

Emus as non-standard seed dispersers and their potential for long-distance dispersal

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Long-distance seed dispersal may have important consequences for species range, migration rates, metapopulation dynamics, and gene flow. Plants have evolved various adaptations for seed dispersal by standard agents, with typical dispersal distances associated with them. Seeds may also be dispersed by non-standard agents for which they do not show any apparent adaptation and may reach long distances. By sampling the droppings of emus *Dromaius novaehollandiae* at three localities in Western Australia, we investigated their potential to act as long-distance dispersers of seeds with adaptations for dispersal modes other than endozoochory, such as unassisted, ant, wind and exozoochory, for which they act as non-standard agents. Seventy-seven plant species with five types of dispersal syndromes were found in the 112 droppings analysed, with at least 68 having viable seeds. Although endozoochory was the most frequent syndrome, the presence of other syndromes was important in terms of number of species (61%) and seeds (50%). Estimates of species richness indicated that an increase in sampling effort would increase the number of species observed, especially among non-endozoochores. As a consequence of their long gut retention times and high mobility, emus can provide long-distance dispersal opportunities that may be especially relevant for species with dispersal modes of typically short distances (unassisted, ant).

Our results suggest that the role of emus as non-standard agents for long-distance dispersal should be taken into account for understanding current geographic ranges, gene flow and metapopulation dynamics of some plant species, as well as for predicting their future responses to climate change and fragmentation.

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Seed dispersal is the movement of seeds away from the parent plant and links the end of the reproductive cycle of adult plants with the establishment of their offspring, thus influencing many key aspects of plant species biology (Nathan and Muller-Landau 2000, Wilson and Traveset 2000). The frequency distribution of the dispersal distances reached by seeds in a population constitutes the dispersal curve and is typically character-

ized by a high frequency of short-distance movements and a long tail of low-frequency long-distance dispersal events (Nathan and Muller-Landau 2000). Most studies of seed dispersal have focused on short-distance dispersal, which primarily influences local recruitment patterns (Herrera et al. 1994, Calviño-Cancela 2002, Gódinez-Alvarez et al. 2002), whereas long-distance dispersal has impacts at larger (landscape-regional-global) spatial

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scales. Long-distance dispersal can influence species metapopulation structure and dynamics, colonization opportunities, gene flow, population divergence, genetic structure, range expansion rates, and rates of speciation and extinction (Hanski 1998, Ouborg et al. 1999, Sork et al. 1999, Cain et al. 2000, He et al. 2004, Bohrer et al. 2005).

Plants have evolved a variety of morphological adaptations for dispersal (van der Pijl 1982), such as wings, plumes or hairs, that increase air resistance and enhance seed dispersal by wind; fibrous pulps and other structures that enhance seed buoyancy and hence dispersal by water; food bodies (elaiosomes) that attract ants that disperse them; hooks or sticky substances that facilitate external adhesion to animals; or fleshy pulps or arils, that attract vertebrate frugivores. These suites of traits have been traditionally classified into dispersal syndromes, such as anemochory (wind), hydrochory (water), myrmecochory (ants), exozoochory (external adhesion to animals), and endozoochory (inside animals). These morphological dispersal syndromes can be considered the standard means of dispersal of a species (Higgins et al. 2003), and differ in the mean dispersal distances they provide (Willson 1993), with animal and wind dispersed species having longer mean dispersal distances than unassisted and ant dispersed seeds (Willson 1993, Hughes et al. 1994). Long-distance dispersal events may result from rare or exceptional behaviour of the standard dispersal agent, such as wind-dispersed seeds travelling long distances in thermal updrafts (Tackenberg 2003), or by non-standard agents, i.e. agents for which the species is not apparently adapted (Higgins et al. 2003). For example, seeds adapted for wind dispersal may float and be dispersed by water reaching longer distances than when dispersed by wind (Carlquist 1967). Similarly, myrmecochores and unassisted species can be dispersed by herbivorous vertebrates over large distances (Vellend et al. 2003, Myers et al. 2004).

In Australia, a high percentage of species are unassisted or myrmecochorous (Berg 1975, Westoby et al. 1990, Jurado et al. 1991), with dispersal distances by standard means typically short (Hughes et al. 1994, Gómez and Espadaler 1998). The reason for the high frequency of these short-distance dispersal modes remains unclear. For ant-dispersal, low soil fertility, moderate fire frequencies and other factors have been suggested to play a role (Westoby et al. 1991). In addition, the relative geological and climatic stability of the region in the past may have led to less necessity for long-distance dispersal and hence less selective pressure to maintain its presence (Hopper et al. 1996, Hopper 2000).

Paleoecological studies have shown that in many cases terrestrial plants have responded to climate changes by migrating rather than evolving to adapt to them (Good 1931, Graham and Grimm 1990). Given the extreme

climate changes predicted and increasing rates of habitat loss and fragmentation, long-distance dispersal will be essential to allow species to move across fragmented landscapes as the climate warms (Thomas et al. 2004, Neilson et al. 2005). For species with no obvious adaptations for long-distance dispersal (e.g. unassisted and ant-dispersed seeds), non-standard agents might play an important role. Thus, a better understanding of dispersal in general, and non-standard dispersal in particular, become essential to understanding the responses of plants to climate change.

Emus *Dromaius novaehollandiae* are large herbivorous birds distributed over much of Australia. Emus are abundant in a wide range of habitats, especially in semi-arid shrublands, and are usually absent from rainforests, extremely dry regions and heavily populated areas (Davies 2002). Emus feed on a great variety of plant material and are known to disperse seeds (reviewed in Davies 2002), although their role as seed dispersers has received little attention (but see Noble 1975, Brunner et al. 1976, McGrath and Bass 1999) and its consequences for plant communities are virtually unknown. In this paper, we investigate the potential for emus to act as non-standard long-distance seed dispersers. Based on samples of emu droppings at three disparate sites in Western Australia, we analyse the richness of species transported by emus, examine the frequency of dispersal events by emus of seeds with adaptations for dispersal modes other than endozoochory (unassisted, ant, wind, exozoochory) and explore the potential of emus as agents for long-distance dispersal events.

Methods

Study sites

Emu droppings were collected at three localities in Western Australia: the Cape Range National Park (CR hereafter), Eneabba Plain (EN), and the Fitzgerald River National Park (FR) (Fig. 1). Sites are situated along a geographic and environmental gradient (rainfall, temperature and soil) in heathland. At CR (21°59'S, 113°57'E), annual rainfall averages 260 mm and is concentrated in summer and autumn. January and July are the hottest and coolest months, with mean maximum temperatures (T_{\max}) of 38°C and 24°C and average minimum temperatures (T_{\min}) of 23°C and 11°C, respectively (Bureau of Meteorology, Learmonth Airport). Geomorphology is dominated by uplands of limestone, heavily dissected by gorges and valleys, surrounded by coastal sandplains and saline mud flats (Wyrwoll et al. 1993). Vegetation is mostly open shrubland over hummock grass, with many species demonstrating tropical affinities (e.g. *Ficus* spp.) in protected valleys (Keighery and Gibson 1993).

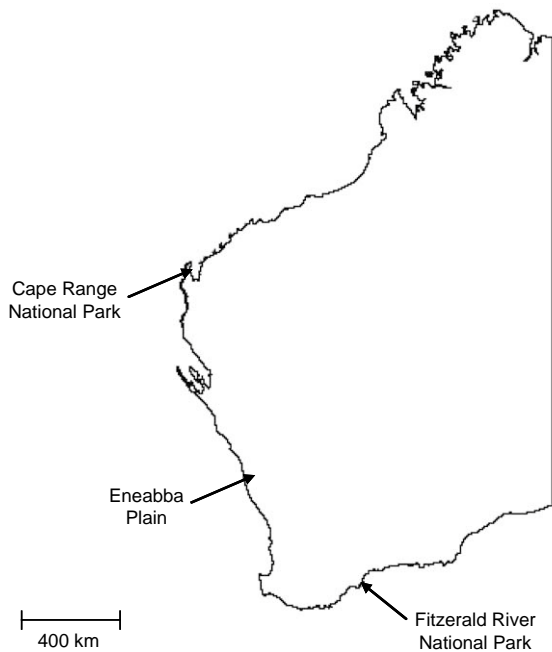


Fig. 1. Location of the three study sites in Western Australia: Cape Range National Park, Eneabba Plain, and the Fitzgerald River National Park.

At EN, the collection area was 10 km north of Eneabba (29°43'S, 115°14'E). Annual rainfall averages 510 mm concentrated during the winter months. January and February are the hottest months ($T_{\max} = 36^{\circ}\text{C}$, $T_{\min} = 19\text{--}20^{\circ}\text{C}$) and June–August the coolest ($T_{\max} = 19\text{--}21^{\circ}\text{C}$, $T_{\min} = 9\text{--}10^{\circ}\text{C}$). Soils vary from acidic, leached sands on low dunes to sandy clays in intervening depressions (Hnatiuk and Hopkins 1981). The vegetation is species-rich heathland and scrub.

At FR, the collection area was in the SW corner of the Fitzgerald River National Park (34°20'S, 119°24'E). Annual rainfall averages 630 mm, with a steep declining rainfall gradient with distance inland, most of it falling in winter. The area is part of an extensive plain of marine sediments and has little topographic relief except where streams have cut gorges exposing soft spongolite rock (Chapman and Newbey 1995). The vegetation of the Marine Plain is mostly species-rich heathland with emergent mallee eucalypts (Chapman and Newbey 1995).

Sample collection and processing

We collected emu droppings at the three localities described above, along tracks and in the vicinity of water sources, where emus concentrate. We collected and analysed 31, 51, and 30 droppings from CR, EN and FR, respectively. We disaggregated the droppings and retrieved diaspores from the faecal material. We quanti-

fied the number of dispersal units (seeds, seeds plus endocarp, multiseeded fruits or infructescences, as they appeared in the droppings) per species in each dropping. The remaining material was set up for a germination trial in order to test whether there were undetected seeds left. Because germination of many species in the study areas occurs only after fire, we used heat and smoke treatments to improve germination (Flematti et al. 2004) and thus the chances of detecting seeds that could pass unnoticed. Samples were heated with boiling water to 75–80°C. After cooling they were spread over a 2–3 cm layer of perlite and coarse sand (1:1 by vol.) on black plastic trays and watered with smoked water, 5 parts water to 1 part smoked water. Twelve controls, with only perlite and coarse sand, were also prepared in order to detect any potential seed rain into the greenhouse. Faecal remains and controls were laid out randomly in the greenhouse, watered daily and checked for seedling emergence.

We performed seed viability tests on 52 species. The aim of these analyses was to check whether emus are actual seed dispersers of these species, proved by the presence of viable seeds in their droppings. We did not perform the tests for 14 species for which only one seed was found in the samples. For another 9 species revealed as seedlings emerging from the remains, we did not perform viability tests but seedling emergence proved the dispersal of seeds in viable condition. For the viability tests, seeds were soaked in water for one night, cut to facilitate stain intake and incubated in a 2% solution of 2,3,5-triphenol-tetrazolium chloride in phosphate buffer for 24 h at 40°C and in the dark (TZ test, Anon. 1985). The number of seeds and replicates used depended on their availability (Appendix 1). We considered the dropping and not the seed as the replicate, so that, when available, samples of seeds from different droppings (replicates) were tested. Only a small number of seeds was available for some species (Appendix 1), which limits the significance of the results for them but at least provides the evidence of legitimate dispersal in cases of positive results.

We classified the species into different categories of dispersal mode according to morphological attributes of the diaspore (Westoby et al. 1990, Jurado et al. 1991), using literature where available for the identified species. Seed identification was based upon comparison with seeds obtained from plants in the study areas, our own collections and consultation with specialists (see Acknowledgements). We used the following categories of dispersal mode: 1) unassisted, with no apparent structures that facilitate dispersal; 2) ant-dispersed, with elaiosome; 3) endozoochorous, with fleshy structures; 4) exozoochorous, with structures that facilitate external adhesion to animals; and 5) wind-dispersed, with structures that enhance air resistance.

Data analyses

We computed observed richness of species (S_{obs}) dispersed by emus and estimated true species richness (S_{est}) per site for endozoochores, non-endozoochores and total species, using species accumulation curves and species richness estimators with the program EstimateS (Colwell 2005). Species accumulation curves represent the cumulative number of species as a function of the number of individuals sampled (dispersal units and seedlings emerging from remains). We generated species accumulation curves (or sample-based rarefaction curves, Gotelli and Colwell 2001) using Mao Tau randomizations (Colwell et al. 2004). In each randomization, samples of individuals (diaspores) are drawn randomly from the data set without replacement (the number of individuals per sample being the average number per dropping and the total number of samples being the total number of droppings analyzed in that locality) and added to the curve in a different order (random). We used 500 runs of randomized sampling order. A curve that does not reach an asymptote indicates that the observed species richness is an underestimate of the true richness, and an increase in the sampling effort would reveal more species. To estimate the true species richness we used Chao2 estimators, that usually perform better than other estimators (Walther and Moore 2005). Chao2 is based on the observed species richness, the frequency of species that occur in only one sample (uniques) and the frequency of species that occur in two samples (duplicates) (Colwell and Coddington 1994). The greater the ratio of uniques to duplicates, the greater the under-sampling and hence the greater the difference between observed and true species richness. Two species from EN had to be excluded from the analyses, as they could not be assigned to any of the dispersal syndromes.

Results

Overall, 77 plant species were detected in the 112 emu droppings analysed, with no viable seeds detected for 9 species (Appendix 1). At CR, a total of 37 species in at least 17 families and 22 genera were detected (with 17570 diaspores in 35 species and 37 seedlings in 5 additional species emerged from dropping remains). At EN, 28 species in at least 17 families and 20 genera were detected (8591 diaspores in 25 species and 7 seedlings in 3 additional species). At FR, 12 species in 9 families and at least 11 genera were detected (5899 diaspores in 10 species and 52 seedlings in 2 additional species).

Frequency of dispersal modes

Species adapted for the five dispersal modes were represented at all sites (Fig. 2a). Endozoochores were

the most frequent group of species in EN (42%) and overall (39%). In CR and FR, endozoochores and unassisted were the most frequent species, with equal frequencies (38 and 33% in CR and FR, respectively). All the other syndromes together, for which emus act as non-standard agents of dispersal, represented the majority of species at each locality (62, 58, and 67%, for CR, EN, and FR, respectively, and 61% overall). Among non-endozoochores, unassisted species were the most frequent at CR, FR and overall (31%) and wind dispersed species at EN (23%). Overall, wind dispersal was the 2nd most frequent dispersal mode among non-endozoochores (16%), followed by ant dispersal (13%). Exozoochory was the least common syndrome, with only 1 species at CR.

When considering the frequency of seeds dispersed, which reflects more directly the quantitative role of emus as seed dispersers, endozoochores were again the most frequent (Fig. 2b), but there were differences among sites. Endozoochory accounted for 97% of all seeds at CR, mainly belonging to *Ficus platypoda* (81%). At EN, endozoochores, ant and wind dispersed seeds were all frequent (40, 32, and 22%, respectively). At FR, wind dispersed seeds were the most frequent (56%), as a consequence of the frequency of *Isopogon trilobus*, with cones containing more than 150 seeds. Excluding this species, endozoochores accounted for 85% of seeds.

Estimates of species richness

Species accumulation curves (Fig. 3) continued to rise with increasing sampling sizes, particularly at CR and EN, indicating that the number of species, both for endozoochores and non-endozoochores, would continue increasing with increasing sample sizes. Estimated species richness (Chao2) was higher than the observed species richness (Table 1) particularly at CR and EN, where the observed species represented 18 and 44% of the estimated true species richness whereas at FR they represented 75%. At all sites, the proportion of the estimated true species richness actually sampled was higher for endozoochores (25, 48, and 100%, at CR, EN and FR, respectively), than for non-endozoochores (14, 38, and 80%, respectively), indicating that the number of non-endozoochores would increase more than the number of endozoochores with increasing sampling effort.

Discussion

Species richness and dispersal modes

The high total number of plant species in emu diets seems to be a consequence of their generalist feeding behaviour (Davies 2002). Emus are omnivorous but mostly herbivorous and, importantly, are not strictly

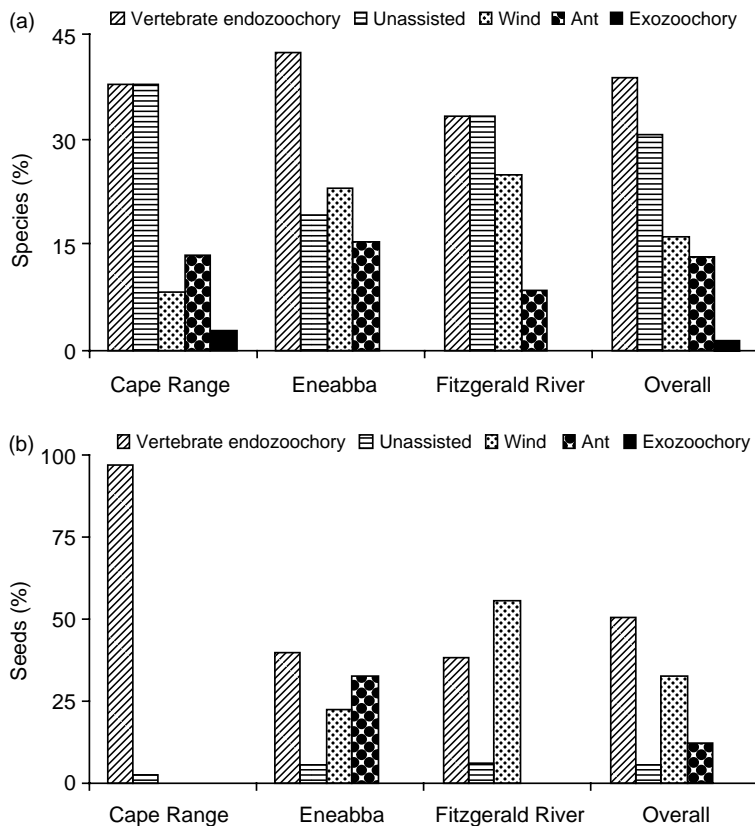


Fig. 2. Proportion of (a) species and (b) seeds with different dispersal syndromes in each locality and overall.

frugivorous, in contrast to cassowaries (Davies 2002), the other large extant Australian ratite, and many other vertebrates involved in seed dispersal. They feed on a great variety of plant material (and occasionally insects) (Davies 2002, this study). For this reason, their role as agents of seed dispersal is not restricted to species with fleshy structures, but instead includes species with a wide variety of seed and fruit morphologies. In our case, five dispersal syndromes were present among the 77 species identified. Thus emus can act as non-standard seed dispersers of many species.

However, emus appear to preferentially ingest endozoochorous diaspores. They live in arid habitats and have been shown to prefer succulent foods, such as fleshy fruits, rather than drier food items (Davies 1978). Endozoochores appear to be overrepresented in the droppings in relation to their occurrence at the study sites. A study carried out in the Eneabba Plain in four communities, each plot with over 10 000 plants, revealed only 0.05% of species ($n=246$) were endozoochores (Lamont et al. unpubl.), in contrast to 42% in our emu droppings samples (80 times higher than expected if sampled at random).

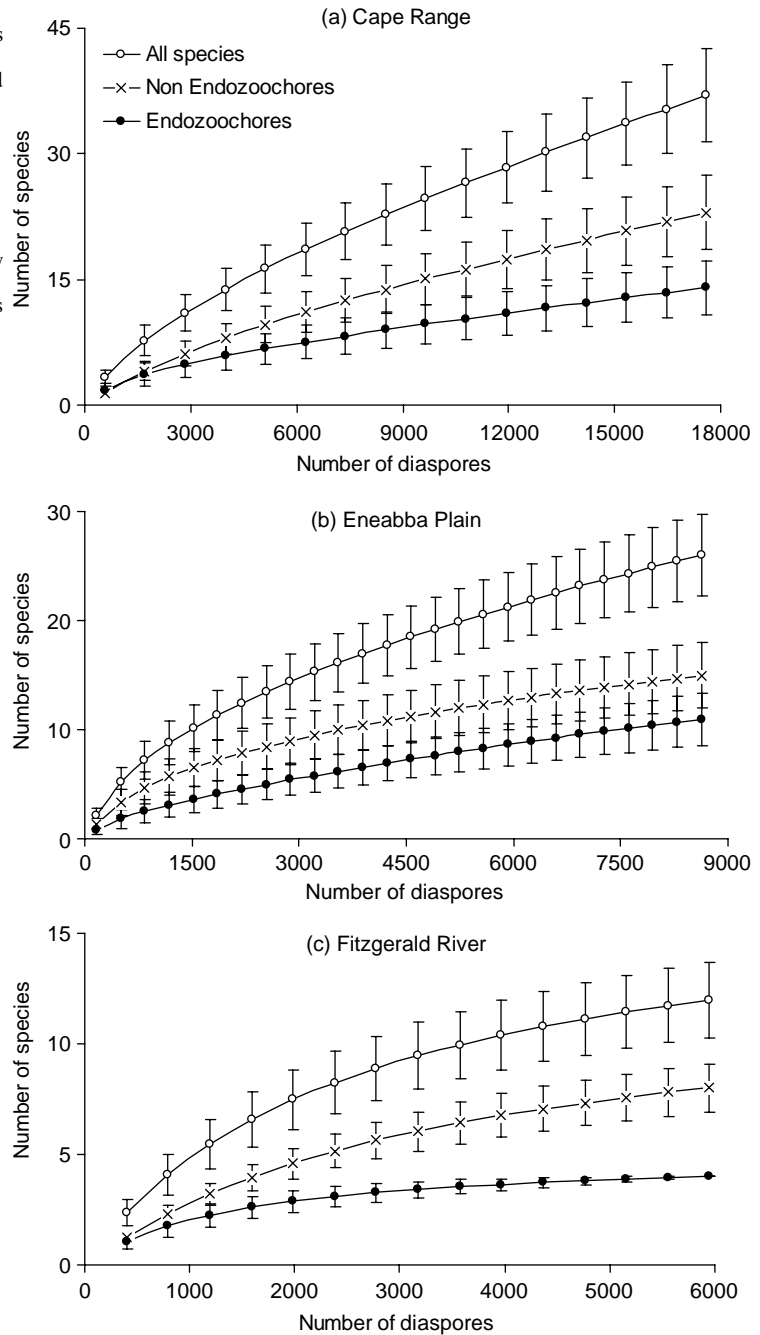
Both the species accumulation curves and the species richness estimators indicate that a higher sampling effort would have revealed more species. Our sampling appears to capture a higher number of endozoochores than non-

endozoochores, which indicates that with additional sampling the number of non-endozoochores would increase more than that of endozoochores, increasing their frequencies shown in the results (Fig. 2).

Herbivorous mammals also have been shown to disperse seeds with various dispersal modes, especially unassisted (Malo and Suárez 1995, Pakeman et al. 2002, Myers et al. 2004). However, they seem to be restricted to small-seeded plant species (usually <2 mm) since larger seeds are damaged by chewing. Herbivorous birds, in contrast, do not chew. In addition, emus are such large birds that they can swallow *Santalum acuminatum* fruits, 2–5 cm in diameter and with seeds 1.5 cm, and *Macrozamia fraseri* seeds, 4–5 cm long and 2.5–3 cm wide. Although ingested seeds can suffer abrasion during digestion, emus were legitimate dispersers of most of the species present in our samples. Only 9 species showed no viability, although for 6 of them the results cannot be considered representative, since only 1 or 2 seeds were tested (1 seed for 2 species and 2 seeds for 4 species). Other large ratites with herbivorous diets, like ostriches in Africa and rheas in South America, as well as extinct ratites, like moas and elephant birds (Noble 1991, Davies 2002), could play a similar role to that played by emus in dispersing a wide variety of diaspores.

As a consequence of their generalist feeding behaviour, emu dependence on particular plant species as

Fig. 3. Species accumulation curves (individual-based rarefaction curves) of seeds isolated from emu droppings from (a) Cape Range National Park, (b) Eneabba Plain, and (c) Fitzgerald River National Park. Each point represents the mean of 500 randomizations of sampling pooling order and error bars show the corresponding standard deviations. Only one out of every two samples is shown. "Endozoochory" includes those species with morphological adaptations for endozoochorous dispersal by vertebrates. "All others" includes those species with other morphological adaptations for dispersal: by exozoochory, wind, ant, or unassisted. "All species" includes all species in the samples.



food sources seems to be weak, at least in the long term. However, some plant species seem to rely on emus for seed dispersal, since the large size of their diaspores prevents other animals from swallowing them (e.g. *Santalum acuminatum*, *Macrozamia fraseri*, see above), and an eventual decline in emu populations (e.g. as a consequence of clearing extensive vegetation for agriculture or urban development) could have an important impact on these plant specialists.

The fact that some diaspores can be frequently dispersed by non-standard means raises questions about the costs and benefits of investing in structures for dispersal. The answer may lie in the relative effectiveness of emus as dispersers (or as non-standard means of dispersal in general) vs the standard means (Schupp 1993). In myrmecochores, for example, an elaiosome would be cost-effective if emus are unreliable dispersers compared with ants, or if emu-dispersed seeds reach less

Table 1. Observed species richness of diaspores in emu droppings and Chao2 estimates (in parenthesis) at the three sites studied: for all plant species (total), for endozoochore, and for species with other dispersal modes (others).

	Cape Range	Eneabba Plain	Fitzgerald River
Total	37 (206)	26* (59)	12 (16)
Endozoochore	14 (55)	11 (23)	3 (4)
Others	23 (168)	15 (40)	9 (10)

* The total number of species detected in the Eneabba Plains was 28, but 2 were excluded from the analysis since their dispersal mode was unknown.

suitable microsites. If dispersal by emus is quantitatively relevant and beneficial at a large scale but poor at a small scale, one might expect the evolution of a double strategy, both to attract emus, increasing the chances of long-distance dispersal, and ants, in order to reach suitable microsites (Vander Wall and Longland 2004). This seems to be the case for *Petalostigma pubescens* (Clifford and Monteith 1989), with a three-phase dispersal process: emus eat the fleshy fruits, seed endocarps dry out in the droppings and explode, liberating the elaiosome-bearing seeds, which are then collected by ants. Such unique life histories highlight the potential selective pressure imposed by emus and the interesting dynamics between the advantages of long-distance and short-distance dispersal of seeds.

Consequences of long-distance dispersal by non-standard agents

Empirical studies have suggested that the migration of a plant species is limited by dispersability, and have reported marked differences in rate of migration among seed dispersal modes, with seeds dispersed by vertebrates (both by endo- and exozoochory) having longer dispersal distances than those dispersed by wind, ants, and unassisted (endozoochory > exozoochory >> wind ≥ ants ≥ unassisted) (Matlack 1994, Willson and Traveset 2000, Takahashi and Kamitani 2004). For example, mean dispersal distances reported for ant-dispersed seeds are usually < 2 m and only exceptionally exceed 50 m (Hughes et al. 1994, Gómez and Espadaler 1998). Dispersal distances may have both evolutionary and ecological consequences, and could be limiting for

species persistence under climate change (Levin et al. 2003, Thomas et al. 2004, Neilson et al. 2005). However, if non-standard means of dispersal are available, dispersal distances by standard mechanisms become less important for understanding patterns of gene flow, extinction and speciation, and responses to climate change may be largely governed by the frequency and dynamics of non-standard dispersal events (Higgins et al. 2003, Vellend et al. 2003).

The chances of long-distance movements of diaspores by emus will depend on emu movement patterns and on the time the diaspores are retained in emu guts (Table 2). Emus can retain diaspores for a minimum of 3–4 h and maximum periods of at least 100 d to many months (Table 2). Although emus are flightless, they are well adapted to move fast and cover great distances (Patak and Baldwin 1993). An emu's normal walking pace is 7 km h⁻¹, and it can reach 45 km h⁻¹ when pursued (Davies 2002). In Western Australia, emus show a nomadic behaviour in periods of food shortage, and can move >600 km to areas of relatively high rainfall where food is available (Davies 1984). Thus, emus may retain seeds over long time periods during which they are likely to move long distances making them ideal agents for long-distance dispersal.

As noted in the introduction, adaptations for endozoochory are poorly represented in Australia's sclerophyll flora while unassisted and ant-dispersed diaspores are common, suggesting that long-distance dispersal is rare (Clifford and Drake 1981, Westoby et al. 1990, Jurado et al. 1991). However, emus may be and have been important in maintaining gene flow and facilitating migration of plant species in Australia. The explicit consideration of emus as agents of long-distance dispersal may contribute to explaining the observed distribution ranges, gene flow and metapopulation dynamics of some species that seem to be inconsistent with the mean dispersal distances predicted according to their standard dispersal mechanisms (Gove et al. pers. comm.). Such long-distance dispersal will be even more important in the future since species will need to migrate as a consequence of climate change across landscapes that are now fragmented (Thomas et al. 2004, Neilson et al. 2005).

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Table 2. Gut retention times by emus.

Food type	Time	Reference
Particulate phase of the diet	5.5 ± 0.4 h	Herd and Dawson (1984)
Wheat	3–50 h	Davies (1978)
Marbles	100 d	Davies (1978)
<i>Santalum spicatum</i> diaspores	Up to 10 months	Davies (1978)
Flat pseudoseeds (0.21, 0.3 and 0.55 g) and spherical beads (0.26 and 2.25 g)	Min. 4 h, median 2 d for those recovered, probably many weeks	Willson (1989)

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