The potential of seed-eating birds to spread viable seeds of weeds and other undesirable plants

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Abstract

The potential for seed-eating birds to spread viable seeds was investigated using captive-feeding trials to determine seed preference, passage time through the gut, and viability of passed seeds for bronzewing pigeons (Phaps chalcoptera), peaceful doves (Geopelia striata), crested pigeons (Ocyphaps lophotes), Senegal doves (Streptopelia senegalensis), zebra finches (Taeniopygia guttata), black ducks (Anas superciliosa) and wood ducks (Chenonetta jubata). Test seeds were bladder clover (Trifolium spumosum), crimson clover (Trifolium incarnatum), gorse (Ulex europaeus), canola (Brassica napus) and red panicum (Setaria italica). Their consumption was compared with that of commercial seed mixes. Although all test seeds were recognizable foods, their consumption usually decreased in the presence of other foods, except for canola, where consumption rates were maintained. Hard-seeded bladder clover was the only species where viable seeds were passed by obligate seedeaters. In contrast, viable seeds of canola and gorse were passed by seed-eating omnivorous/herbivorous ducks, although the germination of passed seeds (42%) was reduced significantly compared with that of untreated control seed (67%). Field validation with wild, urban...
bronzewings and Australian magpies (*Gymnorhina tibicen*) offered canola and commercial seed yielded similar outcomes, with a range of viable seeds recovered from magpie soft pellets. Mean seed passage time in captive birds ranged from 0.5 to 4.3 h for all test seeds and commercial seed mixes, suggesting that these bird species may potentially disperse seed over moderate distances. Despite the low probability of individual birds spreading viable seed, the high number of birds feeding in the wild suggests that the potential for granivorous and seed-eating omnivorous birds to disperse viable seeds cannot be discounted, particularly if exozoochorous dispersal is also considered.

**Keywords:** bird; impact; seed-dispersal; seed-eating; spread; weed

**Introduction**

Seed dispersal, including that of weeds and other undesirable plants, can occur by human activity, wind, water and animal spread (Parsons & Cuthbertson 2001). Vertebrates are often important dispersal agents, spreading seed by endozoochorous (via digestive tract) or exozoochorous (adhesion to animals) means (Calvino-Cancela *et al.* 2006). In particular, the role of frugivorous birds in the dispersal of seed contained within fleshy fruits is well recognized in tropical (Stansbury & Vivian-Smith 2003; Moran *et al.* 2004; Gosper *et al.* 2005; Neilan *et al.* 2006) and non-tropical (Stansbury 2001; Calvino-Cancela 2004; Garcia *et al.* 2005; Milton *et al.* 2007; Ward & Paton 2007; Wotton *et al.* 2008) environments. However, the ability of seed-eating birds (hereafter refers to both obligate seedeaters and seed-eating omnivores) to spread viable seed is less understood. Similarly, the role, or potential role, of seed-eating birds in the establishment and/or maintenance of feral populations of cultivated crops (e.g. canola, *Brassica napus*) has been rarely documented (Buchanan 1989; Stansbury 2001; Gosper *et al.* 2006; Twigg *et al.* 2008). Improved understanding of both these factors would enable the implementation of more informed management strategies for reducing the detrimental impacts of weeds and other undesirable plants. In addition to their impacts on agriculture, invasion by weeds is widely recognized as a major threatening process for natural
ecosystems worldwide (Grice 2004), and is second only to habitat loss and landscape fragmentation as a global threat to biodiversity (Sakai et al. 2001). In Australia, for example, invasive/alien plant species comprise approximately 10% of the flora (Burgman & Lindenmayer 1998), with a number of weed species seriously threatening ecological communities (EPBC Act 1999–Australian Commonwealth, Department of Environment and Water Resources 2007).

While recognizing the importance of the range of seed dispersal strategies utilized by plants, it is nevertheless valuable to employ a reductionist approach to gain greater understanding of some individual factors involved in seed dispersal. Consequently, we examined the potential of seed-eating birds to spread viable diaspores of a number of seed species with a particular focus on weeds and undesirable plants. Assessing this potential is important because: (i) seed-eating birds may disperse and help to maintain weed and undesirable plant populations, (ii) understanding this potential will enable more informed decisions regarding containment zones during exotic plant incursions, (iii) given that some genetically modified (GM) agricultural plant cultivars produce fertile seed (e.g. canola –Winder 2004; Belcher et al. 2005; Hayter & Cresswell 2006), seed-eating birds may spread GM crops beyond containment boundaries thereby enhancing the potential for transgenic flow to wild flora or to non-GM crops (Belcher et al. 2005; Felber et al. 2007; Oeschger & Silva 2007; Twigg et al. 2008), and (iv) such seed dispersal may lead to the establishment of new weed populations which may ultimately impact on conservation values and biodiversity. For the above reasons, this paper assesses the potential role of obligate and omnivorous seed-eating birds in seed dispersal following a series of captive feeding trials with a range of native and introduced bird species.

Our study addresses two current research gaps: (i) the ability of obligate and omnivores seedeaters, rather than frugivorous species, to spread seed, and (ii) the viability of passed seed, as opposed to simply noting its passage. Specifically, our trials assessed the acceptability of a range of seed species as food items to obligate seed-eating and omnivorous birds, the passage time of biomarked (Carmine red) seed through the digestive tract of the birds, and the viability of any seeds, or suspected viable diaspores, found in the associated faecal pellets. We use these outcomes to comment on the likely role
of obligate seed-eating birds, and omnivorous species, in the dispersal of weeds and other undesirable plants. We also discuss the implications of this potential risk to wildlife management strategies, and to the maintenance of biodiversity.

**Methods**

**Museum specimens**

The average size of seeds consumed by free-ranging bronzewing pigeons, crested pigeons and peaceful doves was determined by examining alcohol-preserved crop and stomach contents of specimens held by the Western Australia Museum, which had been collected at various locations in Western Australia. As no zebra finch samples were available, the stomach contents of the closely related finch species, red-eared (*Emblema oculata*) and painted (*Emblema pictum*) Firetails, were used to provide a general indication of the seeds likely to be ingested by zebra finches. There were too few samples available for the Senegal doves, black ducks and wood ducks, or their congeneres, for analysis. The seeds in the crop and stomach contents were sorted, counted and measured to the nearest 0.1 mm (length) using a dissecting microscope with an eyepiece graticule. A frequency histogram was then produced for these data (Fig. 1).

**Origin and housing of birds, and general procedures**

Bronzewing pigeons (*Phaps chalcoptera*), peaceful doves (*Geopelia striata*) and zebra finches (*Taeniopygia guttata*) were purchased from a licensed supplier. Senegal doves (*Streptopelia senegalensis*; introduced species –Long 1981), crested pigeons (*Ocyphaps lophotes*), Pacific black ducks (*Anas superciliosa*) and Australian wood ducks (*Chenonetta jubata*) were wild-caught within the greater Perth metropolitan area. The feeding trials were undertaken in an indoor animal house with a 12:12 photoperiod with ambient temperature maintained at 22 ± 2°C. Because of limited animal house space, the bronzewing pigeons, peaceful doves and Senegal doves were run as Group 1, and the remaining species (Group 2) were run after the completion of the Group 1 trials.
All birds were routinely maintained on an appropriate commercial bird seed mix (standard ration – excluded canola). Pigeon and doves were fed a mix of budgerigar and canary seed, the zebra finches a finch seed mix, and the ducks were maintained on wheat and chicken layer pellets. These rations all had at least 11–15% protein. All birds were provided with commercial ‘grit’ and lawn clippings to aid digestion. Before experimentation, all birds were allowed a 4-week habituation period, and at least 10 days were allowed between trials. Full details of husbandry, cage design and experimental design are given in Twigg et al. (2008).

**Experimental procedures**

Where applicable, all birds were placed in the individual cages for 24–48 h (habituation) before commencing a trial. Following the habituation period, birds were provided with standard rations and/or test seed from ~0800 hour to ~1500 hours. After this time, all food, but not water, was removed before experimentation commenced early the next morning (~0800 hours). Hydration controls (start weights of 20, 30 or 200 g per seed type with two replicates, and protected from being eaten) were also included in all trials to enable correction for the natural changes in hydration which occurred with each seed type. The frequency of faecal pellet collection and other assessments needed to be a compromise between allowing normal feeding behaviour to occur, the time when dyed or undyed seed was ingested, and defecation rates. Consequently, seed consumption and defecation by the birds were monitored at 30- to 60-min intervals over the first 8–14 h of each trial. Where there was a delay in the consumption of test seed, an additional monitoring period was included at approximately 2000 hours.

Because of their smaller body mass, trial conduct was modified slightly for the finches so that they were only exposed to experimental foods for two separate 5- to 7-h periods (Twigg et al. 2008). All other conditions were similar to those described below.

**No-choice tests**

After habituating and ‘pre-feeding’ of the birds as above, depending upon the bird species, 20, 30 or 200 g of test seed only was offered in one of the matching food bowls for 24 h. The amount of test
seed consumed was determined at the end of this 24-h period. Most faecal pellets deposited over the 24-h period were collected for microscopic examination for the presence of whole seed (see below).

Choice with test seed and standard rations

These trials were run over the 48-h period immediately following the weighing of the seed at the end of the 24-h no-choice trials. The appropriate amount (20, 30 or 200 g) of test seed or standard rations was added to the matching food bowls, and observation and collection of faecal pellets continued over the next 24 h. After this period (~0830 hours on next day), food was removed and weighed (including the hydration controls). Where necessary, the amount of seed was readjusted to the nominated amounts, and the food bowls returned to the cages. However, the food trays/bowls were now swapped to the alternate side within the cages to allow for any feed-tray position preference developed by the birds. Observation and collection of faecal pellets continued for another 24 h.

Passage time

Passage time (PT) was determined using test seed treated with a Carmine red dye marker (Merk – Germany, Carmine 1.15933.0025; Microscopy, C.I. 75470; Brugger 1993). Approximately 200 g of test seed was soaked in an excess of 1% aqueous dye solution for 10 min, drained, spread and allowed to dry overnight at room temperature (~23°C). As for most choice experiments, the bronzewing pigeons were trialled as a group within their holding pen. Passage time for all other birds was determined with the birds held in individual cages. Birds were habituated for 24 h with undyed test seed provided during ~0800 hours to ~1500 hours. Early the next morning (~0800 hours), a weighed amount of Carmine red-dyed seed (~20 or ~150 g per bird) was then placed in one food bowl. Depending upon the ingestion rates and passage times, seed consumption and defecation by the birds were monitored at frequent intervals (30–60 min) over the next 8–14 h. The dyed test seed was weighed at approximately hourly intervals until at least 0.4 g of seed was consumed, or when the Carmine dye was first observed in the faecal pellets. Once the consumption of dyed seed was confirmed (i.e. >0.4 g eaten), it was replaced with an excess of the appropriate undyed test seed.
Dyed and undyed faecal pellets were collected over each 24-h trial (including a 2000 hours collection/assessment), and most pellets were examined microscopically for the presence of dyed testa and mesophyll, and the presence of whole seeds. Dyed seed was generally consumed in sufficient amounts by mid to late morning, and the dye appeared in the faecal pellets 1–5 h thereafter. The final observation/collection period occurred at ∼0800 hours the next morning (i.e. ∼24 h from when dyed food was first offered). The visual appearance of faecal pellets, and the observed chronological sequence of pellet deposition, were used as aids when estimating the time when Carmine-dyed testa and mesophyll first appeared and then disappeared from the faeces.

Passage time was determined as the time taken from the estimated time of consumption of dyed seed to when dyed faecal pellets were first observed. Where dye was first present in the faeces at a particular monitoring time, but formal consumption of dyed seed was not recorded until that time, consumption time was estimated as the mid-point between the current and immediately previous observation period.

Because seeds were extracted from the faecal pellets during the PT trials, the potential effect of Carmine red dye on seed germination/viability was examined using 20 grains of wheat and dye concentrations of 0% (distilled water – experimental control), 1%, 5% and 10%. Samples were immersed in excess dye/water for 5 or 10 min. After draining, the individual lots were placed in a 30°C incubator until dry (usually ∼30–60 min), and tested for germination over 14 days (see below).

*Accidental* ingestion

To provide further assessment of the likelihood that the free-ranging omnivorous/herbivorous species could ingest and pass viable seed, the possibility of incidental seed-ingestion was simulated using the two duck species, and wheat and gorse seed. Gorse was mixed in wheat at 1:8 and the mix fed to the ducks as per the PT protocol. The ducks were maintained on the mix until significant amounts were consumed (>20 g) or 24 h had elapsed. After this period the remaining seed was sorted and weighed to estimate the number of gorse seeds ingested. Faecal pellets were also collected to enable assessment of the presence of whole seed.
Faecal pellet inspection

The presence of whole/viable seed in the faecal pellets was assessed by first placing each faecal pellet in a petri dish, and then gently teasing the pellets apart under a dissecting microscope. Firmer pellets were soaked in distilled water for 10–15 min before examination. To ensure that viable seeds were not missed, any particle suspected of being a viable seed/diaspore was plated out and tested using the seed viability test described below. To test that this methodology did not cause unintended destruction of viable seed, 109 faecal pellets (∼3% of all pellets examined) were plated directly onto the filter papers, very lightly teased apart, and monitored for germinating seeds.

Seed germination/viability test

The germination/viability of seed was determined in an incubation room held at 22 ± 1°C with a 12:12 h photoperiod using a procedure similar to that recommended by the international rules governing seed testing (ISTA 2007). Seeds were placed on moistened filter papers held in petri dishes, and were periodically moistened with a 0.1% w/v Benlate fungicide solution (see Twigg et al. 2008). Germination was monitored daily for up to 10 weeks with particular emphasis on day 5 and day 14 (as per International Seed Testing Association rules). This included a record of those seeds which imbibed but did not germinate. All equipment was cleaned thoroughly, soaked in a 1% bleach solution for 24 h, and then rinsed between each use. The viability of any ungerminated seeds remaining at completion of the germination trials was assessed using the Tetrazolium test procedure (ISTA 1996).

Field validation – urban tests

Using techniques similar to those described above, the consumption of canola and standard rations by free-ranging urban birds was assessed to confirm that our animal house-derived data were indicative of the preferences of birds in a more ‘natural environment’[for quarantine reasons, it was not possible to use a declared weed seed such as gorse]. The trials were conducted in the Perth outer suburbs where a number of Australian magpies (Gymnorhina tibicen), bronzewing pigeons (P. chalcoptera) and Australian ringneck parrots (Platycercus zonarius) were feeding freely near an aviary and domestic fowl yard. The trials were conducted over a 4- to 5-week period in early to mid winter.
(June/July), including 1–2 weeks to habituate the birds to feeding at the saucers. Forty grams of seed was offered to the birds on each of four plastic saucers. Seed was provided as a no-choice option for both seed types, then as a choice between these foods. Hydration controls were also included. The position of the saucers was stratified at random at the commencement of each day (i.e. the bowls were in different positions but the two saucers with the same seed type were not adjacent to each other during the choice trials). Feeding by birds was monitored from a ‘hide’, and the seed weighed at the end of each feeding session by each species.

Regurgitated soft pellets were also collected from these magpies over a 10-month period, including the above trial period. The majority of pellets were immediately frozen to prevent fungal contamination during storage. On thawing, they were teased apart under a dissecting microscope and the whole seeds present were enumerated. Additional pellets were also collected and immediately suspended in water, then spread onto a petri dish. Any whole seeds or suspected viable seeds/diaspores were then plated onto the germination filter papers and germination determined as described above.

**Data analysis**

**Seed consumption and hydration controls**

Any spilt seeds were returned to the food bowls before weighing. The amount of the seed remaining for each time period was corrected using the proportional changes which occurred in the hydration controls for each relevant time period before the calculations of the amount of seed eaten were undertaken. Once these corrections were made, the amount of seed eaten was then determined by the subtraction of Time B from Time A weights. Thus, all analyses were carried out using the hydration-corrected weights.

**Choice experiments**

Repeated measure anovas were used to test for significant differences in the observed food preferences (STATISTICA™, Version 5.5, StatSoft™ 1999). Seed consumption was the dependent variable, seed type the between-group factor, and day (day 1, day 2) was the repeated measure
(within-subject factor). Our primary interest was whether the amount of test seed consumed differed significantly from that of the standard rations, rather than whether food consumption varied between the two days of each trial. Thus statistical values are only presented for the between-group factor, seed type.

**Seed germination/viability**

The germination of seed passed through the birds was compared with that of untreated seed using a two-tailed Fisher exact test (STATISTICA™, Version 5.5, StatSoft™ 1999). This test was also used to compare the number of Tetrazolium-positive seeds remaining at the end of the germination trials to that of untreated seed.

**Results**

The size of seeds recovered from the gut of the museum specimens of free-ranging Columbiformes and the finches ranged from <1.0 to >6.0 mm with most seeds in the 1–4.9 mm size range (Fig. 1). The finches and peaceful doves consumed the smallest seed and bronzewings the largest. The number of test seeds per gram ranged from 169 (gorse) to 435 (red panicum). Bladder clover (1.4 mm) was the smallest seed and gorse (3.1 mm) the largest (Table 1).

**Seed consumption (no-choice and choice trials, and accidental ingestion)**

With the exception of gorse, all bird species consumed at least small amounts of the test seeds, indicating that these seeds were recognizable food items (Figs 2–4 and Table 2). Canola was eaten in the greatest amounts. However, the consumption of all test seeds often decreased in the presence of other food, although there was considerable variation between some conspecifics (e.g. wood ducks and canola). Despite bladder clover and crimson clover being acceptable food items, several birds seemed reluctant to consume large amounts of these seeds even in the absence of other food. The contribution of test seed to daily food intake was highly variable ranging from 0% to 19.5% for crimson clover, 0% to 5.7% with bladder clover, 0% to 83.2% for canola and 0% to 3.6% with gorse.
Nevertheless, the number of seeds ingested was often considerable for most bird species ranging to over 15,000 seeds (e.g. wood ducks and canola –Table 3). Of the Columbiformes, crested pigeons displayed the greatest variability in the amount and species of test seed consumed (Fig. 2). Four bird species, zebra finches, black ducks, wood ducks and crested pigeons consumed gorse seed, but this was often in the absence of alternative food. Only the two duck species consistently consumed gorse in the presence of other food, and this was usually in relatively small amounts (Fig. 4.).

Both duck species ingested the gorse seed contained within the gorse/wheat mix and the number of gorse seeds so ingested ranged from 394 to 3250 in the black ducks, and 850 to 1205 in the wood ducks (Table 3). This ingestion comprised 8% to 64% (mean 24.6%, SD 19.6%, n = 7) of expected levels had the ducks ingested seed relative to their proportions in the mix (i.e. 1:8 ratio). This suggests that some individual ducks may have been avoiding gorse seed (i.e. actively selecting wheat), and that some gorse seeds may have been consumed inadvertently.

**Passage time**

Treatment with Carmine red dye did not unduly influence the viability of seed over the range of conditions tested as the number of seeds germinating did not differ between treatments ($F = 0.384$, d.f. 6,20, $P = 0.880$). The overall mean (standard deviation) germination of the Carmine red-treated wheat seed was 18.5 (2.2 SD; 93.0%, $n = 18$ replicates of 20 seeds; range, 88.3–98.8%), compared with 19.2 (1.3 SD; 96.0%, $n = 5$ replicates of 20 seeds; range, 85.0–100%) for the untreated water control. Seed dyed with less than 1% dye for 10 min did not consistently result in marked faeces, and the higher dye concentrations (e.g. 5%) were less acceptable to some birds. Consequently, the 1% Carmine red dye 10-min treatment was used for all passage time trials.

Within a species, passage time of Carmine red-dyed seed through the gut was generally similar for the test seed and standard rations (Table 4; anova d.f. 1,45, $F = 0.942$, $P = 0.337$). There was no evidence of uncoupling of the Carmine red dye and the testa/mesophyll of dyed seed indicating that the presence and absence of dye in the faecal pellets was indicative of true passage time through the digestive tract. Dyed faeces generally appeared within 0.3–5.0 h and were not recorded after a further
1–17 h (Table 4). However, as the disappearance of dye from the faeces is clearly dose dependent, we believe the first appearance of dyed-faeces provides the best estimate of PT. With this proviso and irrespective of seed type, mean PT was least in the smaller birds (e.g. zebra finches, peaceful doves, Senegal doves) and greatest in the larger ducks and bronzewing pigeons (Table 4). Nevertheless, mean PT was generally fairly rapid for all species ranging from 0.44 to 4.3 h.

**Faecal pellets and passed-seed germination**

Over 3300 faecal pellets were examined for the presence of whole seeds, with 2.1% (68 pellets) containing whole seed (Table 3). In all, 435 whole seeds were recovered from the faecal pellets of which 76 (17.5%) germinated (Table 5). However, passed seeds of canola (two-tailed, Fisher exact $P < 0.001$), gorse ($P < 0.001$) and millet ($P < 0.05$) had significantly reduced germination/viability compared with that of uningested ‘control’ seeds plated and monitored over the same period (Table 5). Germination of these passed seeds ranged from 0% (gorse from crested pigeons) to 67% (gorse from wood ducks) but germination was generally around 40% (Table 5). In contrast, and although overall percentages were low, the germination of passed seeds of hard-seeded bladder clover did not differ from that of untreated seeds ($P = 0.806$; Table 5). Faecal contents were often well macerated with relatively large testa, mesophyll, and endosperm fragments, particularly in the wood ducks and crested pigeons.

For bladder clover, 20 untreated control seeds remained at the end of the monitoring period, and 18 (90%) were Tetrazolium-positive compared with 162 (91%) of 178 of the ungerminated passed seeds (two-tailed, Fisher exact $P = 0.700$). In contrast, only 20 (50%) of the 40 remaining passed gorse seeds were Tetrazolium-positive compared with 24 (80%) of 29 uningested seeds (two-tailed, Fisher exact $P = 0.006$). This suggests that passage through birds affected the viability of gorse seed but not that of the hard-seeded bladder clover. Too few passed seeds were recovered for the other seed species to make similar comparisons.
Field validation – urban tests

Free-ranging, semi-suburban, Australian magpies and bronzewing pigeons consumed small amounts of canola in the presence of other food (0.4–1.1 g vs. 0.0–15.3 g standard ration per 10- to 20-min feeding session; Table 6). However, the bronzewing pigeons consumed considerably greater amounts of canola seed when only canola was offered (Table 6). Forty-eight soft pellets regurgitated by magpies over a 10-month period were collected at this site, with 31 (64.5%) containing whole seeds. One hundred and forty-seven seeds were recovered from the 31 seeded pellets, with 4.7 seeds per pellet (3.1 seeds per pellet for all 48 pellets). The germination of seeds was determined for an additional 13 soft pellets. One hundred and thirty-four whole seeds were recovered, of which 44 (35%) germinated. This compares with 36 (77%) of 47 standard ration/wheat seeds monitored over the same period (two-tailed, Fisher exact $P < 0.001$). Viable recovered seeds included wheat, millet, one canola seed and a range of unknown seeds. Fifteen mummified grape seeds were also recovered from three soft pellets.

Discussion

For endozoochorous seed dispersal by birds in the wild, seed must be eaten, and viable seed must be passed beyond the distance it might simply fall if left untouched on the plant. Many published studies concentrate on the first condition only (e.g. Buchanan 1989; Parsons & Cuthbertson 2001). In contrast, our data fulfil the first two conditions, albeit to a varying extent across the bird species tested. The likelihood of the third condition occurring will depend on specific conditions in the field, including plant dispersal, germination, establishment, survival and successful reproduction. These factors are all important in the spread and establishment of new plant (weed) populations at the landscape scale.
Did birds eat test seeds?

Although consumption of test seeds was often low, particularly by the Columbiformes and finches in the presence of other food, test seed species were eaten by most bird species. Further, as indicated by the increased consumption of test seed in the absence of other food, and provided seeds are available, this consumption is likely to increase during times of food shortage. However, irrespective of the bird species, most seed was often well macerated after passage through the digestive tract, and only 435 whole seeds were recovered (range 0% to ∼10%). Parrots and finches are probably least likely to spread viable seeds endozoochorously because, in addition to efficient digestive tracts, they generally de-husk most seeds before consuming the kernel (Forshaw 1969; Long 1984; van der Meij & Bout 2004). In Europe, only a few viable seeds of white clover (*Trifolium repens*), common sorrel (*Rumex acetosa*) and goosefoot (*Chenopodium album*) were recovered from the faeces of house sparrows (*Passer domesticus*—closely related to finches), common pigeons (*Columba domestica*) and pheasants (*Phasianus colcicus*) (Krach 1959).

Were viable seeds passed?

Our study demonstrated that seed-eating birds, particularly the omnivorous/herbivorous species, can pass viable seed. However, the germination of passed seeds was significantly reduced compared with that of control seed, except for the hard-seeded bladder clover. This implies that the number of viable endozoochorously avian-spread soft-seeded diaspores available for establishment in the wild will be reduced. Such an effect has been observed on the Iberian Peninsula where the viability of *Corema album* seed consumed and passed by yellow-legged gulls (*Larus cachinnans*) was only ∼18%, and 4% when passed through blackbirds (*Turdus merula*) (Calvino-Cancela 2004). Nevertheless, the gulls were still considered important seed dispersal agents. In captive mallards (*Anas platyrhynchos*), intact seeds of 21 of 23 species of aquatic plants were recovered from duck faeces over 48 h, with a subsequent germination rate of up to 32% of ingested seeds (Soons *et al.* 2008).

The lack of an obvious effect of passage through crested pigeons on the germination of bladder clover seed suggests that granivorous birds may have limited effect on the viability of hard-seeded species
such as native and introduced legumes. Consequently, they may be important dispersal agents for some of these seeds. The germination of fruit-dispersed seed is often increased once the seeds have passed through the digestive tract of birds (Norconk et al. 1998; Gosper et al. 2005; Calvino-Cancela et al. 2006). Frugivorous birds are well recognized as important seed dispersers, particularly in rainforests (Traveset 1998; Gosper et al. 2005; Neilan et al. 2006), but these birds are also important dispersal agents for several Mediterranean plants/weeds (e.g. bridal creeper (Stansbury 2001); mistletoe (Amyema quandang) (Murphy et al. 1993); Lantana camara (Gosper et al. 2005)).

Positive or negative changes in germination after passage through the digestive tract result from physical (in gizzard) or chemical abrasion and scarification by acids in the gut (Traveset et al. 2001). The failure of some Tetrazolium-positive (indicates seeds can germinate) seeds to germinate during the 10-week germination trials is not surprising as a number factors can influence seed germination. These include the presence of inhibitory chemicals, and the requirement for adequate soil moisture, light and temperature conditions (Hegarty 1987; Kigel & Galili 1995). Nevertheless, the viability of passed soft-seeded species was significantly reduced compared with that of untreated seed.

In contrast to most obligate granivorous birds, our data, and those of Krach (1959) and Soons et al. (2008), suggest that omnivorous/herbivorous species such as ducks, magpies and rooks are less efficient at digesting all ingested seed. Hence, they are more likely to disperse viable seed, including the seeds of weeds and undesirable plants, and this may increase during times of food shortage. In mallards (A. platyrhynchos) from the Netherlands, for example, the smaller, harder aquatic plant seeds were passed more quickly, and had higher germination rates (up to 80% of ingested small seeds germinated), than did comparable larger seeds of aquatic plants (23 plant species assessed (Soons et al. 2008)).

**Viable seed dispersal in the wild**

Although most of our feeding trials were conducted in captivity, we are confident that these outcomes are indicative of the response of wild, free-ranging birds because: (i) passage time estimates were similar between standard rations and test seed, (ii) the results of the small number of field trials were similar to those obtained during the captive feeding trials, (iii) the test seeds used were within the size
range found in the gut of free-ranging birds and/or were within the size range of many weed seeds (many Australian weed seeds range from <1 mm to >8 mm (Parsons and Cuthbertson (2001)), (iv) most test seeds have been recorded in the diet of wild birds (Barker & Vestjens 1989), and (v) the viability/germination of passed seed is unlikely to differ significantly between seeds of the same species fed to captive and free-ranging birds of individual avian species (see Wotton et al. 2008).

The similarity in passage time across our bird species, which generally only varied by 1–2 h between the test seeds and standard rations (usually contained a mix of seeds), suggests that passage time for most seeds ingested by free-ranging individuals of our bird species is unlikely to differ appreciably. Consequently, we believe that the passage times we derived are representative of those of similar wild birds. These estimates may also provide rough guides for other granivorous/omnivorous species. The 0.5- to 4-h mean passage time of test seed and standard rations through the digestive tract of the test birds, together with their known home range size, suggests that these species may potentially disperse seed over moderate distances (see below). However, passage time can be influenced by several factors including the size of the birds and that of the seeds ingested (French 1996; Wotton et al. 2008). For example, the passage time recorded for our finches was similar to that of silvereyes where these rates ranged from 0.1 to 0.5 h (French 1996). Mean retention times in New Zealand pigeons ranged from 0.6 to 0.8 h for small seeds and 1.8 h to 3 h for larger seeds (Wotton et al. 2008). This was similar to that observed for our similar-sized Columbiformes.

Seed dispersal distances greater than 100–200 m are generally considered to be long distance, with most unassisted seed dispersal distances being less than this (Nathan 2006). Nonetheless, dispersal distances will depend upon the size of the home range of the birds involved, particularly their daily use patterns. In temperate climates, the daily distances travelled by our bird species are generally moderate, ranging from 1 to 10 km (R. Johnstone, Western Australian Museum, pers. comm., 2008). However, these distances are often greater in arid environments because many birds need to travel further to obtain food and water (e.g. bronzewing pigeons often travel 50 km in a day (R. Johnstone, pers. comm., 2008)).
For seed dispersal to occur into new areas, seed needs to be ingested, and the birds need to travel outside the current distribution boundaries within a relatively short period (e.g. <1 h). For example, over 60% of new infestations of bridal creeper (*Asparagus asparagoides*) were recorded within 50 m of their source populations (Stansbury 2001). Bridal creeper is an environmental weed in Australia whose seed is contained within a fleshy fruit. Silvereyes (*Zosterops lateralis*) are one of its main seed dispersers, and appear to influence the pattern and rate of its spread. The maximum predicted dispersal distance under this bird/weed system was 12 km (Stansbury 2001). The passage of seeds through the gut of silvereyes can also reduce seed viability (French 1996). Emus also provide a good example of endozoochorous seed dispersal as they can disperse viable seeds of a number of introduced (Brassicaceae, Solanaceae) and native (Mimosaceae, Papilionaceae, Chenopodiaceae) Australian plants over long (>100 km) and moderate distances (<10 km) (Calvino-Cancela et al. 2006). Emus are widely distributed throughout Australia and often have large home ranges (Blakers et al. 1984), which together with their high mobility, generalist diet, long gut retention times (depending upon seed species, this ranges from 3 h to more than several weeks), and high passed seed viability (Calvino-Cancela et al. 2006) accounts for their important role in the dispersal of several plant species. The long gut retention times are consistent with emus being large birds (adults are at least 40 kg) with long intestines (Figuerola et al. 2002). Models of seed dispersal of aquatic plants by mallards (*A. platyrhynchos*) suggest that some ducks can disperse viable seeds of a number of aquatic species over long distances (>500 km; Soons et al. 2008). Such dispersal distances were largely dependent upon the size of seed as smaller seeds are passed more quickly and hence their retention time within the host is reduced (influences seed viability).

The presence of viable seed in the regurgitated soft pellets of omnivorous seedeaters provides another means by which plants may be dispersed. A range of seeds were recovered from the soft pellets of our urban magpies, with approximately 40% being viable. Similarly, pied currawongs (*Strepera graculina*) also spread seeds via regurgitated pellets and, although the viability of such seeds was not determined, this species is a suspected dispersal agent for over 30 alien plants (Buchanan 1989).
Seeds can also be spread secondarily by predators which ingest seeds with their prey, and then pass viable seed (Dean & Milton 1988; Nogales et al. 2002, 2007).

**Will weeds and other undesirable plants be dispersed in the wild?**

In Western Australia, animal-dispersed seeds of declared plants/weeds were the second most commonly recorded dispersal method with 45 species spread by this means (water was the most common dispersal mode with 47 species (Parsons & Cuthbertson (2001)). Over 30 weed species, including at least 15 declared weeds, have been recorded in the diet of Australian birds (Barker & Vestjens 1989; Parsons & Cuthbertson 2001). Further, the range of seeds we tested was within the size range of the seeds of many weed species (Parsons & Cuthbertson 2001). Of course, their presence in the gut does not necessarily imply viable diasporas are passed, or that successful germination and establishment takes place. As stated previously, many factors influence the spread and establishment of new plant populations at the landscape scale.

Gorse was the sole declared weed tested in our trials. Only crested pigeons, finches, black ducks and wood ducks consumed appreciable amounts of gorse seed in the presence of other food. A few whole seeds were recovered from the crested pigeons but none were viable. However, viable gorse seeds were recovered from the faecal pellets of both duck species, particularly those from black ducks. This included seed ingested from the gorse/wheat mix, and when choice and no-choice gorse were offered.

Based on feeding behaviours, pigeons, doves and the small parrots are the species most likely to feed on gorse seed. However, given that gorse is an explosive seed disperser and most seed is retained close to the parent plant, and that no viable gorse seeds were recovered from the Columbiformes during our trials, these granivorous birds may play only a limited role in the dispersal of gorse seed in Australia. Interestingly, in New Zealand, seedling establishment and survival were considered the main determinants of the maintenance and spread of gorse populations, rather than seed dispersal mechanisms per se (Williams & Karl 2002). We are not discounting the role of granivorous birds in dispersing gorse seed as this weed species is included in their diet (Barker & Vestjens 1989; Parsons & Cuthbertson 2001; Williams & Karl 2002). However, we do suggest that caution is required with
such assessments as the germination/viability of seeds found in the faecal pellets/gut contents has rarely been determined. It is unknown whether ducks would feed on gorse seed where plants are present around watering points such as farm dams, but if so, they have the potential to spread viable seeds. Waterbirds are well-recognized dispersal agents for a number of aquatic plants (Figuerola et al. 2002; Soons et al. 2008).

Recent studies suggest that seeds play a more important and effective role in long-distance plant dispersal, and hence in long-distance gene flow, than does pollen (Bacles et al. 2006; Nathan 2006), suggesting the role of vertebrate seed dispersal may be more important than previously thought, particularly in fragmented landscapes (e.g. farmland, small reserves).

**Potential spread of feral populations of agriculture cultivars**

Most of our birds consumed canola seed even in the presence of other food, and viable seeds were recovered from the faecal pellets of wood ducks. This has possible implications for the introduction and/or management of GM canola crops in Australia (Twigg et al. 2008). Canola is self-compatible and capable of autonomous pollination (Williams et al. 1986; Hayter & Cresswell 2006). It is particularly good at colonizing disturbed habitats (Felber et al. 2007) so any dispersal to new sites risks the establishment of new populations. Non-GM canola is considered a minor agricultural weed in some Australian states (OGTR 2002). The main concerns raised regarding GM or non-GM canola include the establishment of feral canola populations within native plant communities resulting in competition with indigenous plants (Claessen et al. 2005; Twigg et al. 2008). The eradication of such plants could be problematical as GM canola is herbicide-resistant to facilitate in-crop weed control. Current models predicting gene flow between GM and non-GM canola crops only allow for wind- and bee- (Apis spp., Bombus spp.) pollination (Hayter & Cresswell 2006). Although proximity alone does not guarantee a GM canola cross-pollination event, the potential for long-distance cross-pollination is likely to increase in areas where birds disperse viable GM canola seed, and this needs to be allowed for in these models (Twigg et al. 2008).
Some caveats and management implications

Our study did not assess the potential for exozoochorous dispersal of seed and, consequently, we may have understated the role of vertebrates in seed dispersal in some cases. Exozoochorous seed dispersal is likely to be important in some situations, at least at a localized scale (e.g. seed adherence to mud on the feet of animals at waterholes). This includes the ongoing maintenance of established weed populations. We also acknowledge that dispersal, germination, establishment, survival and successful reproduction is required for the establishment of new plant (weed) populations, and that vertebrate seed dispersal may or may not be important considerations at the landscape scale.

Although a range of seeds has been identified in the diet (crop and gut contents) of many bird species (Barker & Vestjens 1989; Buchanan 1989; Parsons & Cuthbertson 2001; Williams & Karl 2002), the viability of passed diaspores has rarely been addressed. Consequently, caution is required when assessing the role of such birds as seed dispersal agents because presence in the gut does not necessarily imply that viable diaspores are dispersed. That is, although we readily acknowledge the important role of avian seed dispersal in many situations, this role may be overstated in some instances (e.g. some obligate seed-eating birds).

Passage of seed through birds and other seed consumers also has indirect effects on seed germination rates. Whether seed deposition occurs in an environment which is suitable for plant establishment is at least partially governed by where and how often defecation occurs.

Although options for preventing wild birds from feeding on weed seed are generally limited, a greater understanding of when and where birds are likely to be important considerations is nonetheless valuable. Such knowledge may enable more biological meaningful containment areas to be established during new weed incursions. It will also enable more informed resource allocation during control programmes. For example, our results suggest that, in many situations, seed dispersal by most obligate seed-eating birds may be of lower concern compared with the other modes of seed dispersal (e.g. human spread). Such knowledge helps to focus control efforts and associated expenditure.
The potential for seed-eating animals to disperse GM canola seed (or other similar seeds) could be reduced by ensuring spilt seed is recovered quickly to reduce its ready availability, and by ensuring GM seed is tightly secured during transport, storage and manufacture (Twigg et al. 2008). The persistence of ‘contaminated’ areas will depend upon factors such as seed longevity, crop proximity, spatial arrangement of crops, and the level of cross-pollination (Belcher et al. 2005; Twigg et al. 2008).

Acknowledgements

This work was approved by the DAFWA AEC (Permit # 06FF04/6-06-46). The ducks were collected under licence from the DEC, WA. We thank the Caversham Wildlife Park for loaning us the crested pigeons. We also thank Garry Morse, Kevin Foster, John Moore, Ted Knight and Andy Sutherland, DAFWA, for advice and help with parts of the project. The financial support of the Feral Animal Control Program of the Australian Government's Natural Heritage Trust is gratefully acknowledged. CMT was supported by the 2007 Jennifer Arnold Scholarship.

References


Figure 1. The range in size of seeds found in the gut samples of free-ranging species of Columbiformes and finches* held at the Western Australian Museum. *Pooled samples of red-eared (Emblema oculatum) and painted (Emblema pictum) firetails as no samples were available for the zebra finches. There were no available samples for the black and wood ducks.
Figure 2. The mean and standard deviation of the total amount of test seed (TS) and standard rations (SR) consumed during the no-choice (NC) and choice (C) captive feeding trials with species of Columbiformes. BC, bladder clover; Can, canola; CC, crimson clover; Grs, gorse. The d.f., $F$- and $P$-values are shown for the repeated measure anova comparing the consumption of the different seed types during the choice trials.
Figure 3. The mean and standard deviation of the total amount of test seed (TS) and standard rations (SR) consumed during the no-choice (NC) and choice (C) captive feeding trials with zebra finches. BC, bladder clover; Can, canola; CC, crimson clover; Grs, gorse.
Figure 4. The mean and standard deviation of the total amount of test seed (TS) and standard rations (SR) consumed during the no-choice (NC) and choice (C) captive feeding trials with black ducks and wood ducks. BC, bladder clover; Can, canola; CC, crimson clover; Grs, gorse.
Table 1. Characteristics of the seed species used during the feeding trials

<table>
<thead>
<tr>
<th>Seed species</th>
<th>No. counts</th>
<th>Number of seeds per gram</th>
<th>Seed size (mm)$^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>No. counts</td>
<td>Mean</td>
</tr>
<tr>
<td>Commercial seed mix 1‡</td>
<td>3</td>
<td>179</td>
<td>2.8</td>
</tr>
<tr>
<td>Commercial seed mix 2§</td>
<td>5</td>
<td>303</td>
<td>4</td>
</tr>
<tr>
<td>Bladder clover (<em>Trifolium spumosum</em>)</td>
<td>5</td>
<td>443</td>
<td>6.8</td>
</tr>
<tr>
<td>Crimson clover (<em>Trifolium incarnatum</em>)</td>
<td>4</td>
<td>296</td>
<td>2.7</td>
</tr>
<tr>
<td>Canola (<em>Brassica napus</em>)</td>
<td>5</td>
<td>372</td>
<td>8</td>
</tr>
<tr>
<td>Gorse (<em>Ulex europaeus</em>)</td>
<td>4</td>
<td>169</td>
<td>2.9</td>
</tr>
<tr>
<td>Red panicum (<em>Digitaria italica</em>)</td>
<td>4</td>
<td>435</td>
<td>7</td>
</tr>
</tbody>
</table>

$^1$Measured as the diameter or longest length of each seed species depending upon their shape.

$^2$Parrot/dove mix based on Home Brand (Woolworths, Australia) Canary Bird Seed mix and Budgerigar Bird Seed.

$^3$Finch mix based on several millets, red panicum and sorghum.
Table 2. The number of birds sampling test seed (STS) and the contribution of consumed test seed to daily food consumption, during the food preference trials.

<table>
<thead>
<tr>
<th>Species</th>
<th>NC</th>
<th>C</th>
<th>Minimum</th>
<th>Maximum</th>
<th>NC</th>
<th>C</th>
<th>Minimum</th>
<th>Maximum</th>
<th>NC</th>
<th>C</th>
<th>Minimum</th>
<th>Maximum</th>
<th>NC</th>
<th>C</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peaceful doves</td>
<td>2/4</td>
<td>3/4</td>
<td>0.0</td>
<td>5.7</td>
<td>1/4</td>
<td>1/4</td>
<td>0.0</td>
<td>1.5</td>
<td>4/4</td>
<td>4/4</td>
<td>0.0</td>
<td>7.2</td>
<td>0/4</td>
<td>0/4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Senegal doves</td>
<td>2/3</td>
<td>3/4</td>
<td>0.0</td>
<td>2.4</td>
<td>2/5</td>
<td>0.5</td>
<td>na</td>
<td></td>
<td>5/5</td>
<td>5/5</td>
<td>13.5</td>
<td>83.2</td>
<td>0/5</td>
<td>1/5</td>
<td>0.0</td>
<td>1.6</td>
</tr>
<tr>
<td>Bronzewings</td>
<td>0/3</td>
<td>1/3</td>
<td>0.0</td>
<td>19.5</td>
<td>0/4</td>
<td>3/4</td>
<td>0.0</td>
<td>66.7</td>
<td>0/3</td>
<td>0/2</td>
<td>na</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crested pigeons</td>
<td>4/4</td>
<td>4/4</td>
<td>0.0</td>
<td>11.7</td>
<td>4/4</td>
<td>2/4</td>
<td>0.0</td>
<td>2.1</td>
<td>4/4</td>
<td>4/4</td>
<td>25.5</td>
<td>61.8</td>
<td>3/4</td>
<td>0/4</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>Zebra finches</td>
<td>Not tested</td>
<td>2/3</td>
<td>1/3</td>
<td>0.0</td>
<td>3.7</td>
<td>2/4</td>
<td>1/4</td>
<td>0.0</td>
<td>6.5</td>
<td>3/3</td>
<td>2/3</td>
<td>0.0</td>
<td>3.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black ducks</td>
<td>Not tested</td>
<td>Not tested</td>
<td>3/4</td>
<td>4/4</td>
<td>0.0</td>
<td>12.8</td>
<td>4/4</td>
<td>3/4</td>
<td>0.0</td>
<td>0.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wood ducks</td>
<td>Not tested</td>
<td>Not tested</td>
<td>2/4</td>
<td>3/4</td>
<td>0.0</td>
<td>66.6</td>
<td>1/3</td>
<td>1/3</td>
<td>0.0</td>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The number of birds sampling test seed during the no-choice (NC) and choice (C) captive feeding trials.

The percentage that test seed contributed to the total weight of daily food consumption over the 2 days of the choice (C) trials with standard rations.

ST: Seed test
CR: Crimson clover
BC: Bladder clover
CN: Canola
GR: Gorse

%‡: The percentage that test seed contributed to the total weight of daily food consumption over the 2 days of the choice (C) trials with standard rations.

Table entries marked with ‘na’ indicate that the test was not conducted.
Table 3. The number of faecal pellets examined for whole seed, and the estimated number of seeds ingested, for each bird species tested during the captive feeding trials

<table>
<thead>
<tr>
<th>Trial type/seed species</th>
<th>Parameter</th>
<th>Peaceful doves</th>
<th>Senegal doves</th>
<th>Bronzewing</th>
<th>Crested pigeons</th>
<th>Zebra finches</th>
<th>Black ducks</th>
<th>Wood ducks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>No. seeds ingested – range&lt;sup&gt;c&lt;/sup&gt;</td>
<td>354</td>
<td>44–89</td>
<td>487</td>
<td>1329–2166&lt;sup&gt;d&lt;/sup&gt;</td>
<td>133–879&lt;sup&gt;d&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pellets with seed/no. pellets examined (%)</td>
<td>0/7</td>
<td>0/14</td>
<td>0/5</td>
<td>31/166 (18.7%)</td>
<td>0/29</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>No. seeds ingested – range&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1050–2046&lt;sup&gt;e&lt;/sup&gt;</td>
<td>1409–2891&lt;sup&gt;e&lt;/sup&gt;</td>
<td>521–939&lt;sup&gt;d&lt;/sup&gt;</td>
<td>74–3070</td>
<td>0–15 954</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pellets with seed/no. pellets examined (%)</td>
<td>0/49</td>
<td>0/98</td>
<td>0/47</td>
<td>0/80</td>
<td>2/90 (2.2%)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>No. seeds ingested – range&lt;sup&gt;c&lt;/sup&gt;</td>
<td>811–1048&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0–1724&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0–2954&lt;sup&gt;e&lt;/sup&gt;</td>
<td>34–818&lt;sup&gt;d&lt;/sup&gt;</td>
<td>17–2709&lt;sup&gt;e&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pellets with seed/no. pellets examined (%)</td>
<td>0/83</td>
<td>0/106</td>
<td>0/100</td>
<td>6/229 (2.6%)</td>
<td>1/109 (0.9%)</td>
<td>8/422 (1.9%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No. seeds ingested – range&lt;sup&gt;c&lt;/sup&gt;</td>
<td>207–3116&lt;sup&gt;e&lt;/sup&gt;</td>
<td>394–3250&lt;sup&gt;f&lt;/sup&gt;</td>
<td>850–1 205&lt;sup&gt;f&lt;/sup&gt;</td>
<td>850–1 205&lt;sup&gt;f&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pellets with seed/no. pellets examined (%)</td>
<td>1/244</td>
<td>8/214</td>
<td>3/233</td>
<td>0/4%</td>
<td>8/214</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>No. seeds ingested – range&lt;sup&gt;c&lt;/sup&gt;</td>
<td>149–223</td>
<td>186–893</td>
<td>1190</td>
<td>91–364</td>
<td>261–348&lt;sup&gt;b&lt;/sup&gt;</td>
<td>744–2827</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pellets with seed/no. pellets examined (%)</td>
<td>0/4</td>
<td>0/44</td>
<td>0/2</td>
<td>0/82</td>
<td>2/51 (3.9%)</td>
<td>0/64</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No. seeds ingested – range&lt;sup&gt;c&lt;/sup&gt;</td>
<td>90–215</td>
<td>197–394</td>
<td>1557</td>
<td>269–304</td>
<td>121–182</td>
<td>108–240</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pellets with seed/no. pellets examined (%)</td>
<td>0/31</td>
<td>0/26</td>
<td>0/16</td>
<td>0/142</td>
<td>0/113</td>
<td>0/37</td>
</tr>
<tr>
<td></td>
<td></td>
<td>All pellets with seed/total no. pellets examined (%)</td>
<td>68/3309 (2.1%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

‘Other’ was crimson clover for crested pigeons, and a gorse wheat mix (1 : 8) for the ducks. <sup>a</sup>Grouped birds only used (<i>n</i> = 3). <sup>b</sup>Where possible, the outcomes for the pellets from the choice (standard rations also present) and no-choice trials have been combined. <sup>c</sup>Estimated from the number of seeds per gram (see Table 1), and the amount (g) eaten by those individual birds whose faecal pellets were examined. <sup>d</sup>Mainly standard rations as limited test seed eaten. <sup>e</sup>Assessed as 60% standard rations and 40% test seed eaten during the choice trials. <sup>f</sup>Minimum estimate as measurements only include the amount of dyed seed consumed. Unlimited undyed seed only was provided immediately after the consumption of the Carmine-dyed seed. <sup>g</sup>Minimum estimate as only includes the 1 : 8 gorse wheat mix. Unlimited plain wheat only was provided immediately after obvious consumption of the gorse/wheat mix occurred. <sup>h</sup>Red Panicum was used to determine passage time for the finches. <sup>i</sup>Standard rations were suitable commercial seed mixes for the Columbiformes and finches, and wheat for the ducks (see Methods).
Table 4. Mean (±SD, (range)) estimated passage time of two seed types for the species of Columbiformes, zebra finches and ducks during captive feeding trials with Carmine red marker

<table>
<thead>
<tr>
<th>Species</th>
<th>Seed type</th>
<th>Dye appearance (h)†</th>
<th>Dye disappearance (h)‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peaceful doves (n = 4)</td>
<td>Standard rations</td>
<td>2.63 ± 0.43 (2.3–3.3)</td>
<td>5.46 ± 0.55 (4.8–6.1)</td>
</tr>
<tr>
<td></td>
<td>Canola</td>
<td>1.17 ± 0.20 (1.0–1.4)</td>
<td>6.94 ± 2.36 (4.3–10.0)</td>
</tr>
<tr>
<td>Senegal doves (n = 3 &amp; 4)</td>
<td>Standard rations</td>
<td>0.89 ± 0.34 (0.5–1.1)</td>
<td>5.25 ± 0.87 (4.3–5.8)</td>
</tr>
<tr>
<td></td>
<td>Canola</td>
<td>0.48 ± 0.17 (0.3–0.7)</td>
<td>4.08 ± 0.68 (3.2–4.6)</td>
</tr>
<tr>
<td>Crested pigeon (n = 4)</td>
<td>Standard rations</td>
<td>1.39 ± 0.24 (1.1–1.6)</td>
<td>3.75 ± 1.34 (2.0–5.3)</td>
</tr>
<tr>
<td></td>
<td>Canola</td>
<td>0.77 ± 0.38 (0.6–1.3)</td>
<td>3.02 ± 1.26 (1.6–4.5)</td>
</tr>
<tr>
<td>Bronzewings (group of 3 birds)§</td>
<td>Standard rations</td>
<td>4.3</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Canola</td>
<td>1.3</td>
<td>8.8</td>
</tr>
<tr>
<td>Zebra finches (n = 4)</td>
<td>Standard rations</td>
<td>0.69 ± 0.21 (0.6–1.0)</td>
<td>2.23 ± 1.31 (1.1–3.9)</td>
</tr>
<tr>
<td></td>
<td>Red panicum</td>
<td>0.44 ± 0.10 (0.3–0.5)</td>
<td>2.75 ± 0.29 (2.7–3.3)</td>
</tr>
<tr>
<td>Black ducks (n = 4)</td>
<td>Wheat</td>
<td>2.91 ± 0.79 (1.8–3.5)</td>
<td>2.72 ± 1.78 (1.0–4.8)</td>
</tr>
<tr>
<td></td>
<td>Canola</td>
<td>2.90 ± 1.43 (2.1–5.0)</td>
<td>7.12 ± 0.38 (2.8–12.0)</td>
</tr>
<tr>
<td>Wood ducks (n = 3)</td>
<td>Wheat</td>
<td>1.60 ± 1.60 (0.5–3.4)</td>
<td>8.80 ± 5.12 (3.0–12.8)</td>
</tr>
<tr>
<td></td>
<td>Canola</td>
<td>2.73 ± 0.53 (2.1–3.0)</td>
<td>11.11 ± 4.42 (6.0–14.0)</td>
</tr>
</tbody>
</table>

†The amount of time elapsed (h) from the consumption of dyed seed until the first appearance of dyed faecal pellets.

‡The amount of time elapsed (h) from when dyed faecal pellets first appeared to when dyed pellets were no longer seen.

§ Collected from three birds grouped together in their holding pen.
Table 5. The germination/viability of various seeds after their passage through some Australian birds

<table>
<thead>
<tr>
<th>Seed type</th>
<th>Bird species</th>
<th>No. seeds ingested (range)</th>
<th>Pellets with seed</th>
<th>Seeds recovered</th>
<th>Seeds germinated</th>
<th>Control seed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>No. (range)</td>
<td>%</td>
<td>No.</td>
<td>%</td>
<td>No. tested</td>
</tr>
<tr>
<td>Bladder clover (n = 4)</td>
<td>Crested pigeons</td>
<td>3274 (199–1391)</td>
<td>31</td>
<td>331 (0–176)</td>
<td>10.1</td>
<td>35</td>
</tr>
<tr>
<td>Canola Gorse (n = 4)</td>
<td>Wood ducks (n = 3) Crested pigeons</td>
<td>3816 (600–2544)</td>
<td>29</td>
<td>1065 (0–1056)</td>
<td>3</td>
<td>4 (0–3)</td>
</tr>
<tr>
<td></td>
<td>Black ducks (n = 4) &amp; zebra finches</td>
<td>1486 (118–688)</td>
<td>17</td>
<td>177 (5–56)</td>
<td>5.2</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Millet</td>
<td>225 (51–123)</td>
<td>3</td>
<td>3 (1–1)</td>
<td>1.3</td>
<td>2</td>
</tr>
<tr>
<td>Unknown (n = 2)</td>
<td>Millet</td>
<td>Unknown</td>
<td>5</td>
<td>7</td>
<td>3</td>
<td>42.9</td>
</tr>
<tr>
<td>All passed seeds</td>
<td>Unknown</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

The range is shown for individual birds. n = number of birds included during each monitoring period that whole seed was recovered.

†Fisher exact two-tailed probability for the comparison of the germination of passed versus the control (untreated) seed.

‡Percentage of the seeds recovered.

§Percentage of the seeds ingested.
Table 6. The consumption of standard rations and canola by free-ranging magpies (*Gymnorhina tibicen*) and bronzewing pigeons (*Phaps chalcoptera*) in a semi urban setting

<table>
<thead>
<tr>
<th>Species</th>
<th>Birds feeding†</th>
<th>Amount consumed (g)‡</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Standard rations</td>
<td></td>
</tr>
<tr>
<td>Standard rations only</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpies</td>
<td>3/4–15 min</td>
<td>8.5</td>
</tr>
<tr>
<td>Bronzewings</td>
<td>4/6–30 min</td>
<td>65.4</td>
</tr>
<tr>
<td>Choice – standard rations versus Canola</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpies</td>
<td>3/3–10 min</td>
<td>9.7</td>
</tr>
<tr>
<td></td>
<td>3/3–15 min</td>
<td>11.3</td>
</tr>
<tr>
<td>Magpies</td>
<td>4/4–15 min</td>
<td>6.3</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>27.3</td>
</tr>
<tr>
<td>Bronzewings</td>
<td>1/1–15 min</td>
<td>10.1</td>
</tr>
<tr>
<td>Bronzewings</td>
<td>1/1–10 min</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>1/1–10 min</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>1/1–15 min</td>
<td>15.3</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>27.4</td>
</tr>
<tr>
<td>Canola only</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bronzewings</td>
<td>6/6–30 min</td>
<td>9.6</td>
</tr>
<tr>
<td>Bronzewings</td>
<td>&gt;3/7–~60 min</td>
<td>30.7</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>40.3</td>
</tr>
</tbody>
</table>