugivores, cassowaries are known weed dispersers (Westcott *et al.* in press). Of the 240 fruit species recorded in the cassowary's diet in Australia to date (D.A. Westcott *et al.*, pers. comm.), seven (2.9%) are introduced species and two are declared weeds in the cassowary's Australian range (Queensland Department of Natural Resources and Mines 2003). As the cassowary is known to move relatively large distances, potentially in and out of different landscape types (Bentrupperbäumer 1998, Westcott *et al.* 2005a) and across catchments, land managers need to consider this for effective weed management, particularly for large-seeded species. In addition, tree plantings designed to attract and support cassowaries would be enhanced if they contained high densities of preferred fruiting species. This could be accomplished by providing an over-representation of species with large fruits and/or seeds and a mix of annual, biennial, and continuous fruiting species.

In this study, we have demonstrated that cassowaries consume fruit and seeds from a large number of plant species, and they do not demonstrate diet preferences based upon most fruit characteristics. However they disproportionately feed upon large-seeded species and in lean times, on a high proportion of plant species with extended fruiting periods. Because they disperse seeds, particularly large-seeded species, in larger quantities and over longer distances than any other dispersal vector, sustaining the population density and spatial distribution of cassowaries will greatly contribute to maintaining the potential distribution and density of plant species throughout the species' Australian range.

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SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

Table S1. *Contents of cassowary droppings found in this study.*

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