Interactions between frugivorous birds and weeds in Queensland as determined from a survey of birders

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Summary

We used a questionnaire survey of experienced bird observers to identify the main bird-dispersal agents of introduced plants and weeds in Queensland. From the survey results we gathered information on the foraging habits of different bird groups (small and large generalist frugivores, fruit specialists and seed destroyers). We also examined the relationships between 1) fruit size and the number of bird species utilizing each weed species and 2) weed invasiveness and the number of bird species utilizing each weed species. The study yielded 230 observations of frugivory on introduced and weedy plants. Thirty eight bird species were observed feeding on the fruit of 28 weed species. Weed fruit ranged in size from 2.5 mm (*Rubus fruticosus* L.) to 50 mm (*Opuntia stricta* Haw.). Eighty nine percent of all fruit consumed by frugivores was below 15 mm in diameter. Most fruit was gulped, but birds resorted to pecking or mashing fruit that exceeded gape width. Birds with the most diverse weed fruit diet included the figbird (*Sphecotheres viridis* Vieillot), silvereye (*Zosterops lateralis* Latham), olive-backed oriole (*Oriolus sagittatus* Latham), Lewin's honeyeater (*Meliphaga lewinii* Swainson), pied currawong (*Strepera graculina* White) and regent bowerbird (*Sericulus chrysocephalus* Lewin). Those weed species fed on by the largest number of bird species were camphor laurel (*Cinnamomum camphora* L.), ochna (*Ochna serrulata* (Hoechst.) Walp.), wild tobacco (*Solanum mauritianum* Scop.), umbrella tree (*Schefflera actinophylla* (Endl.) Harms), glossy nightshade (*Solanum americanum* Mill.) and Chinese elm (*Celtis sinensis* Pers.). Bird functional groups differed with regard to flock size, the size of fruit eaten, the habitat type where feeding was observed, the amount of time spent feeding in fruiting plants, the number of fruits consumed and flight distances after a feeding bout. Weed invasiveness was moderately correlated to the number of frugivorous birds observed feeding on each weed species.

Keywords: dispersal syndrome, frugivory, plant functional group, seed dispersal, weed syndrome.

Introduction

In south-eastern Queensland (SEQ), bird-dispersed species represent a diverse and difficult-to-manage group of environmental weeds. In a recent ranking of the 200 most invasive environmental weeds in SEQ, approximately 25% of all species listed, and half of the top 23 species, produce fleshy fruits that are potentially bird-dispersed (Batianoff and Butler 2002). Despite an abundance of bird-dispersed weeds, we have a limited understanding of how avian dispersers contribute to the success of environmental weeds. We know little about the major avian dispersers, their feeding preferences and the seed dispersal patterns that they generate. The large number of weeds involved, their diverse fruit characteristics and the potential for many avian dispersers to contribute to their spread suggests that a multi-species approach to studying the problem of bird-dispersed weeds may reveal previously unidentified functional ecological patterns. These patterns may be useful for generating hypotheses that form the basis for further studies of bird-dispersed weeds, and could provide insight into potential management approaches.

Research on the spread of introduced plants and invasive weeds by frugivorous birds has mostly focused on studies that document the major dispersal vectors of weeds (Carr *et al*. 1992) and on the importance of weeds in the diets of native birds (Symon 1979, Snow 1981, Date *et al*. 1991, Loyn and French 1991, Williams and Karl 1996, Stansbury 1996). Other studies have focused on seed dispersal (Willson and Crome 1989, Stansbury and Scott 1999 and Stansbury 2001), but these have generally dealt with individual weed: disperser relationships and the identification of new mutualisms in the weed's invaded geographic range. The latter studies include research on *Pittosporum undulatum* Vent. dispersed by European Blackbird (*Turdus merula* L.) in Victoria (Gleadow 1982); *Pyracantha angustifolia* C.K.Schneid. and *Crataegus monogyna* Jacq. dispersed by pied currawong (*Strepera graculina* White) in South Australia (Bass 1990); *Schinus terebinthifolius* Raddi dispersed by silvereye (*Zosterops lateralis* Latham) in eastern Australia (Panetta and McKee 1997); and *Asparagus asparagoides* (L.) Wight dispersed by silvereye in south western Australia (Stansbury 2001). Studies of new mutualisms have indicated that weed invasion success may be initially dependent on whether a suitable disperser is present in the new environment and the time it takes for a disperser to adopt the newly arrived plant species (Richardson *et al*. 2000). In some cases, highly effective mutualistic partnerships from the native range may be re-united in the invaded range (Stansbury 2001, Richardson *et al*. 2000).

The role of seed dispersal by birds has been investigated extensively (Snow 1971, Howe 1986, Murray 1987, French *et al*. 1992, Oakwood *et al*. 1993, Wenny 2001, Pizo 2002). More recently, there has been a shift in research focus from specialized dispersal systems to more diffuse mutualistic relationships between groups of plants and dispersers (Howe 1980, Malmborg and Willson 1988), or 'generalized dispersal systems' (Howe 1986) (e.g. Izhaki *et al*. 1991). Such research is relevant to avian weed dispersal relationships, which are predominantly diffuse mutualisms. Generalized dispersal systems tend to involve small, abundant seeds, and low energy fruits that are attractive to a wide range of generalist, opportunistic frugivores and relationships involve bird species with larger populations where fruit makes up a small component of a varied diet (Howe 1986). Consequently, dispersal patterns and seed shadows resulting from a generalized system are more difficult to predict than those from specialized dispersal systems.

Recent studies on the ecology of bird-dispersed plants take a functional group approach, investigating differences in fruit morphology and disperser characteristics (Debussche and Isenmann 1989, Pizo 2002). They have found that larger birds contribute more to the dispersal of plants with larger fleshy fruits (>15 mm diameter), and large-fruited plant species with large seeds have been shown to be visited by fewer total bird disperser species, compared with plants with small fruits with one or few seeds, or with very large fruits and many tiny seeds (Green 1993). These differences are also likely to result in a variation in subsequent seed dispersal patterns (Jordano 1995, Pizo 2002).

Few studies have taken a multi-species, functional group approach to the problem of bird-dispersed weeds. Such an approach may help identify or predict new mutualisms for introduced plants that are not yet invasive, as well as for existing invasive weed species. The identification

of weed:disperser functional groups may enable the prediction of: 1) the likelihood of a fruit-bearing introduced plant being adopted by frugivorous birds; 2) patterns and rates of spread; and 3) identification of factors influencing effective dispersal (i.e. dispersal of viable seed to favourable recruitment microsites) and plant invasiveness. For example, plant invasiveness may be a function of the total number of frugivorous bird species that feed on and potentially spread the plant. Effective dispersal may depend on how a frugivorous bird handles the fruit and treats the seed (i.e., whether it gulps the fruit or pecks at the flesh and if the seed is passed in a viable condition). The size of seed shadows will depend on how long the bird stays in the fruiting plant relative to gut passage rates for ingested seeds. Where disperser behaviour can be predicted, there is the potential for dispersal to be manipulated to decrease the probability of weed spread (Wenny 2001).

This study aimed to provide background information for future exploration of the existence of functional groupings for weed:disperser relationships and potential management opportunities. Specifically, our study used a questionnaire survey of experienced birders to: 1) identify the main bird dispersal agents of introduced plants and invasive weeds in Queensland, Australia and 2) determine whether functional groups of birds (e.g. small and large generalist frugivorous birds, seed destroyers and fruit specialists) behave differently with respect to foraging habits and the range of weed fruits they consume.

Methods

Sample groups

In November 2002, 460 members registered with Birds Queensland were sent a questionnaire designed to obtain records of birds feeding on fruits of introduced plants and invasive weeds (membership database provided by Birds Queensland, Australia). A number of members based in north-eastern New South Wales were included.

Additional records of frugivory were also obtained from 'Faunawatch', a volunteer observer network that focuses on animal and plant interactions in the Noosa Shire SEQ. The Faunawatch database included records of birds seen within introduced plants or weeds, without specifically stating whether birds ate any fruit. In this study, we only included references to birds observed consuming fruits. Records of weed frugivory were also obtained by an information request distributed to the 'enviroweeds' Internet based discussion group and through a network of interested weed researchers and birders.

Questionnaire methodology and design

Distribution of the questionnaire was initially advertised in the Birds Queensland Newsletter distributed in October 2002. The advertisement aimed to raise awareness of the project and encourage member involvement in the forthcoming survey. In November 2002 the questionnaire was sent with a covering letter and colour brochure, which outlined the project in more detail. A reply paid envelope was included. A follow-up article was also placed in the January 2003 Birds Queensland Newsletter. This gave a snapshot of the initial results and prompted members to return their questionnaires. The questionnaire was divided into three parts and followed the methods of Maclean and Genn (1979) and Stansbury and Scott (1999). Part one asked questions about the recipient and provided notes on completing the questionnaire. It also asked whether the respondent would be interested in participating in future structured bird observations. Part two of the questionnaire contained 14 questions and was designed for those respondents who had made only one observation of a bird species feeding on the fruit of one introduced plant or weed species. It included questions on how fruit was handled, how long a bird remained in a fruiting plant, how many fruit were removed during a feeding bout, whether birds fed alone or in pairs or flocks, and how far birds flew after feeding. All questions were multiple-choice, except those that asked for the name of the bird or introduced plant/weed and the month that the observation was made. A final question provided an opportunity for the respondent to supply additional information not asked in the main body of the questionnaire. Part three of the questionnaire was a table designed for respondents who had made several observations of one or many bird species feeding on the fruit of a number of different introduced plants or invasive weeds.

Data analysis

Birds were categorized by morphological attributes such as gape width and whether the species was considered an effective dispersal agent or seed destroyer. This information, along with data from the literature on the influence of fruit size on frugivory, were used to delineate gape width ranges for small and large generalist frugivores. For example, Noma and Yumoto (1997) show that fruit <10 mm in diameter are likely to be utilized by smaller generalist frugivores, whereas Green (1993) suggests that fruit >15 mm diameter are likely to be utilized by fewer, larger frugivorous bird species.

Four functional groups were defined. They included: 1) small generalist frugivores (gape width range: 0.6 to 1.15 cm); 2) large generalist frugivores (gape width range: 1.39 to 2.01 cm); 3) seed destroyers (i.e., parrots and some pigeons that grind seed) (gape width range: 1.03 to 2.39 cm), and 4) fruit specialists (e.g. fruit doves) (gape width range: 0.85 to 1.52 cm) (Appendix 1). Generalist frugivores were bird species with broad diets, comprising fruits from a range of plant species and other items (e.g. insects). Fruit specialists were those birds with fruit comprising almost their entire diet (Barker and Vestjens 1989). Functional groupings were made using both dietary information (Barker and Vestjens 1989, D. Westcott, personal communication) and gape width data. Gape width measurements were taken from skins held by the Queensland Museum (10 skins measured / bird species). Fruits were categorized according to size and measurements were either obtained from fruit samples collected in the field or from the literature (not all fruits were available in the field during the study period).

For each of the questions, Chi square statistics were used to test for differences in feeding preference and foraging habits of birds belonging to the different functional groups. The total number of observations for each question varied depending on the number of responses. Fruit specialists were not included in the functional group analysis due to too few records. Regression statistics were used to: 1) examine the relationship between fruit diameter (i.e., for fruits > or <15 mm) and the number of bird species recorded utilizing each weed species, and 2) examine the relationship between invasiveness scores of 19 weed species (Batianoff and Butler 2002) and the number of bird species recorded utilizing each weed species.

Results

Response rate

After two months approximately 10% (n = 45) of questionnaires were returned. Sixty five percent (n = 29) of the respondents had completed part three of the questionnaire and provided an average of five observations of bird:plant interactions (i.e. 155 separate records). In total the questionnaire produced 169 records of bird:plant interactions. Thirty two were rejected, as these consisted of birds consuming seeds (e.g., grass seed), or fruits of agricultural or native plants. The total number of records for birds feeding on introduced plants and invasive weeds was 137. Of these, 121 included detailed data on the social and foraging behaviour of the birds.

The Faunawatch database produced 71 records of bird:plant interactions. Forty three records were for birds feeding on fruits of introduced plants and invasive weeds. Eight included some data on the social and foraging behaviour of the birds. The email list produced 76 records of bird plant interactions, and included 50 records of birds feeding on fruits of introduced plants and weeds. Nine included some

data on the social and foraging behaviour of the birds.

In summary, all data sources produced a total of 316 observations of frugivory. Of these, 230 were records for birds feeding on fruits of introduced plants and weeds and 138 included some data on the social and foraging behaviour of the birds (Table 1). The low response rate of 10% may reflect low rates of observation of bird:weed interactions during the time of the survey (the survey was conducted in summer months when many introduced plants and invasive weeds had finished fruiting).

General bird:weed interactions

The respondents' confidence was high, with 96% of observers stating they were 'reasonably sure' or 'very sure' about the observations they had made. Gape width measurements used to assign birds to different functional groups showed a continuous relationship between bird species and gape width (Figure 1).

Generalist frugivorous birds were observed feeding on a wide range of weed fruits, both in number of species and size of fruits. In all, 38 bird species were observed feeding on the fruit of 28 weed species. Frugivores with the most diverse weed fruit diets included the figbird (*Sphecotheres viridis* Veillot) (observed feeding on 15 weed species); silvereye (*Zosterops lateralis*) (12 weed species); olive-backed oriole (*Oriolus sagittatus* Latham), Lewin's honeyeater (*Meliphaga lewinii* Swainson) and pied currawong (*Strepera graculina*) (all observed feeding on seven weed species); and regent bowerbird (*Sericulus chrysocephalus* Lewin) (five weed species) (Appendix 1).

Those weed species fed on by the largest number of bird species were camphor laurel (*Cinnamomum camphora* L.) (fed on by 20 bird species); ochna (*Ochna serrulata* (Hoechst.) Walp.) (12 bird species); wild tobacco (*Solanum mauritianum* Scop.) (nine bird species); umbrella tree (*Schefflera actinophylla* (Endl.) Harms) (eight bird species); glossy nightshade (*Solanum americanum* Mill.) (seven bird species); and Chinese elm (*Celtis sinensis* Pers.) (six bird species). Consumed weed fruit ranged in size from 2.5 mm (*R. fruticosus* L.) to 50 mm (*O. stricta* Haw.). Approximately 89% of all fruit consumed by frugivores was below 15 mm in diameter (Appendix 1).

Functional group analysis

The flock sizes observed during feeding differed significantly with bird functional group ($\chi^2 = 14.73$, df = 4, P = 0.005). Fifty percent of observations of small generalist frugivores and 80% of observations of large generalist frugivores were of one or two individuals. Conversely, approximately 82% of observations of seed destroyers were of flock sizes of three or more individuals (Figure 2).

Table 1. Numbers of frugivory observations obtained from each source (questionnaire, Faunawatch database and email list). 'Detailed observations' refers to sources that provided information on foraging habits of frugivores.

	Weeds + native plants	Weeds only	Weeds (detailed observations only)
Questionnaire	169	137	121
Faunawatch	71	43	8
Email list	76	50	9
Total	316	230	138

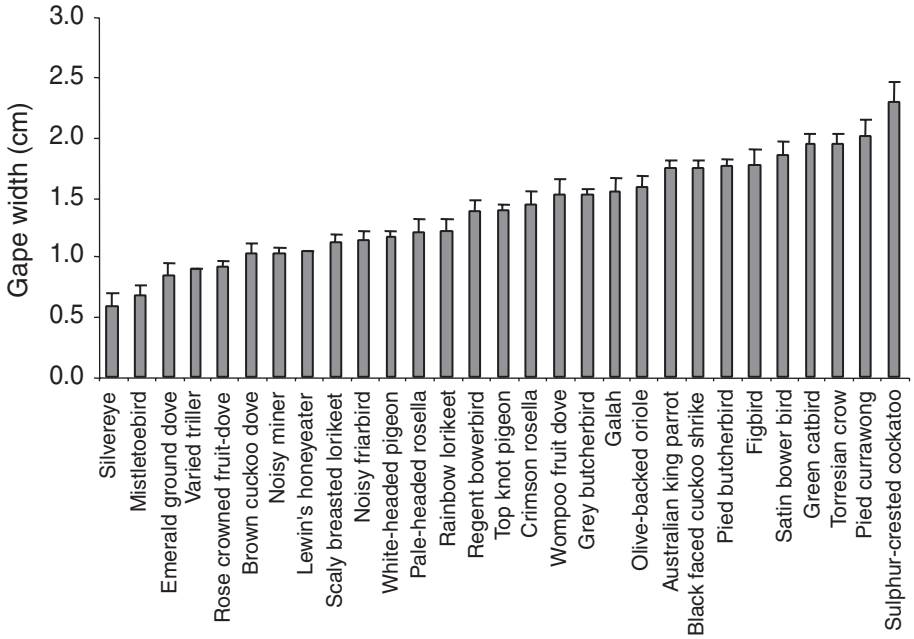

Figure 1. Gape-widths (± standard deviation) of frugivorous bird species in south-eastern Queensland.

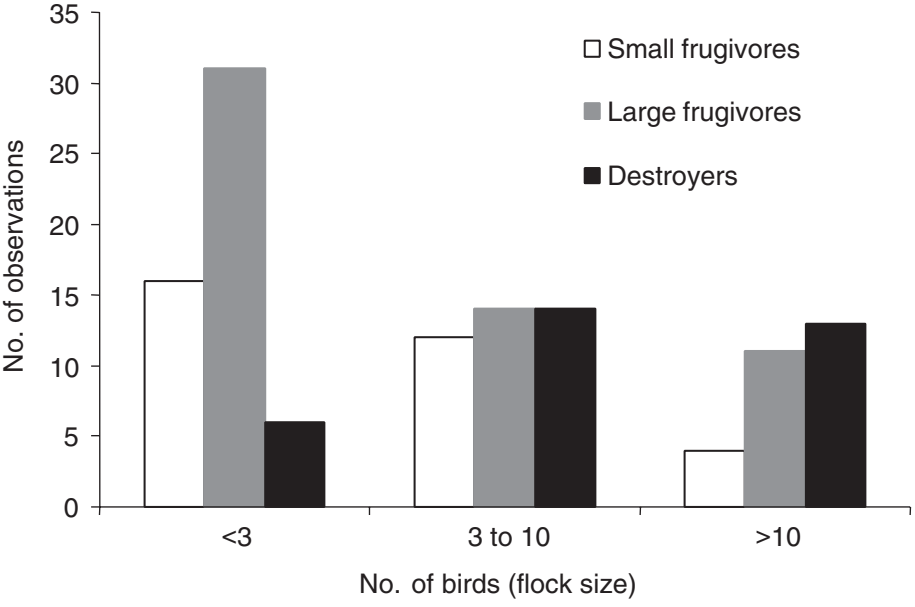

Figure 2. Flock size of frugivorous birds belonging to different dispersal syndromes observed feeding on introduced plants and invasive weeds.

There was also a significant difference with respect to bird functional group and the type of habitats in which feeding was observed ($\chi^2 = 20.96$, df = 4, P <0.001). The greatest proportion of weed frugivory observations (41%) were made in urban areas, 26% were made in rural areas and 32% in parkland or native bushland. For all observations of large generalist frugivores, approximately 62% were made in urban areas, 19% in rural areas and 19% in parklands or native bushland. Conversely, only 20% of all observations of small generalist frugivores were made in urban residential areas, 27% in rural habitats and 54% in parkland or native bushland. Observations of seed destroyers were more evenly distributed across the three habitat types (Figure 3).

The amount of time spent feeding in fruiting plants differed significantly between bird functional groups ($\chi^2 = 9.36$, df = 4, P <0.05). For all observations of feeding time in fruiting plants, approximately half of all birds (49%) stayed longer than five minutes. Seed destroyers and large generalist frugivores tended to feed for longer periods in source plants, with 40% of all seed destroyers and 72% of all large generalist frugivores feeding for periods greater than five minutes. In contrast, only 21% of small generalist frugivores were observed feeding for periods greater than five minutes. Most observations (57%) of small generalist frugivores were for feeding periods of between one and five minutes and 21% were for periods of less than one minute (Figure 4).

Only 41 respondents provided details on the number of fruit consumed during a feeding bout (data not tested for statistical significance). Forty three percent of large generalist frugivores and 78% of seed destroyers removed more than five fruits during a feeding bout. Conversely, small generalist frugivores removed more than five fruits only 36% of the time, between three and five fruits 45% of the time, and less than three fruits 18% of the time.

There was no difference between bird functional groups with regard to the location within the fruiting plant where feeding was observed ($\chi^2 = 3.19$, df = 3, n.s.). All bird groups were more often observed in central or top parts of plants. Approximately 90% of birds were observed consuming fruit at the source, with only 2% removing fruit and flying to another plant or perch before consumption.

Forty four respondents provided details on flight distance after a feeding bout (data not tested for significance). Eighty three percent of observations of small generalist frugivores ($n = 10$) were for flight distances of less than 50 m from the source plant. For large generalist frugivores, equal proportions of observations were for flight distances of less than 50 m and greater than 50 m ($n = 25$). There were seven observations of flight distance for seed destroyers; five of these were for distances less than 50 m.

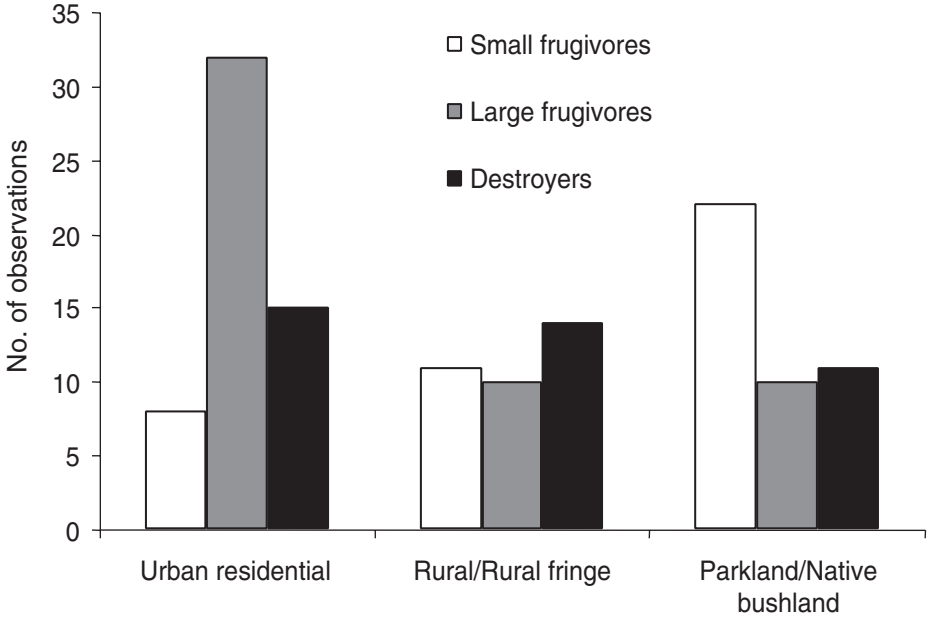

Figure 3. Observations of frugivory by birds belonging to different dispersal syndromes in relation to habitat type.

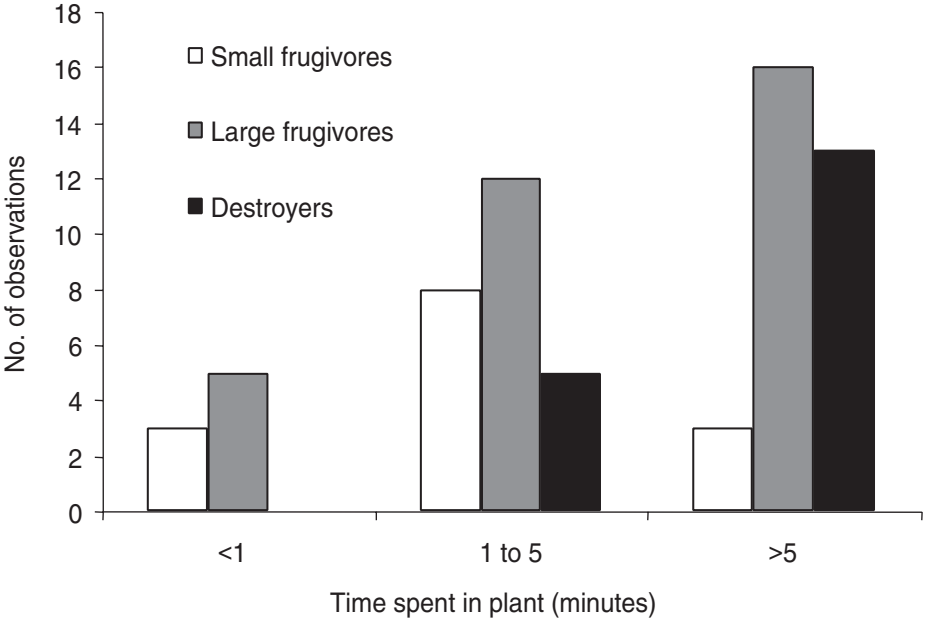

Figure 4. Observations of the amount of time spent feeding in fruiting weed species by frugivorous birds belonging to different dispersal syndromes.

The role of fruit size

There was a significant difference between bird functional groups with regard to the size of fruit consumed ($\chi^2 = 12.67$, df = 3, P <0.05). Ten small generalist frugivores were observed feeding on 18 weed species with a fruit diameter range of 2.5–11.4 mm. Fourteen large generalist frugivores were observed feeding on 22 weed species with a fruit diameter range of 2.5–50 mm. Eleven seed destroyers were observed feeding on 12 weed species with a fruit diameter range of 4–25 mm. Three fruit specialists were observed feeding on two weed species, 7 mm and 9 mm diameter. Overall, small fruit (<15 mm diameter) were utilized by a larger number of frugivorous bird species (Figure 5).

There were no differences between bird functional groups with regard to fruit handling techniques ($\chi^2 = 0.87$, df = 2, n.s.). Across all bird groups 'gulp' was the most common handling technique (89% of records). Large generalist frugivores accounted for 60% of gulping observations, compared to 22% for seed destroyers and

18% for small generalist frugivores. No small generalist frugivores were recorded gulping fruit that was greater than 12.5 mm in diameter. Silvereyes (gape width 6 mm), were reduced to pecking the flesh of larger fruits such as *S. mauritianum* (diameter 11.4 mm).

Weed invasiveness and frugivory

Weed invasiveness was moderately correlated to the number of frugivorous birds observed feeding on each weed species ($R^2 = 0.31$, $F = 7.47$, $df = 1, 17$, $P = 0.014$) (Figure 6). It should be noted that three weed species were potentially over-represented in the analysis. *Solanum mauritianum* and *O. serrulata* were both in fruit during the period of the survey, and *C. camphora* data were obtained from an independent, intensive study on that species. If all three weeds are treated as outliers and removed from the analysis, the invasiveness of the remaining 16 weed species was more strongly correlated to the number of frugivorous birds observed feeding on each weed species ($R^2 = 0.39$, $F = 9.11$, $df = 1, 14$, $P = 0.009$).

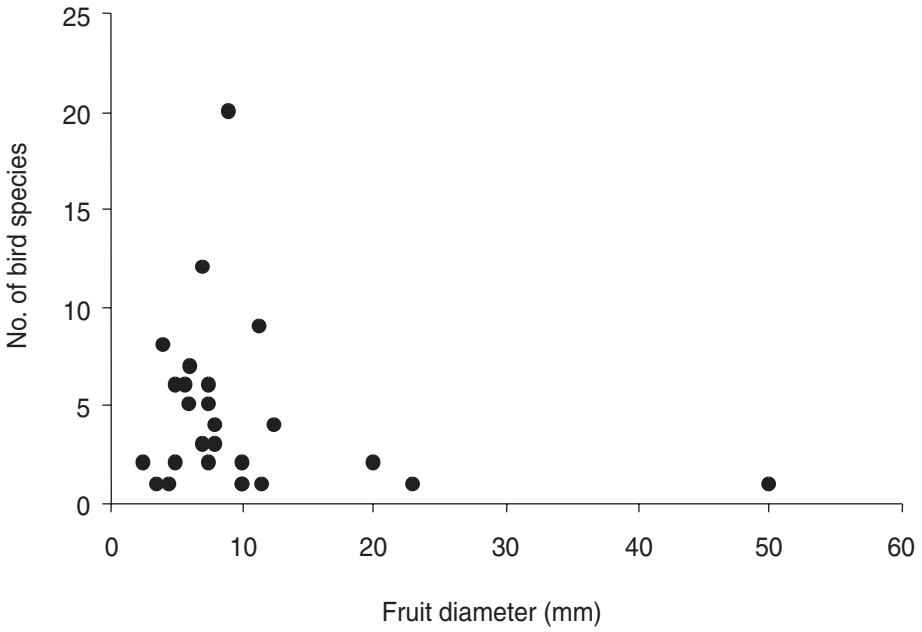

Figure 5. Observations of frugivory by birds in relation to weed fruit size.

Discussion

The results of the questionnaire support the theory of generalized relationships between frugivorous birds and introduced fruit-bearing plants. Queensland Birders indicated that generalist frugivores, such as the figbird, silvereye, olive-backed oriole, Lewin's honeyeater, pied currawong and regent bowerbird, were the most frequently observed birds, feeding on between five and 15 weed species. Fruit of one weed species could also be consumed by up to 20 different species of frugivorous bird. Similar observations of generalist frugivory have also been reported by Snow (1971) and Green (1993). Snow (1971) reported that a single fruiting plant species may be consumed by up to between 20 and 51 different bird species, especially in the tropics. Green's (1993) study of avian seed dispersal in sub-tropical rainforest in Queensland, recorded a total of 34 bird species feeding on the fruits of 23 plants species. Green also noted that for most plant species, the rate of visitation by potential dispersers was far higher than the rate of visitation by fruit thieves or seed predators.

Relationships between native frugivorous birds and introduced plants that favour seed dispersal are likely to be largely coincidental and associated with a generalized dispersal system. Introduced plants with fruits that are utilized by generalized dispersal syndromes are also likely to be more invasive than those relying on specialist dispersal agents, as suggested by Renne *et al.* (2002), following their studies on dispersal of Chinese tallow (*Sapium sebiferum* (L.) Roxb.). Similarly, plant species that are not reliant on specific vectors

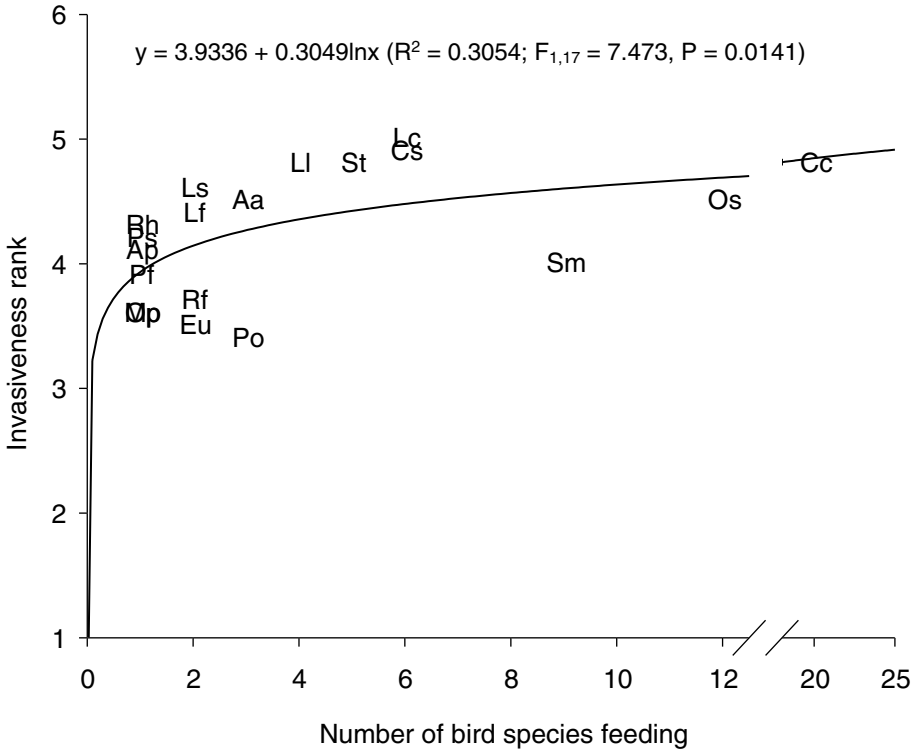

Figure 6. Weed invasiveness relative to the number of available bird dispersers. Letters refer to genus and species (Aa = *Asparagus aethiopicus* **L., Ap =** *Asparagus plumosus* **Baker, Cs =** *Celtis sinensis*, **Cc =** *Cinnamomum camphora*, **Eu =** *Eugenia uniflora* **L., Lc =** *Lantana camara*, **Ll =** *Ligustrum lucidum* **Aiton, Ls =** *Ligustrum sinense* **Lour., Lf =** *Lycium ferocissimum* **Miers, Mp =** *Murraya paniculata* **L., Os =** *Ochna serrulata*, **Op =** *Opuntia stricta*, **Pf =** *Passiflora foetida* **L., Ps =** *Passiflora suberosa*, **Po =** *Phytolacca octandra* **L., Rh =** *Rivina humilis* **L., Rf =** *Rubus fruticosus*, **St =** *Schinus terebinthifolius*, **Sm =** *Solanum mauritianum*. **Invasiveness scores from Batianoff and Butler (2002). (Note: Overlapping letters denote Op and Mp, which share the same point).**

have a greater chance of being effectively dispersed in a new environment (Noble 1989).

Identifying plant functional groups

The results presented here also show that small fruit (<15 mm in diameter) were utilized by a larger number of frugivorous bird species and that no small generalist frugivores were recorded gulping fruit that was greater than 12.5 mm in diameter. Both questionnaire results and independent field observations also showed that regent bowerbirds shift from gulping small weed fruits such as *O. serrulata* (diameter 5–7 mm), *Passiflora suberosa* L. (8–12 mm) and *L. camara* L. (diameter 5–6 mm), to mashing larger fruits such as *S. mauritianum* (diameter 11–14 mm) and *Passiflora foetida* L. (>15 mm diameter), which approach or exceed the bird's gape width (diameter 14 mm) (Stansbury, Vivian-Smith and Porter, unpublished data). This does not seem to be the case for some fruit specialists, such as rose-crowned fruit doves (*Ptilinopus regina* Swainson), which have extendable muscular gapes (diameter 9 mm) and are able to gulp fruit (such as those of *S. mauritianum*) that exceed gape width.

Our results support those of previous studies examining fleshy fruit traits and choices by birds and mammals, which point to fruit size as the most important trait determining fruit choice (Debussche and Isenmann 1989, Green 1993). Green (1993) noted that large-fruited plant species (>15 mm diameter) with large seeds, were visited less frequently and by fewer disperser species, compared to plants with either small fruits with one or few seeds or very soft fruits with many tiny seeds. Similarly, Noma and Yumoto (1997) showed that small-gaped birds consumed only fruits <6 mm in diameter, whereas large gaped birds consumed a wide range of fruits, including smaller fruits. Rey *et al.* (1997) observed that song thrushes (*Turdus philomelos* Brehm), blackcaps (*Sylvia atricapilla* L.), European robins (*Erithacus rubecula* L.) and Sardinian warblers (*Sylvia melanocephala* Gmelin) shifted from gulping to pecking as fruit size in European olives (*Olea europaea* L.) increased.

Identifying dispersal syndromes

The results of the questionnaire show distinct differences in the foraging habits of different groups of frugivorous birds. Small generalist frugivores were more often observed feeding solo or in pairs. They were limited to gulping smaller fruit and spent significantly shorter periods feeding within fruiting plants. They consumed fewer fruit during a feeding bout, mostly in the upper parts of plants. After a feeding bout, they flew shorter distances (<50 m) to a nearby plant before perching.

Large generalist frugivores were also more often seen feeding solo or in pairs and spent significantly longer periods within fruiting plants. Feeding for longer periods within fruiting plants can increase the likelihood that seeds will be defecated beneath the parent plant, particularly when gut passage times are short. This frugivore group primarily gulped larger quantities of fruit of varying sizes compared to other groups of birds, feeding from within both central and top parts of plants. After a feeding bout they generally flew greater distances (>100 m) before perching, suggesting both the mean and modal dispersal distances are greater than those generated by small generalist frugivores.

Seed destroyers differed significantly from generalist frugivores in observed flock size and were more often observed feeding in flocks of three or more individuals. Seed destroyers were also observed to spend significantly longer time feeding within fruiting plants, compared to small generalist frugivores. Despite limited data on patterns of movement after a feeding bout, observations indicate that movements are often less than 100 m, suggesting that resultant seed shadows (assuming that not all seeds are destroyed) may be concentrated around preferred fruiting plants. Green (1993) made similar observations of differences in frugivore behaviour, noting that most birds did not stay long in the plant after consuming fruit, but that non-passerines (usually seed predators or thieves), stayed significantly longer than passerines. Rate of visitation was also significantly greater for passerines.

Weed seed dispersal is likely to be dependent on fruit handling techniques, foraging habits and territorial or migratory movements of different groups of frugivorous birds; such factors have been shown to play an important role in the final distribution of a plant species (French 1990, Courtney and Sallabanks 1992). Smaller fruits are usually consumed by a greater range of frugivorous birds which produce seed shadows following a continuous leptokurtic distribution from the seed source (mode near the parent plant), along with localized increases under perches (Howe and Smallwood 1982, Murray 1986, Howe 1989). Larger sized fruit are usually consumed by larger frugivorous birds which produce seed shadows clumped under the roosting place and can be located both near to and far away from the seed source (Hoppes 1988, Debussche and Lepart 1992, Debussche and Isenmann 1994). Both the mean and modal distance of the seed shadow from the parent plant may be broadly determined by the dispersal syndrome (Willson 1993), although considerable variation in both individuals and species is reported (see Willson and Traveset 2000). Factors such as the number of dispersers, their social behaviour, fruit handling techniques, gut passage rates, movement distances, and landscape patchiness can all interact to determine the scale and shape of the seed shadow (see Willson and Traveset 2000, e.g. Westcott and Graham 2000).

Future research directions

The analysis of fruit traits presented here has primarily focused on fruit size as a determinant in fruit choice by different groups of frugivorous birds. However, there are likely to be additional fruit traits that determine fruit choice, such as the type of fruit displays, fruit phenology or fruit chemistry (e.g. nutritional value and presence of secondary metabolites). As an example, future studies could investigate whether display characteristics enhance the attractiveness of a weed fruit crop to frugivorous birds. Display characteristics worthy of investigation could include bi-coloured displays (Willson and Melampy 1983, Janson 1987) (e.g., *O. serrulata* and *A. asparagoides*); pre-ripe 'fruit flags' (Stiles 1982, Facelli 1993); and intensive or synchronous fruit displays (Knight 1986a, Stansbury and Scott in preparation). Display traits may increase fruit removal rates and successful seed dispersal, contributing to the likelihood of an introduced plant becoming invasive (Knight 1986b).

Seed treatment studies

While this study has identified which groups of frugivorous birds are feeding on and potentially spreading seed of introduced plants and invasive weeds, it has not provided information on gut passage effects of identified frugivorous birds and how these may affect dispersal and recruitment. Gut passage rates have been identified as a key factor influencing the shape of the seed shadow (Westcott and Graham 2000). The relationship between seed size, gut passage rate and dispersal distance for different fruit syndromes is worthy of further investigation. For example, large seeds take up more room in the gut and require a longer time to be digested. Hence, they are usually regurgitated or defecated soon after being swallowed (Wheelwright and Orians 1982). Rapid gut passage can prevent stomach acids from adversely affecting seeds of some plants but do not promote distant dispersal. Small seeds are usually passed through the gut, taking some time before defecation. Longer gut retention periods can increase seed scarification, potentially increasing germination rates of some plant species (Panetta and McKee 1999, Traveset and Verdú 2001). Valuable progress towards a better understanding of bird-dispersed weeds will be made from future research, that: 1) determines the effects (negative or positive) of gut passage on weed seed viability and germinability, and 2) quantifies gut

passage times for fruit and seed consumed by different groups of frugivorous birds.

Large scale patterns of weed spread

Foraging habits and seed shadows generated by different groups of frugivorous birds are likely to vary considerably according to landscape patterns and structure (With 2002). For example, disturbed habitats such as forest gaps and edges are recognized as favoured feeding sites for many bird species (Malmborg and Willson 1988, Brothers and Spingam 1992). Such habitats are therefore likely to receive disproportionately larger amounts of weed seed through directed dispersal (McDonnell and Stiles 1983, Howe 1989, Wenny 2001, With 2002). This is exemplified by the spread of *P. undulatum* beyond its native range in south-east Australia, where it invades bushland edges in urban areas (Rose 1997) and by *S. mauritianum* which is commonly associated with roadside reserves, forest gaps and habitat edges in SEQ (Stansbury personal observation).

Similarly, habitat fragmentation may assist in the containment of weeds that are spread vegetatively or dispersed by birds with very limited foraging ranges. Conversely, for weeds dispersed by birds with larger foraging ranges, habitat fragmentation may result in an increase in weed invasion rates. Here, habitat fragments potentially act as stepping stones for frugivorous birds and associated weed species (Date *et al.* 1991, Stansbury 1996, With 2002), allowing them to forage further than they otherwise would. These forms of directed dispersal may be much more common than the literature suggests and have possibly been overlooked owing to a lack of detailed data on seed shadows generated by particular bird species (Wenny 2001). In order to predict the effects of landscape patterns and processes on the spread of bird-dispersed weeds it is crucial that future studies aim to quantify how foraging habits of birds within various functional groups differ under different landscape conditions. This could be achieved through the use of radio-tracking devices attached to frugivorous birds belonging to different functional groups or measured using seed traps placed under natural or imitation perches at varying distances from a seed source. The bird movement data (including both foraging and post-foraging movement patterns) could be combined with data on gut passage rates for different groups of avian frugivores, and types and sizes of weed seeds, to model seed shadows generated by different dispersal syndromes (Westcott and Graham 2000, Westcott and Dennis 2003).

Predicting plant invasiveness

It is clear from the results presented in this study that plant invasiveness is correlated to the number of available dispersal agents. It is also recognized that plant species that are not reliant on specific vector species have a greater chance of retaining their dispersal ability in a new environment (Noble 1989), and that early adoption of fruit of introduced plants by native frugivorous birds may play a very important role with respect to weed invasion success. Future efforts to assess the risk of fruit-bearing introduced plants becoming invasive weeds should consider the number of dispersal vectors in the plant's native range as a predictor of potential for adoption by frugivores in the new environment.

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Appendix 1. Weed frugivory matrix depicting 38 bird species (vertical axis) observed feeding on the fruit of 28 weed species (horizontal axis). Birds have been categorized according to four functional groups based on gape width, feeding behaviour and biology: Small generalist frugivores, Large generalist frugivores, Seed destroyers and Fruit specialists. Weeds have been listed based on fruit size: large-fruited species (left), small-fruited species (right). Row totals show the number of weed species fed on by each bird species and the total number of observations for each bird species. Column totals show the number of bird species observed feeding on each weed fruit and the total number of frugivory observations for each weed species.

		Fruit Size (mm)	50.00	*	23.00	20.00	11.42	12.50	11.50	10.00	10.00	10.00	9.00	8.00	8.00	7.50	7.50	7.50	7.06	7.00	6.19	6.00	5.75	*	5.00	5.00	4.50	4.00	3.59	2.50		
		Weed species	*Opuntia stricta* (common prickly pear)	*Spathodea campanulata* (African tulip tree)	*Passiflora foetida* (stinking passion flower)	*Eugenia uniflora* (Brazilian cherry)	*Solanum mauritianum* (wild tobacco)	*Capsicum frutescens* (birds eye chillie)	*Passiflora suberosa* (cork passionflower)	*Murraya paniculata* cv. *exotica* (murraya)	*Lycium ferocissimum* (African boxthorn)	*Pittosporum venulosum*	*Cinnamomum camphora* (camphor laurel)	*Phytolacca octandra* (inkweed)	*Ligustrum lucidum* (broad leaf privet)	*Pyracantha angustifolia* (firethorn)	*Celtis sinensis* (Chinese celtis)	*Cotoneaster glaucophyllus* (cotoneaster)	*Ochna serrulata* (ochna)	*Asparagus aethiopicus* (basket asparagus)	*Solanum americanum* (glossy nightshade)	*Schinus terebinthifolius* (broad leaf pepper)	*Lantana camara* var. *camara* (lantana)	*Solanum nigrum* (blackberry nightshade)	*Schinus molle* (pepperina)	*Ligustrum sinense* (small leaf privet)	*Asparagus plumosus* (asparagus fern)	*Schefflera actinophylla* (umbrella tree)	*Rivina humilis* (baby pepper)	*Rubus fruticosus* (blackberry)	No. of weed sp. eaten by each bird spp.	No. of observations
Bird group	Gape width	Bird sp.																														
Small	0.6	Silvereye					3						1	2		1	1		2		1	3	4	1	1				1	12	21
generalist	0.69	Mistletoebird											1	1					1		1	1								5	5
frugivores	0.91	Varied triller						1															1							2	2
	1.03	Noisy miner																	1									3		2	4
	*	Indian mynah						1																						1	1
	*	Metallic starling						1																						1	1
	1.05	Lewin's honeyeater											2						2	1	1		4				1		1	7	12
	*	Spiny-cheeked honeyeater																					4		1					2	5
	*	Striped honeyeater																							1					1	1
	1.15	Noisy friarbird													1															1	1
Large	1.39	Regent bowerbird					1						1								2		2					1		5	7
generalist	1.53	Grey butcherbird					1																							1	1
frugivores	1.58	Olive-backed oriole			1								2				2		2	2		1						1		7	11
	*	Yellow oriole						1																						1	1
	1.74	Black-faced cuckoo-shrike											3																	1	3
	1.76	Pied butcherbird											1						1											2	2
	1.78	Figbird				2		1		3		1	6		2		4	1	3			3	1		1	1		6		1	15	36
	1.85	Satin bower bird					3						2		2										1			1		5	9
	1.95	Green catbird					1						1								1							1		4	4
	*	Spotted catbird					2																							1	2
	*	Common koel				2							1						1											3	4
	1.95	Torresian crow	1								1		1				1		2											5	6
	2.01	Pied currawong									1		2			1	1		2						1	2				7	10
	*	Magpie																	3											1	3
Seed	1.03	Brown cuckoo-dove					9							1							1									3	11
destroyers	1.18	White-headed pigeon											6				1				1									3	8
or thieves	1.4	Top knot pigeon											4																	1	4
	1.13	Scaly-breasted lorikeet											1															1		2	2
	1.21	Pale-headed rosella					1		1									1	2											4	5
	*	Eastern rosella																1												1	1
	1.55	Galah		2																										1	2
	1.22	Rainbow lorikeet		1																		3						9		2	13
	1.44	Crimson rosella																1												1	1
	2.29	Sulphur crested cockatoo		1																										1	1
	1.74	Australian king parrot					6						1		2			1												4	10
Fruit	0.85	Emerald ground dove											1																	1	1
specialists	0.92	Rose-crowned fruit-dove											1							2										2	3
	1.52	Wompoo fruit dove											1																	1	1
No. bird spp. eating each weed sp.			1	1	1	2	9	4	1	1	2	1	20	3	4	2	6	5	12	3	7	5	6	1	6	2	1	8	1	2		
No. of observations			1	4	1	4	27	5	1	3	2	1	39	4	7	2	10	5	22	5	8	11	16	1	6	3	1	23	1	2		

* Gape width or fruit diameter measurements not taken.