

# Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options

Carl R. Gosper, Chris D. Stansbury and Gabrielle Vivian-Smith\*

CRC for Australian Weed Management,  
Alan Fletcher Research Station, Queensland  
Department of Natural Resources and Mines,  
PO Box 36, Sherwood, Queensland 4075,  
Australia

## ABSTRACT

The ecology of seed dispersal by vertebrates has been investigated extensively over recent decades, yet only limited research has been conducted on how suites of invasive plants and frugivorous birds interact. In this review, we examine how plant fruit traits (morphology, colour and display, nutritional quality, accessibility and phenology), avian traits (fruit handling techniques, gut passage time and effect, bird movements and social behaviour and dietary composition) and landscape structure (fruit neighbourhood, habitat loss and fragmentation and perch tree effects) affect frugivory and seed dispersal in invasive plants. This functional approach could be used to develop generic models of seed dispersal distributions for suites of invasive plant species and improve management efficiencies. Four broad research approaches are described that could direct management of bird-dispersed invasive plants at the landscape scale, by manipulating dispersal. First, research is needed to quantify the effect of biological control agents on dispersal, particularly how changes in fruit production and/or quality affect fruit choice by frugivores, dispersal distributions of seed and post-dispersal processes. Second, we explore how seed dispersal could be directed, such as by manipulating perch structures and/or vegetation density to attract frugivorous birds after they have been foraging on invasive plant fruits. Third, the major sources of seed spread could be identified and removed (i.e. targeting core or satellite infestations, particular habitats and creating barrier zones). Fourth, alternative food resources could be provided for frugivores, to replace fruits of invasive plants, and their use quantified.

## Keywords

Biological invasions, exotic species, frugivore, fruit, landscape, mutualism, plant invasions, seed dispersal.

\*Correspondence: Gabrielle Vivian-Smith, CRC for Australian Weed Management, Alan Fletcher Research Station, Queensland Department of Natural Resources and Mines, PO Box 36, Sherwood, Queensland 4075, Australia. Tel.: + 61733750737. Fax: + 61733796815. E-mail: gabrielle.vivian-smith@nrm.qld.gov.au

## INTRODUCTION

Birds are recognized as the main dispersal agent of many invasive plant species (Glyphis *et al.*, 1981; Buchanan, 1989; Dean & Milton, 2000; Stansbury, 2001; Renne *et al.*, 2002) (the definition of invasive plant is as per Richardson *et al.*, 2000a). Despite this, our understanding of how birds contribute to the success of invasive alien plants is limited, leading to ineffective management of invasive plant spread. Invasive plant dispersal by birds can be via generalized mutualistic or non-mutualistic relationships. Mutualistic spread occurs through intentional fruit consumption and subsequent seed dispersal. In this review, we consider bird-dispersed invasive plants within the framework of mutualistic spread of fleshy-fruited plants (the term 'fleshy-fruited' here after includes arillate seeds and seeds with elaiosomes that are attractive to vertebrate dispersers). Non-mutualistic spread occurs through unintentional ingestion, such

as when birds are consuming other foods, or by epizoochory, such as adhesion to feet and feathers (e.g. Vivian-Smith & Stiles, 1994). These methods of dispersal are likely to produce different patterns of seed spread and require quite different management.

Complex dispersal patterns of fleshy-fruited invasive plants should be expected, as studies in systems without invasive plants emphasize a variety of frugivorous species consuming fruits from a single plant species (Snow, 1971; Kitamura *et al.*, 2002). This appears to be the case in several studies to date, where there are many bird-dispersed invasive plants in a particular area, and multiple disperser species with a wide range of estimated dispersal efficiencies (White & Stiles, 1992; Williams & Karl, 1996; Renne *et al.*, 2002; Stansbury & Vivian-Smith, 2003). An understanding of the ecology underlying disperser behaviours and dispersal effectiveness may thus help to determine opportunities and limitations for invasive plant management.

We review the literature on the ecology of bird-dispersed plants, discussing fruit and frugivore traits, and landscape factors, which influence bird behaviour and shape dispersal patterns. These will, in turn, influence the development of improved management strategies for bird-dispersed invasive plants. In conclusion, we identify research opportunities that will assist in invasive plant management.

## Theoretical background

The role of seed dispersal by birds and mammals has been investigated extensively (Snow, 1971; Herrera, 1984; Howe, 1986; Wenny, 2001; Pizo, 2002). A large body of this work focuses on diffuse mutualistic relationships, or 'generalized dispersal systems', between broad groups of plants and dispersers (Howe, 1986; Malmborg & Willson, 1988), and is most relevant to the dispersal ecology of fleshy-fruited invasive plants.

Highly generalized avian seed dispersal systems involve fruits with small seeds that are produced in large quantities and are consumed by a wide range of frugivorous birds (Howe, 1986). Such dispersal systems may rely on chance relationships with common birds where fruit is a component of a varied diet. Consequently, seed shadows (spatial distribution of seeds dispersed from a plant; Nathan & Muller-Landau, 2000) resulting from a generalized system are more difficult to predict than when only one or a few disperser species are involved. Most relationships between frugivorous birds and invasive plants involve a generalized dispersal system (Noble, 1989; Richardson *et al.*, 2000b; Renne *et al.*, 2002), although exceptions exist where plants reliant on one or few biotic dispersal agents become invasive (Setter *et al.*, 2002; Markus & Hall, 2004).

Mutualisms involving bird-mediated seed dispersal facilitate many plant invasions (Richardson *et al.*, 2000b). Birds benefit from this relationship by having a new food source, and the plant may benefit by having its seeds dispersed. Mutualistic seed-dispersal relationships include when native dispersers shift their foraging patterns to use the fruits of an invasive species, mimicking processes occurring in the plant's natural range (numerous examples in Richardson *et al.*, 2000b; Stansbury & Vivian-Smith, 2003). They also occur when a plant species is reunited in the invaded range with species or genera with which it forms partnerships in its native range (Richardson *et al.*, 2000b), for example *Rubus* spp. and blackbirds (*Turdus merula* L.) and foxes (*Vulpes vulpes* L.) in Australia. New mutualisms occur through totally new types of associations between plant and bird species. An example is the accidental spread of seeds of wind-dispersed pines, *Pinus* spp., by seed predated cockatoos, *Calyptrorhynchus* spp., in Australia (Richardson *et al.*, 2000b).

Mutualisms may enhance a plant's invasive potential via increased dispersal effectiveness (Mandon-Dalger *et al.*, 2004). Seeds may be deposited away from the parent or to favourable recruitment microsites (Howe & Smallwood, 1982; Wenny, 2001), or receive favourable seed treatment (Panetta & McKee, 1997; Mandon-Dalger *et al.*, 2004). Moreover, dispersal of native fleshy-fruited plant species occupying the same habitat may be negatively affected as a consequence of competition for dispersal

services from the invasive plant species. Few studies have compared fruit removal rates in co-occurring native and invasive plant species, and these have produced inconsistent results (Sallabanks, 1993; Vila & D'Antonio, 1998; cf. Greenberg *et al.*, 2001). This, combined with difficulties in identifying the reasons for frugivore preferences due to the multiple traits involved and taxonomic considerations, hinders generalizations as to whether invasive fruit are preferred over native fruit.

Invasive plant management may be improved via a better understanding of mutualisms by enabling us to predict: (1) the likelihood of a fleshy-fruited introduced plant being adopted by a frugivorous bird and its potential to become invasive, and (2) dispersal effectiveness, potential dispersal distributions and rates of spread of invasive plants.

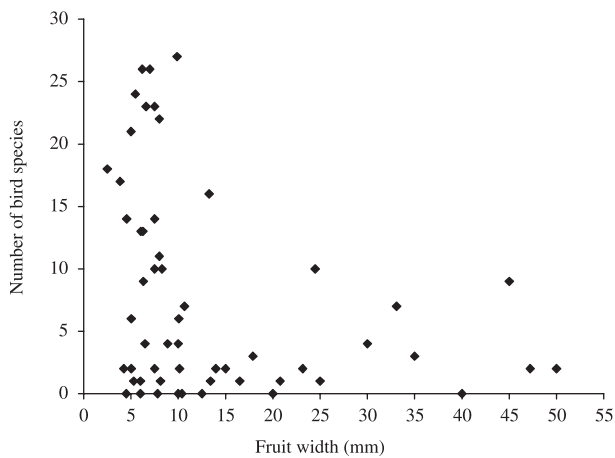
## A functional approach

Research-to-date on bird-dispersed invasive plants does not fully reflect the typical situation of interacting multiple invasive plants, native plants and bird species. Rather, it has largely focused on the individual species level and includes: (1) determining the importance of invasive plants in the diets of birds (Buchanan, 1989; Dean & Milton, 2000; Mandon-Dalger *et al.*, 2004); (2) documenting the dispersal vectors and spread of individual fleshy-fruited invasive plant species (Glyphis *et al.*, 1981; Stansbury, 2001; Renne *et al.*, 2002); and (3) quantifying patterns of invasive plant seed rain (Willson & Crome, 1989; Stansbury, 2001) or plant distribution (Dean & Milton, 2000). Exceptions are the work of Debussche and Isenmann (1990), White and Stiles (1992) and Williams and Karl (1996), who examine use of fruits of invasive and native species by a suite of dispersers.

A multispecies approach to studying the problem of bird-dispersed invasive plants may allow the identification of sets of species that are functionally similar in ways that are relevant to invasive plant management, and improve management approaches. These features may include morphological, behavioural or reproductive traits, population dynamics and responses to environmental conditions (Weiher *et al.*, 1999). In the following section, we review traits of fleshy-fruited plants, avian frugivores and landscape structure that contribute to plant invasions.

## FRUIT TRAITS

Fruit traits that contribute to plant invasions include those that increase the probability or quality of seed dispersal. These traits can operate by attracting birds to fruit sources and encouraging them to consume fruits (or fruit parts), or by inducing frugivores to leave fruit-bearing plants after only a few fruits have been consumed (Wheelwright & Orians, 1982). The key cues used by birds to select fruit appear largely generalized (Howe & Smallwood, 1982; Wheelwright & Orians, 1982; French, 1991), hence the existing extensive literature from natural systems is of relevance when considering frugivory of invasive species. Despite widespread similarities in fruit traits across many bird-dispersed plant taxa, generalizations about what traits underlie bird choices remain elusive (Levey & Martínez del Río, 2001). We



**Figure 1** Invasive plant fruit size relative to the number of frugivorous bird species observed using them in subtropical eastern Australia. Observations of frugivory were compiled from published sources ( $n = 20$ ) and personal observations of the authors (sources available from the authors on request). The invasive plants included were derived from combining lists published by Batianoff and Butler (2002) and the New South Wales North Coast Weeds Advisory Committee (2000). Fruit width data taken from measurements (C. Gosper and G. Vivian-Smith, unpublished data) and from local floras (Stanley & Ross, 1983–89; Harden, 1990–93).

present a highly simplified outline of those considered important below, but encourage readers unfamiliar with the frugivory literature to read more comprehensive reviews on this topic (e.g. Herrera, 2001; Levey & Martínez del Río, 2001).

Aspects of fruit morphology, such as fruit and seed size, seed load (ratio of indigestible seeds to pulp) and seed geometry, affect choices by birds (Herrera, 1984; Howe, 1989; Murray *et al.*, 1993). Smaller fruits (less than about 15 mm in width) predominate among both indigenous (Silva & Tabarelli, 2000) and invasive (Fig. 1) assemblages of vertebrate-dispersed plants and are accessible to a larger variety of fruit-eating birds (Green, 1993; Kitamura *et al.*, 2002). Plants with large fruit (excluding those having many tiny seeds) have few bird dispersers in both native (Green, 1993; Rey *et al.*, 1997) and invasive (Fig. 1) assemblages of bird-dispersed plants.

Birds have excellent colour vision, and visual signals influence fruit choice (Siitari *et al.*, 1999; Schmidt *et al.*, 2004). Advanced visual cues have been noted for invasive plant species in South Africa (Knight, 1986), and in genera of bird-dispersed invasive plants that produce mimetic fruits (e.g. *Abrus* spp. Galetti, 2002); such cues could increase fruit removal rates and seed dispersal of invasive plant species.

The nutritional quality of fruit pulp is relative to the digestive abilities of frugivores, and may play an important role in fruit choice (Martínez del Río & Restrepo, 1993). Nutritional characteristics can also directly affect seed shadows, as secondary metabolites can affect gut passage time and seed deposition density (Wahaj *et al.*, 1998). A better understanding of the role of fruit nutrient content in fruit choice and the complexity of bird digestive systems (Levey & Martínez del Río, 2001), along with

the accurate measurement of nutrient parameters (e.g. proteins; Izhaki *et al.*, 2002), may improve the identification of potentially invasive species and seed dispersal distributions. The nutritional quality of invasive plant fruits is currently poorly documented, especially in comparison with co-occurring native plants (but see White & Stiles, 1992; Vila & D'Antonio, 1998; Gosper, 2004a).

Fruit crop size, fruit density, fruit accessibility and plant structure are additional traits that affect fruit choices by birds (Denslow, 1986; Sargent, 1990; Stanley & Lill, 2001), and are likely to vary between invasive and native plants. In several studies, invasive plants have produced more fruits than their native congener, and this may have contributed to their greater dispersal (Sallabanks, 1993; Vila & D'Antonio, 1998). In South Africa, invasive plants also tended to have larger and more conspicuous fruit displays than native species (Knight, 1986).

Timing of fruit production and the length of time that fruit are available may influence the fruit choices, abundance and behaviour of dispersers (Snow, 1971; Burns, 2002). Invasive plant fruit production alters local patterns of fruit availability (White & Stiles, 1992; Williams & Karl, 1996; Gosper, 2004a), and fleshy-fruited invasive plants may have distinct phenological patterns that make them attractive to specific groups of frugivores. Those species that fruit when native fruit production is limited may be more readily consumed by frugivores, contributing to their more rapid spread. Changes in fruit availability with increases in invasive and cultivated plants may have resulted in recent changes in the migratory behaviour of blackcaps (*Sylvia atricapilla* L.) (Debussche & Isenmann, 1990). Blackcaps also shifted from native to introduced fruit from early spring to summer, as native fruit became scarcer. However, European robins (*Erithacus rubecula* L.), which are less dependent on fruit, did not (Debussche & Isenmann, 1990). These findings indicate that the effects of phenology on the adoption of fleshy-fruited invasive plants may vary with both habitat (availability and phenology of native fruits) and the characteristics of dispersers.

## FRUGIVORE TRAITS

Frugivore traits that contribute to plant invasions are those that determine the capacity of birds to disperse seeds and the seed shadows they generate. These include fruit handling techniques, gut passage rates and effects, movements and dietary composition. Some of these traits also vary when the same bird species feeds on different fruits.

The methods that birds use to handle fruits have substantial implications for seed dispersal and plant invasions. Frugivores can be categorized as seed gulpers, seed discarders (after consuming pulp) or seed predators. The fruit-handling method used by a particular bird species and its efficiency can vary with fruit and seed size (Avery *et al.*, 1993; Rey *et al.*, 1997). Seed gulpers swallow whole fruits, or fruit parts containing seeds, and defecate or regurgitate viable seeds after holding the seeds in their gut for a period. Seed discarders take part or all of the fruits' attractant (pulp, aril or elaiosome) without ingesting the seed(s). Seeds are either separated during mandibulation and dropped beneath the parent plant or elsewhere, or are left attached to the parent plant

(Jordano, 1995). Dropped seeds are subsequently available for secondary dispersal (Norconk *et al.*, 1998). Seed predators lethally damage the seed during foraging, either during mandibulation (e.g. many parrots) or during gut passage (e.g. some pigeons, *Columba* spp., and other genera, which have a strong muscular gizzard). Some seeds handled by these species, however, may escape damage (Norconk *et al.*, 1998) and be dispersed.

Both seed treatment within the gut and the time taken for gut passage affect dispersal distance and effectiveness (Murphy *et al.*, 1993). Gut passage time can be affected by fruit traits (such as secondary compounds, nutrient content and seed size, geometry and load), bird diets and digestive strategies (Wahaj *et al.*, 1998; Levey & Martínez del Rio, 2001). Greater gut passage times increase both the potential for long distance dispersal (Levey & Sargent, 1987) and seed scarification by gut acids (Traveset *et al.*, 2001). Among invasive plants, gut passage increases germination rates in broad-leaved pepper (*Schinus terebinthifolius* Raddi) (Panetta & McKee, 1997) and lantana (*Lantana camara* L.) (Mandon-Dalger *et al.*, 2004) compared to whole fruits, but has little effect in *Ochna serrulata* (Hochst.) Walp. (C. Gosper *et al.*, unpublished data).

Seeds voided by birds may be deposited in clumps of various aggregations (with conspecifics or different species) or singly, depending on bird diets, digestive strategies and fruit traits. This may affect subsequent seedling recruitment. For example, seeds of the invasive pond apple (*Annona glabra* L.) had greater probabilities of germination when deposited singly than in clumps by the southern cassowary (*Casuaris casuaris* L.) (D. Westcott *et al.*, unpublished data).

The movements of birds after feeding on fruits (if they transport seeds and deposit them undamaged) have important implications for invasive plant spread. Plants may facilitate directed dispersal (i.e. dispersal to microsites that favour seedling recruitment) by attracting animal vectors with particular behaviours and habitat preferences, which may lead to a predictable pattern of seed spread (Wheelwright & Orians, 1982, e.g. Wenny, 2000). However, other studies have shown that the distribution of seed by dispersers has not always supported maximal plant recruitment (Rey & Alcántara, 2000; Wenny, 2000). Birds that linger in a plant after feeding could be less effective dispersers than species that spend shorter periods at the fruiting plant (Pratt & Stiles, 1983). In south-east Queensland, the amount of time spent in a fruiting invasive plant varied, with smaller seed dispersers spending less time than larger seed dispersers or seed predators/discarders (Stansbury & Vivian-Smith, 2003).

Dietary composition can be used to identify functionally similar frugivores. This could include the proportion of fruit in their diet and their fruit preferences (e.g. carbohydrate- or lipid-rich fruits; Levey & Martínez del Rio, 2001). Such information could be used to predict groups of potential or likely dispersers and associated dispersal patterns of invasive species.

## LANDSCAPE EFFECTS ON SEED DISPERSAL

Landscape processes, through their effects on frugivore community composition and behaviour, are likely to substantially influence

seed deposition patterns of invasive plants. Dispersal processes can also operate over variable scales (Kollman, 2000; Burns, 2004). Most models of invasive plant spread, however, assume a homogeneous environment and do not take into consideration how environmental variation may affect dispersal patterns across the landscape (Higgins & Richardson, 1996; With, 2002).

Fruit neighbourhood may affect dispersal of invasive plant species; it can refer to either the distance between fruits within a plant, or the distance between fruiting plants within a local area. Sargent's (1990) work suggests that for invasive plants with abundant dispersers, fruit removal rates are likely to progressively increase with increasing infestation size. Furthermore, habitats heavily invaded by fleshy-fruited plants are also likely to receive more seeds than less infested habitats. Seed dispersal and invasive plant spread are thus likely to increase as the patches become larger or when the diversity of fleshy-fruited invasive plants increases. Gosper (2004b) found greater rates of removal of invasive bitou bush (*Chrysanthemoides monilifera* (L.) Norlindh) fruit from extensive stands than from areas where it had been largely removed, although the cause of this difference (e.g. changes in fruit density, vegetation structure, etc.) was not identified. These two studies suggest that there could be a critical abundance level of invasive plants (if fleshy fruits in the system are limiting), above which there is an increase in frugivorous bird activity, seed dispersal, and ultimately, further invasion. In contrast, Greenberg *et al.* (2001) did not find an increase in fruit removal with greater neighbourhood fruit density in the invasive Oriental bittersweet (*Celastrus orbiculatus* Thunb.).

Habitat loss and fragmentation can alter the abundance and composition of the frugivorous bird community (Restrepo *et al.*, 1999; Moran *et al.*, 2004) and the rate of consumption of fleshy fruits (Galetti *et al.*, 2003). Impacts on seed dispersal through changes in frugivore populations are unlikely to be uniform across fruit traits (Silva & Tabarelli, 2000; Galetti *et al.*, 2003). Dispersal of early successional species can also be promoted in fragmented landscapes (McClanahan, 1986). These interacting effects of landscape processes and fruit traits may be relevant in plant invasions, but they are not well understood.

In some cases, habitat fragmentation may create movement barriers, helping to contain invasive plants. More extensive spread of the fleshy-fruited shrub Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder) in Ohio was associated with higher forest cover and connectivity (Hutchinson & Vankat, 1998). In other cases, habitat fragmentation may have the opposite effect, resulting in an increase in invasion rates. Rapid adoption of invasive plant fruits by some birds and increased invasive plant spread across the landscape has been attributed to habitat loss and an associated reduction in native fleshy fruit availability (Richardson *et al.*, 2000b). Habitat fragments potentially act as stepping-stones for frugivorous birds as they forage across a landscape (Date *et al.*, 1991; With, 2002), and hence may become foci of invasive plant seed dispersal (the nascent foci concept of Moody & Mack, 1988). Disturbed habitats such as forest gaps and edges have more rapid removal of fruits (Galetti *et al.*, 2003), are favoured feeding sites for many frugivorous birds (Malmborg & Willson, 1988; Brothers & Spingarn, 1992) and are therefore

likely to receive proportionately larger amounts of invasive plant seed (With, 2002). Over time, the proliferation of invasive plants in habitat fragments would allow frugivorous birds to forage over a greater range, increasing the potential for infilling between these outlying fruit sources.

The 'perch tree effect' is the enhancement of seed deposition under perch or roost structures, although seeds are not always deposited in environments favourable for recruitment (Holl, 1998). Increased seed deposition by birds occurs beneath habitual roosts and perches (Wenny, 2001), beneath isolated trees and in windbreaks in pastures (Debussche & Isenmann, 1994; Harvey, 2000), and beneath perches within successional landscapes (McDonnell & Stiles, 1983; McClanahan & Wolfe, 1987). The presence of other microhabitat components (e.g. shrub cover within patches; Jordano & Schupp, 2000) can also strongly influence seed deposition patterns.

Seed deposition below perches is important for the spread of invasive species (Ferguson & Drake, 1999). Bridal creeper (*Asparagus asparagoides* (L.) Druce) is often found under the crown of isolated tuarts (*Eucalyptus gomphocephala* DC.) (Stansbury, 2001), with these isolated trees acting as stepping stones for an important disperser, the silvereye (*Zosterops lateralis* Latham). The under-canopy microhabitat aids *A. asparagoides* survival, growth and fruit production (Stansbury, 1999). Similarly, in South Africa, invasive *Opuntia ficus-indica* (L.) Mill. density was substantially greater under telegraph and transmission poles, which acted as perches for corvid and primate dispersers (Dean & Milton, 2000).

### SEED DISPERSAL PATTERNS: LINKING FRUIT, FRUGIVORE AND LANDSCAPE CHARACTERISTICS

Regardless of the mode of seed dispersal, seeds of terrestrial plants usually fall in a continuous leptokurtic distribution with the mode under or near the parent plant and with a steady decline with distance (Howe & Smallwood, 1982; Howe, 1989). Rare, long-distance dispersal events may be particularly significant for the spread of invasive plants (Myers *et al.*, 2004; Trakhtenbrot *et al.*, 2005). However, capturing these rare events in studies of dispersal patterns is inherently difficult (Cain *et al.*, 2000; Nathan & Muller-Landau, 2000).

Plants with similar fruits might be used by a similar variety of frugivores, and subsequently might have similar distributions of dispersed seed (Pizo, 2002). The linking of fruit and frugivore traits has the potential to allow the estimation of seed shadows for assemblages of invasive plant species with their assemblages of dispersers (Westcott & Dennis, 2003). When several bird species are involved in dispersal, it is possible for seed shadows to be concentrated close to a source plant, but also with clumps further away deposited by different species (Debussche & Isenmann, 1994; Nathan & Muller-Landau, 2000).

For a given fruit type, it could be expected that the mean dispersal distance generated by small, facultative frugivores that ingest seeds would be closer to the source than for large, facultative frugivores. Differences in the initial flight distances between

small and large frugivores after feeding on native (Green, 1993) and invasive (Stansbury & Vivian-Smith, 2003) fruits have been reported. Obligate frugivores are more likely to disperse seeds in a pattern reflecting the distribution of fruit sources (which are often patchy) than for birds that also use other foods. This should result in a more clumped seed shadow of larger spikes (compared to facultative frugivores) at varying distances and with a longer tail. Seed-discarding birds are likely to generate seed shadows with comparatively short tails, as many seeds are dropped directly beneath the parent plant and only occasional fruit are carried away for processing elsewhere. For all these frugivores, small spikes in seed numbers dispersed at varying distances from the source could result from birds spending time at favoured sites, such as other food sources or perch trees.

Few studies have investigated the seed shadows of invasive plants; however, such investigations could provide useful management insights. For example, Setter *et al.* (2002) combined gut passage rates of *Annona glabra* seeds through southern cassowaries with bird movement data. They estimated that these birds might regularly disperse seeds up to 350 m from source plants, and occasionally 1200 m. This has important management implications, as it showed birds could disperse *A. glabra*, which is also dispersed by water, between watersheds. In order to predict the effects of landscape patterns and processes on the spread of bird-dispersed invasive plants, we need to better understand the foraging habits of different groups of frugivorous birds in differently patterned landscapes (With, 2002; Westcott & Dennis, 2003). This would require quantifying the seed shadows generated by various invasive plant–disperser relationships within tracts of native habitat as well as within fragmented landscapes (Westcott & Dennis, 2003).

### FUTURE RESEARCH DIRECTIONS AND MANAGEMENT APPLICATIONS

Seed dispersal by vertebrates and plant invasions deserve substantially more research (Richardson *et al.*, 2000b). We believe a functional approach to this issue could be particularly valuable in directing invasive plant management activities. Our understanding of invasive plant and disperser relationships would benefit from detailed analyses of fruits (chemistry, morphology and phenology), frugivore fruit choice and handling (Pizo, 2002), and gut passage combined with bird movements and/or seed deposition. This would provide greater predictive capability in relation to seed dispersal patterns and invasive plant spread that could then be integrated into management programs. Research in these areas is also likely to enable better prediction of the likelihood of adoption of fruit of new plant introductions by bird dispersers, their invasive potential and management priority. An assessment of an introduced plant's opportunity for dispersal by birds is an important component of the invasive plant screening procedure (Pheloung *et al.*, 1999), as plant invasiveness is correlated with the number of dispersal agents (Stansbury & Vivian-Smith, 2003).

To assist management of existing invasions at the landscape scale, adaptive management and research on bird-dispersed

invasive plants should focus on studies that manipulate plant spread. An appropriate aim for these approaches is to maximize their impact on seed dispersal — reducing it to a minimum. Experimental tests of these concepts would examine both their utility in invasive plant management and our conceptual understanding of invasive plant dispersal. They are in addition to current control options available to land managers. We propose studies that focus on four major themes: reducing fruit production or fruit quality, directing seed deposition, identifying and removing the major sources of seed spread and providing alternative resources for frugivores.

Each of these research opportunities is based on the assumption that invasive plant spread is dispersal limited. This assumption is most likely to be met at the extremities of the invaded range and for new incursions, which is where management intervention is often most effective. Seed dispersal determines the potential for invasive spread, although whether invasive spread is realized depends on post-dispersal processes (Nathan & Muller-Landau, 2000). For most species, the relative importance of dispersal and post-dispersal processes on plant demography are unknown, although in a study within the natural range of olives (*Olea europaea* L.), the importance of post-dispersal processes is illustrated by the final spatial pattern of recruitment being different from the frugivore-generated dispersal pattern (Rey & Alcántara, 2000). Additionally, other means of dispersal, even if rare (e.g. human-mediated or secondary dispersal; Nathan & Muller-Landau, 2000; Trakhtenbrot *et al.*, 2005) will need to be considered in delineating incursions and applying the management approaches described below.

Any management actions that reduce fruit production or affect fruit quality in invasive plants potentially affects seed dispersal, provided that frugivore populations are not satiated at the lower production level. Fewer fruits are available, which may affect both the number of seeds dispersed and the dispersal distribution of those seeds through fruit density effects on frugivore behaviour. Biological control agents for bird-dispersed invasive plants have been introduced, with questionable effectiveness, as a means of reducing fruit production (Hoffmann *et al.*, 1998), fruit quality (Day *et al.*, 2003) or for seed predation (Mays & Kok, 1988). Sublethal herbicide application or pruning is an option for culturally significant plants (Scanlon & The Camphor Laurel Taskforce, 2001). Research is needed to determine: (1) how fruit-infesting biological control agents affect fruit choice, as birds may select either for or against infested fruits (Sallabanks & Courtney, 1992; García *et al.*, 1999); (2) whether the establishment of biological control agents changes the dispersal distribution of seeds; and (3) how fruit-infesting biological control agents affect post-dispersal processes.

The proposition of manipulating dispersal has received support from Wenny (2001), who states: 'Where disperser behaviour can be predicted, dispersal can be manipulated ...'. Wenny (2001) also suggests that directed dispersal may become more common in highly disturbed landscapes and would most benefit plants with a generalized dispersal system. Land managers could use this information to structure weed surveys for targeting satellite outbreaks and eradication, or manipulate landscape structure to

capture seeds. We speculate that it may be possible to use strategically placed perch structures as invasive plant seed sinks in habitats that are unsuitable for seedling recruitment or where recruitment can be managed. For smaller frugivores, provision of dense vegetation may be more appropriate, as this may encourage them to remain in an area while they void any ingested seeds. More research is needed on the structure of such 'seed sinks', at both the patch and the landscape scale, as factors such as patch shape, size, density, composition and landscape connectivity could affect the accumulation of bird-dispersed seeds (Harvey, 2000). Sites for these features might include the boundary of sources of dispersed seeds, such as existing infestations or urban areas. This strategy might reduce the amount of seed penetrating further into a remnant habitat or to other favourable recruitment sites. Additionally, after killing woody invasive plants, is it more beneficial to leave dead plants *in situ* to provide perches, potentially enhancing recruitment of native plant species? Such an approach would be useful only if there are native fruits available (Robinson & Handel, 2000) and would be constrained by the perches also promoting the deposition of invasive plant seeds (Ferguson & Drake, 1999).

Moody and Mack (1988) demonstrated theoretically the importance of controlling isolated populations of invasive plants for reducing their rate of spread. This approach could also effectively be applied to creating dispersal 'barrier zones' (Sharov & Liebhold, 1998) around important habitats by removing those plants within the maximum dispersal distance of the bird(s). The use or enhancement of natural or anthropogenic barriers to bird movement in the landscape may provide opportunities to limit invasive plant spread (Hutchinson & Vankat, 1998). In a model developed as a decision-making tool, Higgins *et al.* (2000) demonstrate that invasive plant management at sites with low densities of juvenile plants was more cost-effective than other scenarios based on plant density and age. Shea *et al.* (2002), however, suggest that for some bird-dispersed invasive plants, it may be the core populations that contribute most to spread, particularly when they attract greater concentrations of dispersers. More rapid removal of fruits can occur in high than low density stands (Gosper, 2004b). Clearly, further work is required to test whether it is best to remove satellite or core populations of bird-dispersed invasive plants and how this might vary with different invasive plant–disperser relationships (Shea *et al.*, 2002). Additionally, fruits may be removed more rapidly in some habitats than others (C. Gosper *et al.*, unpublished data), reflecting differences in frugivore communities. Removing invasive plants from those habitats with the greatest dispersal effectiveness is another strategy for prioritizing management efforts.

Knowledge of the frugivore–invasive plant relationship can also be used to recommend replacement native plants that provide frugivores with appropriate fruit resources. This has been suggested as a management strategy for the invasive tree, Russian olive (*Elaeagnus angustifolia* L.), in the south-western USA (Brock, 1998). Invasive plant removal can affect frugivore abundance (Gosper, 2004b). From both an ecological and a social perspective, a prudent strategy before broad-scale control programs might be to identify and make efforts to provide suitable alternative food

sources for frugivores, as the importance of invasive plant fruit to fauna can be a significant public issue and galvanize opposition to invasive plant control. The rate that frugivores adopt these new resources could then be measured to assess the success of this management approach.

## ACKNOWLEDGEMENTS

We thank Dane Panetta, Tony Grice and David Westcott for advice on earlier drafts. The input of David Richardson, Doug Levey, W.R.J. Dean and three anonymous referees significantly improved the paper. The CRC for Australian Weed Management and the Queensland Department of Natural Resources and Mines provided funding support.

## REFERENCES

- Avery, M.L., Goocher, K.J. & Cone, M.A. (1993) Handling efficiency and berry size preferences of cedar waxwings. *Wilson Bulletin*, **105**, 604–611.
- Batianoff, G.N. & Butler, D.W. (2002) Assessment of invasive naturalised plants in south-east Queensland. *Plant Protection Quarterly*, **17**, 27–34.
- Brock, J.H. (1998) Invasion, ecology and management of *Elaeagnus angustifolia* (Russian olive) in the southwestern United States of America. *Plant invasions: Ecological mechanisms and human responses* (ed. by U. Starfinger, K. Edwards, I. Kowarik and M. Williamson), pp. 123–136. Backhuys Publishers, Leiden.
- Brothers, T.S. & Spingarn, A. (1992) Forest fragmentation and alien plant invasions of Central Indiana old growth forests. *Conservation Biology*, **6**, 91–100.
- Buchanan, R.A. (1989) Pied currawongs (*Strepera graculina*): their diet and role in weed dispersal in suburban Sydney, New South Wales. *Proceedings of the Linnean Society of New South Wales*, **111**, 241–255.
- Burns, K.C. (2002) Seed dispersal facilitation and geographic consistency in bird–fruit abundance patterns. *Global Ecology and Biogeography*, **11**, 253–259.
- Burns, K.C. (2004) Scale and macroecological patterns in seed dispersal mutualisms. *Global Ecology and Biogeography*, **13**, 289–293.
- Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany*, **87**, 1217–1227.
- Date, E.M., Ford, H.A. & Recher, H.F. (1991) Frugivorous pigeons, stepping stones, and weeds in northern New South Wales. *Nature Conservation 2: the role of corridors* (ed. by D.A. Saunders and R.J. Hobbs), pp. 241–245. Surrey Beatty & Sons, Chipping Norton.
- Day, M.D., Wiley, C.J., Playford, J. & Zalucki, M. (2003) *Lantana: Current management status and future prospects*. Australian Centre for International Agricultural Research, Canberra.
- Dean, W.R.J. & Milton, S.J. (2000) Directed dispersal of *Opuntia* species in the Karoo, South Africa: are crows the responsible agents? *Journal of Arid Environments*, **15**, 305–311.
- Debussche, M. & Isenmann, P. (1990) Introduced and cultivated fleshy-fruited plants: consequences of a mutualistic Mediterranean plant–bird system. *Biological invasions in Europe and the Mediterranean basin* (ed. by F. di Castri and M. Debussche), pp. 399–416. Kluwer Academic Publishers, Dordrecht.
- Debussche, M. & Isenmann, P. (1994) Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos*, **69**, 414–426.
- Denslow, J.S. (1986) Fruit removal rates from aggregated and isolated bushes of the red elderberry *Sambucus pubens*. *Canadian Journal of Botany*, **65**, 1229–1235.
- Ferguson, R.N. & Drake, D.R. (1999) Influence of vegetation structure on spatial patterns of seed deposition by birds. *New Zealand Journal of Botany*, **37**, 671–677.
- French, K. (1991) Characteristics and abundance of vertebrate-dispersed fruits in temperate wet sclerophyll forest in south-eastern Australia. *Australian Journal of Ecology*, **16**, 1–13.
- Galetti, M. (2002) Seed dispersal of mimetic fruits: parasitism, mutualism, aposematism or exaptation? *Seed Dispersal and frugivory: ecology, evolution and conservation* (ed. by D.J. Levey, W.R. Silva and M. Galetti), pp. 129–144. CAB International, Wallingford.
- Galetti, M., Alves-Costa, C.P. & Cazetta, E. (2003) Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. *Biological Conservation*, **111**, 269–273.
- García, D., Zamora, R., Gómez, J.M. & Hódar, J.A. (1999) Bird rejection of unhealthy fruits reinforces the mutualisms between juniper and its avian dispersers. *Oikos*, **85**, 536–544.
- Glyphis, J.P., Milton, S.J. & Siegfried, W.R. (1981) Dispersal of *Acacia cyclops* by birds. *Oecologia*, **48**, 138–141.
- Gosper, C.R. (2004a) Fruit characteristics of invasive bitou bush, *Chrysanthemoides monilifera* (Asteraceae), and a comparison with co-occurring native plant species. *Australian Journal of Botany*, **52**, 223–230.
- Gosper, C.R. (2004b) *Consequences of weed invasion and control on plant–bird interactions and bird communities*. PhD Thesis, Department of Biological Sciences, University of Wollongong, Wollongong, Australia. (<http://www.library.uow.edu.au/theses/>).
- Green, R.J. (1993) Avian seed dispersal in and near subtropical rainforests. *Wildlife Research*, **20**, 535–557.
- Greenberg, C.H., Smith, L.M. & Levey, D.J. (2001) Fruit fate, seed germination and growth of an invasive vine — an experimental test of ‘sit and wait’ strategy. *Biological Invasions*, **3**, 363–372.
- Harden, G.J. (ed.) (1990–93) *Flora of New South Wales. Vols 1–4*. New South Wales University Press, Kensington.
- Harvey, C.A. (2000) Windbreaks enhance seed dispersal into agricultural landscapes in Monteverde, Costa Rica. *Ecological Applications*, **10**, 155–173.
- Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs*, **54**, 1–23.
- Herrera, C.M. (2001) Seed dispersal by vertebrates. *Plant–animal interactions: an evolutionary approach* (ed. by C.M. Herrera and O. Pellmyr), pp. 185–208. Blackwell Science, Oxford.

- Higgins, S.I. & Richardson, D.M. (1996) A review of models of alien plant spread. *Ecological Modelling*, **87**, 249–265.
- Higgins, S.I., Richardson, D.M. & Cowling, R.M. (2000) Using a dynamic landscape model for planning the management of alien plant invasions. *Ecological Applications*, **10**, 1833–1848.
- Hoffmann, J.H., Moran, V.C. & Zeller, D.A. (1998) Evaluation of *Cactoblastis cactorum* (Lepidoptera: Phycitidae) as a biological control agent of *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa. *Biological Control*, **12**, 20–24.
- Holl, K.D. (1998) Do perching structures elevate seed rain and seedling establishment in abandoned tropical pasture. *Restoration Ecology*, **6**, 253–261.
- Howe, H.F. (1986) Seed dispersal by fruit-eating birds and mammals. *Seed dispersal* (ed. by D.R. Murray), pp. 123–183. Academic Press, Wollongong.
- Howe, H.F. (1989) Scatter and clump-dispersal and seedling demography hypothesis and implications. *Oecologia*, **79**, 417–426.
- Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–228.
- Hutchinson, T.F. & Vankat, J.L. (1998) Landscape structure and spread of the exotic shrub *Lonicera maackii* (Amur honeysuckle) in southwestern Ohio forests. *American Midland Naturalist*, **139**, 383–390.
- Izhaki, I., Tsahar, E., Paluy, I. & Friedman, J. (2002) Within population variation and interrelationships between morphology, nutritional content, and secondary compounds of *Rhamnus alaternus* fruits. *New Phytologist*, **156**, 217–223.
- Jordano, P. (1995) Spatial and temporal variation in the avian-frugivore assemblage of *Prunus mahaleb*: patterns and consequences. *Oikos*, **71**, 479–491.
- Jordano, P. & Schupp, E.W. (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, **70**, 591–615.
- Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma, N. (2002) Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia*, **133**, 559–572.
- Knight, R.S. (1986) Fruit displays of indigenous and invasive alien plants in the south-western Cape. *South African Journal of Botany*, **52**, 249–255.
- Kollman, J. (2000) Dispersal of fleshy-fruited species: a matter of scale? *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 29–51.
- Levey, D.J. & Martínez del Rio, C. (2001) It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *Auk*, **118**, 819–831.
- Levey, D.J. & Sargent, S. (1987) Seed size and fruit handling techniques of avian frugivores. *American Naturalist*, **129**, 471–485.
- Malmborg, P.K. & Willson, M.F. (1988) Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodlot. *Condor*, **90**, 173–186.
- Mandon-Dalger, I., Clergeau, P., Tassin, J., Rivière, J.N. & Gatti, S. (2004) Relationships between alien plants and an alien bird species on Reunion Island. *Journal of Tropical Ecology*, **20**, 635–642.
- Markus, N. & Hall, L. (2004) Foraging behaviour of the black flying-fox (*Pteropus alecto*) in the urban landscape of Brisbane, Queensland. *Wildlife Research*, **31**, 345–355.
- Martínez del Rio, C. & Restrepo, C. (1993) Ecological and behavioral consequences of digestion in frugivorous animals. *Vegetatio*, **107/108**, 205–216.
- Mays, W.T. & Kok, L.T. (1988) Seed wasp on multiflora rose, *Rosa multiflora*, in Virginia. *Weed Technology*, **2**, 265–268.
- McClanahan, T.R. (1986) The effect of a seed source on primary succession in a forest ecosystem. *Vegetatio*, **65**, 301–309.
- McClanahan, T.R. & Wolfe, R.W. (1987) Dispersal of ornithochorous seeds from forest edges in central Florida. *Vegetatio*, **71**, 107–112.
- McDonnell, M.J. & Stiles, E.W. (1983) The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia*, **56**, 109–116.
- Moody, M.E. & Mack, R.N. (1988) Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology*, **25**, 1009–1021.
- Moran, C., Catterall, C.P., Green, R.J. & Olsen, M.F. (2004) Fate of feathered fruit-eaters in fragmented forests. *Conservation of Australia's forest fauna*, 2nd edn (ed. by D. Lunney), pp. 699–712. Royal Zoological Society of New South Wales, Sydney.
- Murphy, S.R., Reid, N., Yan, Z. & Venables, W.N. (1993) Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers: effects on seedling establishment. *Oecologia*, **93**, 171–176.
- Murray, K.G., Winnett-Murray, K., Cromie, E.A., Minor, M. & Meyers, E. (1993) The influence of seed packaging and fruit color on feeding preferences of American robins. *Vegetatio*, **107/108**, 217–226.
- Myers, J.A., Vellend, M., Gardescu, S. & Marks, P.L. (2004) Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion and migration of plants in eastern North America. *Oecologia*, **139**, 35–44.
- Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.
- New South Wales North Coast Weeds Advisory Committee (2000) North Coast Environmental Weed Survey. (<http://www.fncw.nsw.gov.au/index.html>). Accessed 21 July 2005.
- Noble, I.R. (1989) Attributes of invaders and the invading process: terrestrial and vascular plants. *Biological invasions: a global perspective*, SCOPE 37 (ed. by J.A. Drake, H.A. Mooney, F. di Castri, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 301–310. John Wiley and Sons, Chichester.
- Norconk, M.A., Grafton, B.W. & Conklin-Brittain, N.L. (1998) Seed dispersed by neotropical seed predators. *American Journal of Primatology*, **45**, 103–126.
- Panetta, F.D. & McKee, J. (1997) Recruitment of the invasive ornamental *Schinus terebinthifolius* is dependent upon frugivores. *Australian Journal of Ecology*, **22**, 432–438.
- Pheloung, P.C., Williams, P.A. & Halloy, S.R. (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management*, **57**, 239–251.

- Pizo, M.A. (2002) The seed dispersers and fruit syndromes of Myrtaceae in the Brazilian Atlantic Forest. *Seed dispersal and frugivory: ecology, evolution and conservation* (ed. by D.J. Levey, W.R. Silva and M. Galetti), pp. 129–144. CAB International, Wallingford.
- Pratt, T.K. & Stiles, E.W. (1983) How long fruit-eating birds stay in the plants where they feed — implications for seed dispersal. *American Naturalist*, **122**, 797–805.
- Renne, I.J., Barrow, W.C., Randall, L.A.J. & Bridges, W.C. (2002) Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. *Diversity and Distributions*, **8**, 285–295.
- Restrepo, C., Gomez, N. & Heredia, S. (1999) Anthropogenic edges, treefall gaps, and fruit–frugivore interactions in a neotropical montane forest. *Ecology*, **80**, 668–685.
- Rey, P.J. & Alcántara, J.M. (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*, **88**, 622–633.
- Rey, P.J., Gutiérrez, J.E., Alcántara, J. & Valera, F. (1997) Fruit size in wild olives: implications for avian seed dispersal. *Functional Ecology*, **11**, 611–618.
- Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M. (2000b) Plant invasions — the role of mutualisms. *Biological Reviews of the Cambridge Philosophical Society*, **75**, 65–93.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000a) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.
- Robinson, G.R. & Handel, S.N. (2000) Directing spatial patterns of recruitment during an experimental urban woodland reclamation. *Ecological Applications*, **10**, 174–188.
- Sallabanks, R. (1993) Fruiting plant attractiveness to avian seed dispersers: native vs. invasive *Crataegus* in western Oregon. *Madroño*, **40**, 108–116.
- Sallabanks, R. & Courtney, S.P. (1992) Frugivory, seed predation, and insect–vertebrate interactions. *Annual Review of Entomology*, **37**, 377–400.
- Sargent, S. (1990) Neighbourhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology*, **71**, 1289–1298.
- Scanlon, T. & The Camphor Laurel Taskforce (2001) *Camphor laurel kit*. NSW North Coast Weeds Advisory Committee, Lismore. (<http://www.northcoastweeds.org.au/camphorkit.htm>).
- Schmidt, V., Schaefer, H.M. & Winkler, H. (2004) Conspicuousness, not colour as foraging cue in plant–animal interactions. *Oikos*, **106**, 551–557.
- Setter, M., Bradford, M., Dorney, B., Lynes, B., Mitchell, J., Setter, S. & Westcott, D. (2002) Pond apple — are the endangered cassowary and feral pig helping this weed to invade Queensland's Wet Tropics? *Thirteenth Australian weeds conference papers and proceedings* (ed. by H. Spafford Jacob, J. Dodd and J.H. Moore), pp. 173–176. R.G. and F.J. Richardson, Melbourne.
- Sharov, A.A. & Liebhold, A.M. (1998) Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecological Applications*, **8**, 1170–1179.
- Shea, K., Possingham, H.P., Murdoch, W.W. & Roush, R. (2002) Active adaptive management in insect pest and weed control: intervention with a plan for learning. *Ecological Applications*, **12**, 927–936.
- Siitari, H., Honkavaara, J. & Viitala, J. (1999) Ultraviolet reflection of berries attracts foraging birds. A laboratory study with redwings (*Turdus iliacus*) and bilberries (*Vaccinium myrtillus*). *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **266**, 2125–2129.
- Silva, J.M.C. & Tabarelli, M. (2000) Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature*, **404**, 72–74.
- Snow, D.W. (1971) Evolutionary aspects of fruit-eating by birds. *Ibis*, **113**, 194–202.
- Stanley, M.C. & Lill, A. (2001) Accessibility as a factor influencing frugivory by silvereyes (*Zosterops lateralis*): field comparisons with aviary experiments. *Australian Journal of Zoology*, **49**, 171–182.
- Stanley, T.D. & Ross, E.M. (1983–89) *Flora of south-eastern Queensland. Vols 1–3*. State of Queensland, Department of Primary Industries, Brisbane.
- Stansbury, C.D. (1999) *The invasiveness and biogeographical limits of the environmental weeds bridal creeper Asparagus asparagoides and bridal veil A. declinatus in south-western Australia*. PhD Thesis, Department of Geography, University of Western Australia, Perth.
- Stansbury, C.D. (2001) Dispersal of the environmental weed bridal creeper *Asparagus asparagoides* by silvereyes *Zosterops lateralis* in south-western Australia. *Emu*, **101**, 39–45.
- Stansbury, C.D. & Vivian-Smith, G. (2003) Interactions between frugivorous birds and weeds in Queensland as determined from a survey of birders. *Plant Protection Quarterly*, **18**, 157–165.
- Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173–181.
- Traveset, A., Riera, N. & Mas, R.E. (2001) Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology*, **15**, 669–675.
- Vila, M. & D'Antonio, C.M. (1998) Fruit choice and seed dispersal of invasive vs. non-invasive *Carpobrotus* (Aizoaceae) in coastal California. *Ecology*, **79**, 1053–1060.
- Vivian-Smith, G. & Stiles, E.W. (1994) Dispersal of salt marsh seeds on the feet and feathers of waterfowl. *Wetlands*, **14**, 316–319.
- Wahaj, S.A., Levey, D.J., Sanders, A.K. & Cipollini, M.L. (1998) Control of gut retention time by secondary metabolites in ripe *Solanum* fruits. *Ecology*, **79**, 2309–2319.
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *Functional Ecology*, **10**, 609–620.
- Wenny, D.G. (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs*, **70**, 331–355.

- Wenny, D.G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research*, **3**, 51–74.
- Westcott, D.A. & Dennis, A.J. (2003) The ecology of seed dispersal in rainforests: implications for weed spread and a framework for weed management. *Weeds of rainforests and associated ecosystems* (ed. by A.C. Grice and M.J. Setter), pp. 19–23. Cooperative Research Centre for Tropical Rainforest Ecology and Management, Cairns.
- Wheelwright, N.T. & Orians, G.H. (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints of coevolution. *American Naturalist*, **119**, 402–413.
- White, D.W. & Stiles, E.W. (1992) Bird dispersal of fruits of species introduced into eastern North America. *Canadian Journal of Botany*, **70**, 1689–1696.
- Williams, P.A. & Karl, B.J. (1996) Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand Journal of Ecology*, **20**, 127–145.
- Willson, M.F. & Crome, F.H.J. (1989) Patterns of seed rain at the edge of a tropical Queensland rain forest. *Journal of Tropical Ecology*, **5**, 301–308.
- With, K.A. (2002) The landscape ecology of invasive spread. *Conservation Biology*, **16**, 1192–1203.