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FUNCTIONAL VARIATION AMONG RAINFOREST FRUGIVORES

**Can Functional Traits Predict Ecological Interactions? A Case Study Using Rainforest
Frugivores and Plants.**

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ABSTRACT

In rainforest, the large numbers of species of fleshy-fruited plants and frugivorous animals result in a very large number of potential fruit-frugivore interactions, which are challenging to survey in the field. Yet, knowledge of these relationships is needed to predict consequences of changes in the frugivore assemblage for seed dispersal. In the absence of comprehensive dietary information, it may be possible to delineate between frugivores that disperse different plants using 'functional traits', or morphological and behavioural attributes of frugivores that interact with differences in salient characteristics of plant species. Here we use data on the consumption of 244 Australian rainforest plant species by 38 bird species to test for associations between patterns of frugivory and birds' (1) degree of frugivory; (2) gape width; and (3) seed treatment (seed crushing or seed dispersing). Degree of frugivory and gape width explain 74% of the variation in the sizes of fruits consumed by frugivorous birds. Among birds that consume a substantial dietary proportion of fruit, birds with wider gapes consume larger fruits. In contrast, this relationship was not shown by birds for which fruit is only a minor dietary component. Degree of frugivory and gape width, together with seed treatment also strongly predict the overall taxonomic composition and diversity of plants consumed by bird species. Functional classifications of frugivore species may prove useful in developing a predictive understanding of fruit-frugivore interactions in other rainforest regions where detailed dietary information is not available for most frugivores.

Keywords: Australia; bird; degree of frugivory; diet composition; gape width; seed dispersal

1 IN SPECIES-RICH SYSTEMS, UNDERSTANDING OF ECOLOGICAL INTERACTIONS IS CONSTRAINED BY
2 the high number of potential interactions between species. In an area of tropical or subtropical
3 rainforest for example, fleshy-fruited plants number in the hundreds of species and there are
4 likely to be at least 50 - 100 frugivore species that potentially consume the fruits of these plants
5 (*e.g.*, Corlett 1998, Silva *et al.* 2002, Moran *et al.* 2004a, Dennis & Westcott 2006, 2007). The
6 resultant number of potential fruit-frugivore interactions is very high and, given the added
7 difficulty of collecting this information in the field, logistically problematic. Yet, knowledge of
8 the dietary composition of frugivore species is required in order to predict consequences of
9 changes in the frugivore assemblage for seed dispersal, because the role that a frugivore species
10 plays in the dispersal of seeds from a plant species depends initially upon whether or not it
11 consumes fruits from that plant.

12 In the absence of comprehensive dietary information, it may be possible to delineate
13 between groups of frugivores that disperse different plant taxa using particular characteristics, or
14 ‘functional traits’. Such traits include morphological or behavioural attributes of frugivores that
15 interact with differences in salient characteristics of plant species and affect aspects of the
16 frugivore species’ role in seed dispersal (van der Pijl 1982, Dennis & Westcott 2006).
17 Information regarding the morphology and behaviour of frugivore species is more readily
18 available than detailed dietary information (*e.g.*, Dunning 1993, Corlett 1998). Identification of
19 consistent relationships between these frugivore attributes and their patterns of plant species
20 consumption would enable the development of functional classifications of frugivore species
21 based on these attributes.

22 There is substantial variation among rainforest plant species in the sizes of fruit they
23 produce and among the capacity of frugivore species to handle fruits of different sizes (van der

1 Pijl 1982). Among frugivorous birds, which are an important and diverse component of the
2 rainforest frugivore assemblage, gape width imposes an intractable upper threshold on the size of
3 fruits that birds can swallow whole (Wheelwright 1985, Levey 1987). Consequently, the
4 substantial variation among bird species in their gape widths (Wheelwright 1985, Moran *et al.*
5 2004b) is related to dietary differentiation among frugivorous bird species (Wheelwright 1985,
6 Kitamura *et al.* 2002).

7 Although some authors have considered that differences among frugivore species'
8 capacity to handle larger fruits is the main determinant of variation in the plant species that they
9 consume (van der Pijl 1982, Gautier-Hion *et al.* 1985, Bollen *et al.* 2004), such dietary variation
10 among frugivore species cannot be explained by fruit size alone (Kitamura *et al.* 2002). Dietary
11 variation may also be associated with interspecific differences in the energetic, nutritional or
12 chemical content of fruits, interacting with differences among frugivore species in their capacity
13 to digest plant toxins, lipids and sugars, and in their degree of nutritional dependence on fruit
14 (Izhaki & Safriel 1989, Martínez del Río & Restrepo 1993, Cipollini & Levey 1997, Levey &
15 Martínez del Río 2001). In particular, highly frugivorous species may actively select fruits that
16 have specific energetic or nutritional values in order to obtain a complete diet (Morton 1973,
17 McKey 1975, Bairlein 1996). In contrast, frugivores whose diets include non-fruit items such as
18 animal prey or seeds (*i.e.*, through seed crushing) may obtain substantial amounts of energy,
19 minerals and nutrients from these sources (Izhaki & Safriel 1989) and hence be less selective of
20 particular plant species. In addition to the potential for seed crushing to affect a frugivore
21 species' dietary composition, it also clearly affects its potential to disperse viable seed.

22 Because of the limited availability of dietary information for most frugivore species in
23 most regions, it has not previously been possible to test for consistent associations between

1 frugivore and fruit traits in relation to patterns of consumption of plant species. However, a
2 substantial amount of information on the consumption of fleshy fruited plants by frugivorous
3 birds in subtropical Australia is available and has been partly compiled for each species in the
4 Handbook of Australian, New Zealand and Antarctic Birds (HANZAB) series (Marchant &
5 Higgins 1993, Higgins & Davies 1996, Higgins 1999, Higgins *et al.* 2001), although it has not
6 been synthesised across any regional bird assemblage. In addition, the frugivorous bird
7 assemblage of subtropical Australia is large enough ($n = 38$) that substantial variation in dietary
8 composition among bird species can be evaluated using statistical tests. Furthermore, the
9 frugivorous bird assemblage and floristic composition of rainforest in subtropical Australia bear
10 many affinities with tropical rainforests in northern Australia and Papua New Guinea, and to a
11 more limited extent, in other regions. In any case, the approach used here is predominantly based
12 on traits of plants and frugivores that should be transferable across regions, independently of
13 variation in taxonomic composition.

14 Moran *et al.* (2004b) developed a functional classification of the frugivorous bird species
15 from subtropical Australian rainforests based on the functional attributes of gape width, degree
16 of frugivory and seed treatment. Here, we use a database comprising observations of fruit
17 consumption by these bird species to test the relationships between these functional attributes
18 and bird species' specific patterns of plant consumption. Specifically, we test whether the birds'
19 gape width, degree of frugivory and seed treatment are associated with their patterns of fruit size
20 consumption, the overall plant species composition of their diets, and the frequency of particular
21 plant families in their diets. This work is the first to relate this particular dimension of functional
22 variation among frugivore species (dietary composition) to interspecific differences in easily

measured morphological and behavioural attributes across an entire assemblage of rainforest birds.

METHODS

SPECIFIC PATTERNS OF FRUIT CONSUMPTION BY FRUGIVOROUS BIRDS.— The eastern Australian subtropics contain the continent's second-largest area of rainforest, and some 70% of the region's rainforest plant species are fleshy-fruited (Butler 2003). Detailed descriptions of the flora and of fruit characteristics of subtropical Australian plant species are provided in Williams *et al.* (1984), Floyd (1989) and Cooper and Cooper (1994). Although Australia lacks frugivorous primates and the large, terrestrial mammalian frugivores found in other regions of the world, the average size and structural characteristics of fruits in the tropical rainforests of Australia are broadly similar to those in tropical forests elsewhere (Westcott *et al.*, 2008). Plants from subtropical Australian rainforests have not been included in systematic cross-regional comparisons of fruit traits, but there appear to be fewer very large-fruited species in Australian subtropical rainforests, compared with the Australian tropics (C. Moran, pers. obs.).

We obtained records of the consumption of native plant species by 38 frugivorous bird species (the complete avian frugivore assemblage found in subtropical Australian rainforest landscapes; Moran *et al.* 2004a, Moran 2007) from 151 published sources, together with several unpublished data sets (see Appendices in Moran 2007). Most records were from opportunistic field observation of fruit consumption, although some were from targeted surveys of particular plant or frugivore species. A small number of records had been obtained from the gut contents of frugivorous birds.

Because of the large geographic range of many of the bird species from subtropical Australian rainforests, frugivory records may have been collected from a region extending from

temperate southern Australia (*e.g.*, French 1990) to tropical Papua New Guinea (Frith *et al.* 1976). The data set included records accumulated during a period of more than 140 years, with the earliest account published by Gould (1865). For a given frugivore species, the data potentially included foraging records from multiple years, seasons and geographic locations. Data were potentially biased towards more conspicuous bird and plant species, or taxa that had been the subject of detailed studies, although the large number and temporal scale of sources and records should offset most biases.

We collapsed 3152 observations of frugivory into a binary data matrix containing the presence or absence of each of the 244 native fleshy-fruited plant species in the known diet of each of the 38 frugivorous bird species. We included records for species of tree, shrub, vine and herb that are native to the rainforests of subtropical Australia. We measured the diaspore size (the functional dispersal unit) for each plant species as the shorter axis (typically diameter) of the whole fruit, where it would be necessary to swallow the fruit whole in order to disperse the seed(s). However, in the case of soft fruits with multiple small seeds that can be dispersed after piecemeal consumption (*e.g.* many species in the Solanaceae and Moraceae; Levey 1987), we used the diameter of individual seeds as the diaspore size. All *Ficus* species were considered in this category. Similarly, for dehiscent, arillate fruits such as *Alectryon* spp. (family Sapindaceae), the diameter of an individual seed plus the fleshy aril was used. Diaspore size data were collected from published literature (Williams *et al.* 1984, Floyd 1989, Cooper & Cooper 1994, Hauser & Blok 1998, Butler 2003), supplemented with data from field collections (S. McKenna, C. Moran) and biological web sites. The median value of the range of reported diaspore size values was used in analyses. Records would have been excluded from analyses if the fruit was

1 too large to be swallowed whole by a given bird species and the rind was too thick to enable
2 piecemeal consumption, although there were no instances of this in the data.

3 In order to examine whether each bird species appeared to be consuming the largest fruits
4 that it could handle, we calculated the proportion of plant species consumed that had a diaspore
5 width at least 75% of their gape width (*i.e.*, the fruits were large relative to the gape of the bird).
6 This measure was intended to distinguish between a positive association between gape and fruit
7 size that was generated by the random selection of available fruits that could be handled, rather
8 than more active selection of the largest fruit that could be handled.

9
10 FUNCTIONAL ATTRIBUTES OF BIRD SPECIES.— The 38 bird species were categorised based on
11 three attributes considered to influence their patterns of fruit consumption (Moran *et al.* 2004b).

12 Gape width was measured on ten museum specimens of each bird species and ranged from 6.0
13 mm (*Zosterops lateralis*) to 32.8 mm (*Scythrops novaehollandiae*). For sexually dimorphic
14 species (*e.g.*, *Ptilonorhynchus violaceus*), measurements were taken from five male and five
15 female specimens. Each species' degree of frugivory was classified into one of three categories:
16 11 bird species had a fruit-dominated diet ('major frugivores'), 15 had a diet comprising two or
17 more main food types, one of which was fruit ('mixed-diet frugivores'), and 12 had a diet
18 dominated by food other than fruit, but which occasionally included fruit ('minor frugivores').

19 The relative level of dependence of each bird species on fruit was determined primarily from
20 qualitative descriptions in the literature (Blakers *et al.* 1984, Marchant & Higgins 1993, Higgins
21 & Davies 1996, Higgins 1999, Higgins *et al.* 2001). Each bird species was also categorised as
22 being either a seed-disperser or seed-crusher, based on information contained in these texts about

the destruction of seeds during either feeding (bird species in the families Cacatuidae, Psittacidae) or digestion (certain species in the Columbidae; *Alectura lathami*).

We used bird species' gape width, degree of frugivory and seed treatment behaviour to form three 'seed dispersal potential classes' (high, medium, low; after Moran *et al.*, 2004b). We grouped bird species into one of three gape size categories; large (>15 mm wide; n = 17), medium (10–15 mm; n = 14) and small (<10 mm; n = 7), to reflect species' relative capacities to handle fruits of different sizes, in particular larger fruits which reportedly are at risk of limited dispersal elsewhere (*e.g.*, da Silva and Tabarelli 2000, Corlett 2002, Kitamura *et al.* 2002). Cut-points between categories were based on the distribution of gape widths among bird species, rather than information about diet or fruit size. The 15 mm cut-point for the large gape size category reflects the low proportion of larger-gaped birds in the Australian subtropics: only three species had gapes >20 mm whereas frugivore assemblages in some other regions contain higher numbers of bird species with gapes above this size (*e.g.*, Corlett 2002, Westcott *et al.* 2008). The 'high' seed dispersal potential class comprised major frugivores with large or medium gapes and mixed-diet frugivores with large gapes. The 'medium' seed dispersal potential class comprised major frugivores with small gapes and mixed-diet frugivores with medium or small gapes. All minor frugivores and all seed-crushers were grouped into the 'low' seed dispersal potential class (*i.e.*, there were no seed crushers among the species in the high and medium seed dispersal potential classes).

DATA ANALYSES. — To establish whether a bird species' frugivory level, gape size and seed treatment were independent of one another, we tested pair-wise and three-way interactions using a log linear model in the statistical package SPSS 14.0 (2001). The factors were frugivory level

(three levels, major, mixed and minor), gape width classes (three levels, small (<10 mm), medium (10 – 15 mm) or large (>15 mm)) and seed treatment (two levels, seed-disperser and seed-crusher). The data were the number of bird species (total 38) within each cell of the three-way table of factors.

We used one-way analyses of covariance (ANCOVA) to test the effect of the independent variable frugivory level on the following dependent variables: (1) the average size of diaspores consumed; (2) the proportion of plant species consumed that had diaspores with a width $\geq 75\%$ of the bird species' gape width; and (3) the total number of plant species consumed. Species' gape widths (actual width in mm) were used as the covariate in analyses. The frugivory levels were again major (n=10 with *Scythrops novaehollandiae* excluded from analyses because of its strongly different patterns of diaspore size consumption relative to the size of its gape), mixed-diet (n=15) and minor (n=12). Tests of homogeneity of regression slopes were used to indicate the interaction between frugivory level and gape width. The Eta-squared statistic was used as a measure of the amount of variability in the dependent variables that was explained by frugivory level and gape width.

Using analysis of variance (ANOVA), we tested for differences among seed dispersal potential classes in (1) the number of native plant species and (2) the average size of diaspores potentially dispersed. For these analyses, seed-crushers were assumed to disperse no seeds (and hence the number of plant species potentially dispersed by these frugivores was taken as zero, irrespective of the number of plant species consumed).

We used t-tests to assess differences between major and mixed-diet frugivores (with bird species as replicates) in the number of plant species consumed from families which were represented by at least four species in the data set. Parametric t-tests were used for families with

>15 plant species in the data set (three families), and randomisation-based t-tests (with 1000 iterations) were used for the 18 plant families with 4 – 14 plant species using the Pop-tools add-in in MS Excel (Hood 2003). The randomisation technique iteratively allocated values (*i.e.*, the number of plant species from the given family consumed by each frugivore species) to different positions in the data array to assess the likelihood that recorded values were the result of stochasticity. Using ANOVA, we also tested for differences between the three seed dispersal potential classes in terms of the numbers of species from each of these plant families. Where there was significant effect of seed dispersal potential on the number of plant species consumed, we used Least Significant Difference (LSD) tests to assess pairwise differences.

A classification tree for frugivore species, based on the similarity of plant species in their diets, was generated using the complete linkage algorithm (Manly 1994) and Bray-Curtis similarity metric in PRIMER (Clarke & Warwick 2001). We excluded plant species that had been recorded in the diet of less than three frugivore species, and frugivores that had been recorded consuming less than three plant species, leaving a matrix of 35 bird species and 151 plant species. We also tested the effect of (1) degree of frugivory (major, mixed-diet and minor frugivores); (2) gape width category (large, medium and small); and (3) seed dispersal potential class (high, medium and low) on the plant species composition of frugivore diets using Analysis of Similarity (ANOSIM) in PRIMER.

The relationship between bird species' gape widths (mm) and body mass (g) was tested using Pearson's correlation coefficient in SPSS (2001). Tests were conducted separately for seed dispersers and seed crushers. Body mass data were obtained from Baker *et al.* (1997), except for *Coracina lineata*, which was obtained from Dunning (1993).

RESULTS

An average of 5.2 (S.E. 0.30) frugivorous bird species was recorded consuming each native plant species. Only four of the 244 plant species, all figs, were consumed by at least half of the 38 bird species: *Ficus macrophylla* (consumed by 26 bird species), *F. platypoda* (25), *F. obliqua* (23) and *F. fraseri* (21). None of the plant species in the data set were consumed by all of the 38 bird species.

The functional attributes and patterns of native plant species consumption of frugivorous bird species are shown in Table 1. None of the interactions between bird species' frugivory level, gape width and seed treatment were significant in the loglinear model (likelihood ratio $\chi^2 = 6.38$, $p = 0.90$ for three-way interaction; pair-wise chi-squared tests showed no interaction between gape width and frugivory level ($\chi^2 = 0.38$, $p = 0.98$), frugivory level and seed treatment ($\chi^2 = 0.82$, $p = 0.66$), nor gape width and seed treatment ($\chi^2 = 2.51$, $p = 0.29$). Therefore, relationships between bird species' attributes and their patterns of plant species consumption were tested independently.

EFFECT OF GAPE WIDTH AND FRUGIVORY LEVEL ON THE FRUIT SIZES AND NUMBER OF PLANT

SPECIES CONSUMED. — We excluded *Scythrops novaehollandiae* from analyses of the relationship between diaspore size, gape width and frugivory level because it showed a strongly different pattern from other major frugivore species. Despite its very wide gape (32.8 mm), *S. novaehollandiae* predominantly consumed plants with very small diaspores (average 2 mm).

This was a consequence of the dominance of *Ficus* spp. in its diet (83%; Table 1), with the *Ficus* diaspore being the small seed embedded in soft fruit, which we assumed could be dispersed via piecemeal consumption of the fruit.

ANCOVA (without *S. novaehollandiae*) showed that the average size of diaspores consumed varied significantly among the three frugivory levels. Major and mixed-diet frugivores consumed larger diaspores than minor frugivores (Fig. 1; Table 2). In addition, the average width of diaspores that was consumed by a bird species increased with its gape width at a ratio of approximately 1:2 (e.g., a 2 mm increase in gape width was associated with a 1 mm increase in the average size of diaspores consumed: Table 2), with no significant interaction between gape width and frugivory level. These two factors together explained 74% of the variation in diaspore size consumption (Eta- squared 0.43 and 0.31, respectively).

The consumption of plant species with diaspores that were close to the limit of a bird species' handling capacity was also influenced by frugivory level. A moderate proportion of the plant species consumed by major and mixed-diet frugivores (0.31 and 0.20, respectively) had diaspores that were close to their maximum handling capacity. In contrast, minor frugivores consumed a low dietary proportion (0.04) of plant species with diaspores that were at least 75% the width of their gapes (Fig. 1; Table 2). Together, frugivory level and gape width explained 65% of the variation in consumption of diaspores that were close in size to bird species' handling capacity (Eta- squared 0.39 and 0.26, respectively).

The minimum number of native plant species recorded in a frugivores diet was two (in: *Cacatua roseicapilla*, *Philemon corniculatus* and *Entomyzon cyanotis*, all minor frugivores), compared with a maximum of 128 in the mixed-diet *Meliphaga lewinii* (Table 1). On average, major and mixed-diet frugivores consumed a higher number of plant species than minor frugivores (Table 2; Fig. 1; Eta-squared 0.34). There was a significant relationship between the number of native plant species consumed by a frugivore and its gape width (Table 2), although this relationship was not strong (Eta-squared 0.12). There was large variation in the number of

native plant species consumed by individual major and mixed-diet frugivore species, whereas minor frugivores consistently consumed relatively low numbers of plant species (Fig. 1). The major and mixed-diet frugivore species with low dietary plant species richness tended to consume plants from a narrow range of plant taxa; for example, the major frugivore *Dicaeum hirundinaceum* mostly consumed plant species from the family Loranthaceae and the mixed-diet *Coracina lineata* consumed a high dietary proportion of *Ficus* spp. (70%; Table 1).

FRUGIVORE FUNCTIONAL ATTRIBUTES IN RELATION TO SPECIFIC PATTERNS OF FRUIT

CONSUMPTION. — There were few differences between major and mixed-diet frugivores in the numbers of species consumed from different plant families (Table 3). Major frugivores consumed higher numbers of native plant species from the Lauraceae than mixed-diet species, whereas mixed-diet frugivores consumed a higher number of native plant species from the families Celastraceae and Sapindaceae (Table 3). Note that we excluded three major frugivore species (*Chalcophaps indica*, *Scythrops novaehollandiae* and *Dicaeum hirundinaceum*) and five mixed-diet frugivore species (*Alectura lathami*, *Leucosarcia melanoleuca*, *Platycercus adscitus*, *Coracina lineata* and *Lalage leucomela*) from the analysis because they ate comparatively few plant species (Table 1). We did not compare data for minor frugivores because they consumed low numbers of plant species from most families (Table 1).

The UPGMA classification based on plant species consumption assembled frugivore species into five groups that broadly corresponded with frugivory level. Most major frugivores were classified together in Group 2, most mixed-diet frugivores were in Group 3 and most minor frugivores were in Group 4 (Fig. 2). Group 5 comprised species from all three frugivory levels; both major frugivore species in Group 5 were small-gaped, and the three mixed-diet species were

1 either small-gaped or seed crushers. Group 1 contained two major frugivore species *Ptilinopus*
2 *superbus* (a seed disperser) and *Columba leucomela* (a seed crusher), which had diets that were
3 relatively dissimilar to other major frugivores. ANOSIM showed that the overall plant species
4 composition of frugivore diets varied among frugivory levels (Global $R = 0.23$, $p < 0.001$;
5 pairwise comparisons: major versus mixed-diet frugivores $R = 0.09$, $p = 0.07$; major versus
6 minor frugivores $R = 0.27$, $p = 0.002$; mixed-diet versus minor frugivores $R = 0.34$, $p = 0.001$).
7 Diet composition also varied among gape size categories (Global $R = 0.14$, $p = 0.02$), although
8 the difference was only significant in pairwise comparisons between small and large-gaped
9 frugivores ($R = 0.30$, $p = 0.01$) and small and medium-gaped frugivores ($R = 0.27$, $p = 0.01$; for
10 large versus medium-gaped frugivores $R = -0.01$, $p = 0.53$).

11 Birds that were classified as having high and medium seed dispersal potential were likely
12 to disperse a higher average number of native plant species (56.8 and 46.2, respectively) than
13 birds in the low seed dispersal potential class (1.7; ANOVA $F = 21.8$, $p < 0.0001$). Birds in the
14 high seed dispersal potential class were likely to disperse plants with larger diaspores ($n = 12$;
15 average diaspore size 7.7 mm) than birds in either the medium ($n = 6$; 4.9 mm) or low ($n = 20$;
16 1.4 mm) classes (ANOVA $F = 28.1$, $p < 0.0001$). ANOSIM showed no statistical difference
17 among the three seed dispersal potential classes in terms of their overall dietary composition
18 (Global $R = 0.05$, $p = 0.20$; Fig. 2). However, birds in the low seed dispersal potential class were
19 only likely to disperse relatively low numbers of plant species from all families tested (Table 3).
20 Birds in the high seed dispersal potential class were likely to disperse the highest numbers of
21 plant species from the families Arecaceae, Lauraceae and Sapotaceae. Birds in the high and
22 medium seed dispersal potential classes were likely to disperse high numbers of plants from
23 Elaeocarpaceae, Lamiaceae, Oleaceae and Rubiaceae, whereas birds classed as having medium

seed dispersal potential were likely to disperse highest numbers of plant species from Celastraceae, Euphorbiaceae, Rhamnaceae and Rosaceae (Table 3).

RELATIONSHIP BETWEEN BIRD GAPE WIDTH AND BODY MASS. — There was a strong positive correlation between the gape width and body mass of seed dispersing bird species (Pearson's $R = 0.85$, $p < 0.0001$, $n = 25$). The relationship was not as strong for seed crushing species ($R = 0.55$, $p = 0.05$, $n = 13$), which tended to have a smaller gape width to body mass ratio than dispersers (Fig. 3).

DISCUSSION

GAPE WIDTH AND FRUGIVORY LEVEL AS KEY PREDICTORS OF THE SPECIFIC DIETARY COMPOSITION OF FRUGIVOROUS BIRDS. — Variation among frugivorous bird species of subtropical Australia in their consumption of plant species is strongly related to the birds' gape widths and relative degree of frugivory. This study shows that, although many of the rainforest plant species in subtropical Australia are consumed by multiple frugivorous bird species, there is less overlap among frugivorous bird species in their patterns of plant species consumption than implied in earlier classifications of taxonomic disperser groups (*e.g.*, van der Pijl 1982). Furthermore, these results show that variation in patterns of plant species consumption by frugivores are strongly influenced by deterministic factors, rather than being the result of random variation, as suggested by the null model proposed by Burns (2006). On the other hand, there is greater overlap among groups of frugivores in their patterns of fruit consumption than predicted in early models based on close coevolutionary relationships between plant and frugivore species (*e.g.*, McKey 1975).

There was a strong positive association between a bird species' gape width and the average size of fruits that it consumed. However, this pattern varied between groups of bird

1 species depending on their degree of frugivory. Minor frugivores tended to consume relatively
2 small fruits, even if their gape was wide. In contrast, major and mixed-diet frugivorous bird
3 species consume many fruits that are as large as they can handle, similar to the pattern reported
4 for frugivorous birds in a neotropical rainforest (Wheelwright 1985). Optimal foraging theory
5 suggests that a bird's net energy yield would be higher when large compared with small fruits are
6 consumed because of the need to locate and handle fewer fruits to obtain a given amount of
7 energy (Martin 1985), which may explain why all but the minor frugivores showed a bias
8 towards the consumption of fruits at the upper limit of their handling capacity.

9 In most previous studies which have attempted to relate patterns of fruit size selection to
10 frugivore attributes (*e.g.*, da Silva & Tabarelli 2000, Dennis & Westcott 2006), frugivory level
11 has not been explicitly considered. The results presented here show that the combination of
12 frugivory level and gape width explained 74% of the variation in sizes of fruits consumed by bird
13 species. If frugivory level were not incorporated, predictions based on gape width alone would
14 over-estimate the potential dispersal of large seeds by minor frugivores with large gapes.

15 For most of the frugivorous bird species in subtropical Australia, gape width is strongly
16 positively associated with body mass. Hence, body mass may be useful as a surrogate measure of
17 bird species' relative seed size handling capacities in situations where data on bird species' body
18 mass is more accessible than gape width measurements (*e.g.*, Dunning 1993). Note that body
19 mass overestimates this capacity for seed crushing birds, although this would not affect
20 predictions relating to seed dispersal if seed crushers were treated as having limited potential to
21 disperse viable seed (*e.g.*, Moran *et al.* 2004b, this study).

22 Consistent with the proposal by McKey (1975) that a bird's relative degree of frugivory
23 is likely to be related to substantial variation in dietary composition, the present work shows

1 broad dietary similarity among bird species that were similar in gape width and degree of
2 frugivory. Between functional groups, there was a clear difference in the plant species consumed
3 by minor frugivores and other birds. The dietary composition of major and mixed-diet birds was
4 more similar, although major frugivores tended to consume high number of plant species from
5 the family Lauraceae, whereas mixed-diet frugivores consumed more plants from the
6 Celastraceae and Sapindaceae. Note that while Lauraceae is a family known for the high lipid
7 content of fruit pulp (Stiles 1993), plants in both Celastraceae (Corlett 1996) and Sapindaceae
8 (Snow 1981) also have high lipid content. In subtropical Australia, as in other regions (Fuentes
9 1994), birds other than major frugivores may also consume lipid-rich fruits, contrary to early
10 hypotheses of strict lipid or carbohydrate preferences between specialist and generalist avian
11 frugivores (McKey 1975).

12 Most rainforest vertebrates consume fruit from *Ficus* species, at least occasionally
13 (Shanahan *et al.* 2001). The minor frugivore species in our study tended to consume a low
14 number of plant species overall, and predominantly ate *Ficus* species. There were also certain
15 major and mixed-diet species that consumed high dietary proportions of figs, notably *Scythrops*
16 *novaehollandiae*. This agrees with the observation by Brown and Hopkins (2002) that some non-
17 crushing, highly frugivorous bird species in Papua New Guinea appeared to specialise on figs.
18 Whereas *Ficus* fruits have traditionally been considered a relatively poor source of nutrition,
19 Wendeln *et al.* (2000) showed that certain species of neotropical *Ficus* may provide a
20 nutritionally complete diet for highly frugivorous vertebrates (although it is unknown whether
21 this is the case for any Australian species).

22 In this study, two of the three seed-crushing species that were classed as major frugivores
23 (*Macropygia amboinensis* and *Chalcophaps indica*) had diets that were more similar to those of

1 mixed-diet species than to those of other major frugivore species. If the dietary differences
2 detected between major and mixed-diet frugivores result from the need of the former to select
3 fruits with particular nutritional value, the similarity between these two seed-crushing major
4 frugivores and other mixed-diet species may reflect their ability to derive nutrition from the
5 seeds they ingest, as well as from the fruit pulp (Snow 1981).

6
7 ADDITIONAL BIRD CHARACTERISTICS THAT MAY INFLUENCE PATTERNS OF CONSUMPTION OF PLANT
8 SPECIES. — The major frugivore bird species in this study included the *Ptilinopus* fruit-dove
9 species and *Lopholaimus antarcticus*, which are among the most highly frugivorous birds in the
10 world (Crome 1975). In the present study, these species shared a substantial proportion of plant
11 species with the mixed-diet birds *Ailuroedus crassirostris*, *Sericulus chrysocephalus* and
12 *Ptilonorhynchus violaceus* (all in the bowerbird family Ptilonorhynchidae) and *Strepera*
13 *graculina*. Similar patterns of dietary overlap have been shown for fruit-dove and bowerbird
14 species from these same genera in Papua New Guinea (Pratt & Stiles 1985, Brown & Hopkins
15 2002). This similarity in patterns of plant species consumption between these bird taxa may be
16 related to a substantial increase in the degree of frugivory of the four mixed-diet species during
17 the non-breeding season (Blakers *et al.* 1984, Innis & McEvoy 1992, Frith *et al.* 2004),
18 associated with an increased consumption of plant taxa with the nutritional attributes selected by
19 species that have fruit-dominated diets throughout the year (Bairlein 1996).

20 The dietary similarity between close taxonomic relatives with similar functional traits
21 (*e.g.*, *Ptilinopus magnificus*, *Ptilinopus regina* and *Lopholaimus antarcticus* (family
22 Columbidae); species in the family Ptilonorhynchidae) may also be associated with
23 phylogenetically-derived tolerance of secondary chemical compounds (Bernays & Chapman

1994). It is plausible that fruit chemistry, including secondary compound content, would influence patterns of fruit consumption (Izhaki and Safriel 1989). However, further testing of any such relationships within the study region would require better information on the chemical characteristics of Australian rainforest fruits. Taxonomic relatedness among species may explain some of the additional dietary variation within the groups formed using functional attributes. For example, in the present study, both *Sphecothebes viridis* and *Ptilinopus magnificus* have wide gapes and fruit-dominated diets. In the context of the entire avian frugivore assemblage, these two species have relatively similar dietary composition. However, the plant species in the known diet of *S. viridis* comprise only 44% of those known for *P. magnificus* (Moran *et al.* 2009).

BIRD SPECIES' SEED DISPERSAL POTENTIAL IN RELATION TO THEIR FUNCTIONAL ATTRIBUTES. —
Moran *et al.* (2004b) proposed that frugivorous bird species which have a similar degree of frugivory, gape width and seed treatment would be likely to disperse similar seeds to one another. It was also predicted that seed dispersal roles would vary substantially among species that differ in these attributes, and that species groupings based on combinations of these attributes could therefore be ranked in terms of their seed dispersal potential (Moran *et al.* 2004b). It was expected that, among species that do not crush seeds, a bird's seed dispersal potential would be positively associated with its degree of frugivory and gape width, and would also be associated with higher rates of dispersal, dispersal of many plant species, especially those with large diaspores, and those belonging to certain families (*e.g.*, Lauraceae). The present study shows that such a classification of bird species' seed dispersal potential on the basis of functional attributes does correspond with their likely role in seed dispersal, based on records of the plant species they actually consume. The realised extent of seed dispersal by a given frugivore species

1 is also likely to be influenced by factors such as the number of fruits that it consumes and its
2 patterns of landscape and microhabitat use (Schupp 1993, Dennis & Westcott 2006).

3 The functional classification of frugivorous birds described here identifies a primary
4 dimension of functional variation among frugivorous bird species. Because it is founded on
5 broad principles that should be consistent across taxa and regions, the existence of such a
6 relationship between avian functional attributes and patterns of plant species consumption can be
7 tested wherever sufficient data are available regarding plant-frugivore interactions. Such a
8 classification cannot substitute for detailed, species-specific dietary information. However, the
9 collection of such information is extremely time-consuming, especially in mega-diverse tropical
10 systems, and scientists are frequently asked to inform management decisions in the absence of
11 comprehensive data. This functional approach provides a systematic, general and simple means
12 of identifying strong relationships among plants and frugivores, allowing for comparison across
13 different geographic regions where different animal taxa perform similar functional roles.

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1 Table 1. *The functional attributes and summary of patterns of native plant species consumption of 38 frugivorous bird species in*
 2 *Australian subtropical rainforests.*

Bird order, family ^a	Bird species ^a	Frugivory level	Gape (mm) ^b	Seed treatment ^c	Relative seed dispersal potential ^d	No. plant spp. ^e	Average diaspore size (mm) ^f	Diaspore size range ^g		% of plant species ^h			
								Min.	Max.	No. <10	No. ≥ 10	≥75% gape	<i>Ficus</i> spp.
O. Galliformes													
F.Megapodiidae	<i>Alectura lathami</i>	Mixed	18.3	C	Low	9	9.44	1	27.5	6	3	33	11
O. Columbiformes													
F.Columbidae	<i>Columba leucomela</i>	Major	11.8	C	Low	39	9.29	1	18.5	19	20	59	8
	<i>Macropygia amboinensis</i>	Major	10.1	C	Low	63	5.48	1	12.5	56	7	25	10
	<i>Chalcophaps indica</i>	Major	8.5	C	Low	9	6.39	1	14.5	6	3	44	33
	<i>Geopelia humeralis</i>	Minor	6.6	C	Low	3	2.83	1	4.0	3	0	0	33
	<i>Leucosarcia melanoleuca</i>	Mixed	9.3	C	Low	9	6.65	1	14.0	5	4	44	33
	<i>Ptilinopus magnificus</i>	Major	19.0	D	High	81	10.01	1	27.5	34	47	15	10
	<i>Ptilinopus superbus</i>	Major	12.6	D	High	26	9.08	1	22.5	13	13	54	12
	<i>Ptilinopus regina</i>	Major	11.5	D	High	74	8.75	1	22.5	41	33	49	12
	<i>Lopholaimus antarcticus</i>	Major	17.5	D	High	73	10.25	1	27.5	31	42	23	10
O. Psittaciformes													
F.Cacatuidae	<i>Cacatua roseicapilla</i>	Minor	15.5	C	Low	2	5.00	1	9.0	2	0	0	50
	<i>Cacatua galerita</i>	Minor	22.9	C	Low	11	7.45	1	27.5	9	2	9	10
F.Psittacidae	<i>Trichoglossus haematodus</i>	Minor	12.2	C	Low	12	5.25	1	14.0	10	2	17	33
	<i>Trichoglossus chlorolepidotus</i>	Minor	11.3	C	Low	8	4.00	1	7.5	8	0	0	38
	<i>Alisterus scapularis</i>	Mixed	17.4	C	Low	59	7.82	1	20.0	37	22	8	5
	<i>Platycercus elegans</i>	Mixed	14.4	C	Low	42	7.20	1	27.5	31	11	24	10
	<i>Platycercus adscitus</i>	Mixed	12.1	C	Low	5	5.00	2	8.5	5	0	0	0
O. Cuculiformes													
F.Cuculidae	<i>Eudynamis scolopacea</i>	Major	18.2	D	High	25	7.04	1	20.0	19	6	8	24
	<i>Scythrops novaehollandiae</i>	Major	32.8	D	High	6	2.00	1	7.0	6	0	0	83
O. Passeriformes													
F.Meliphagidae	<i>Anthochaera chrysoptera</i>	Minor	9.9	D	Low	3	3.50	2	6.0	3	0	0	0
	<i>Philemon corniculatus</i>	Minor	11.5	D	Low	2	7.25	6	8.5	2	0	0	0

Bird order, family ^a	Bird species ^a	Frugivory level	Gape (mm) ^b	Seed treatment ^c	Relative seed dispersal potential ^d	No. plant spp. ^e	Average diaspore size (mm) ^f	Diaspore size range ^g		% of plant species ^h			<i>Ficus</i> spp.
								Min.	Max.	No.	No. ≥	≥75% gape	
										<10	10		
F.Campephagidae	<i>Entomyzon cyanotis</i>	Minor	13.1	D	Low	2	1.00	1	1.0	2	0	0	100
	<i>Manorina melanocephala</i>	Minor	10.2	D	Low	7	4.29	1	9.0	7	0	29	43
	<i>Meliphaga lewinii</i>	Mixed	10.5	D	Medium	106	6.65	1	20.0	82	24	32	9
	<i>Coracina novaehollandiae</i>	Minor	17.4	D	Low	10	3.45	1	8.0	10	0	0	50
	<i>Coracina lineata</i>	Mixed	13.5	D	Medium	10	2.05	1	6.5	10	0	0	70
F.Artamidae	<i>Lalage leucomela</i>	Mixed	9.1	D	Medium	10	4.50	1	8.5	10	0	20	30
	<i>Cracticus torquatus</i>	Minor	15.3	D	Low	3	4.83	4	6.0	3	0	0	0
F.Paradisidae	<i>Strepera graculina</i>	Mixed	20.1	D	High	50	8.20	1	27.5	32	18	6	20
	<i>Ptiloris paradiseus</i>	Mixed	16.7	D	High	33	6.57	1	17.5	26	7	9	12
F.Oriolidae	<i>Oriolus sagittatus</i>	Mixed	15.8	D	High	30	5.11	1	12.5	26	4	7	20
	<i>Sphecotheres viridis</i>	Major	17.8	D	High	74	7.11	1	18.5	52	22	7	14
F.Corvidae	<i>Corvus orru</i>	Minor	19.5	D	Low	10	4.15	1	9.0	9	1	0	50
F.Ptilonorhynchidae	<i>Ailuroedus crassirostris</i>	Mixed	19.5	D	High	104	9.08	1	35.0	60	44	9	9
	<i>Sericulus chrysocephalus</i>	Mixed	13.9	D	Medium	108	7.62	1	27.5	73	35	28	9
	<i>Ptilonorhynchus violaceus</i>	Mixed	18.5	D	High	106	8.81	1	35.0	58	48	10	8
F.Dicaeidae	<i>Dicaeum hirundinaceum</i>	Major	6.9	D	Medium	6	4.33	1.5	7.0	6	0	33	0
F.Zosteropidae	<i>Zosterops lateralis</i>	Mixed	6.0	D	Medium	37	4.45	1	9.0	37	0	59	19

1 ^a ‘O’ is order, ‘F’ is family. Taxonomy and nomenclature follow Christidis and Boles (1994).

2 ^b ‘Gape’ is gape width at the junction of the upper and lower mandibles. Measurement incorporates gape distensibility for Ptilinopus species.

3 ^c ‘D’ is seed disperser, ‘C’ is seed crusher.

4 ^d After Moran *et al.* (2004b), indicating the relative potential of bird species to disperse high numbers of plant species, large diaspores and plants from certain families (see text).

6 ^e ‘No. plant spp.’ the total number of native plant species recorded in the diet of each bird species.

7 ^f ‘Average diaspore size’ is the average size (mm) of diaspores (‘fruits’ see text) consumed.

- 1 ^g ‘Diaspore size range’ shows the minimum (‘Min.’) and maximum (‘Max.’) sizes of diaspores consumed and the number of plant species with diaspores < 10
2 mm and $\geq$ 10 mm consumed by each bird species.
- 3 ^h ‘% of plant species. $\geq$ 75% gape’ is the percentage of the plant species recorded in the diet of each bird species with diaspores greater than or equal to 75% of
4 its gape width; and ‘% of plant species *Ficus* spp.’ is the percentage of native plant species consumed that were from the genus *Ficus*

1 Table 2. Results of Analysis of covariance (ANCOVA) testing for effects of gape width and
2 frugivory level on: (1) the average size of diaspores consumed; (2) the dietary proportion of
3 diaspores that were close in size to the limit of a bird species' handling capacity ($\geq 75\%$ of gape
4 width); and (3) the number of native plant species consumed. β is the slope of the relationship
5 between gape width and the variable tested. Mean values and correlations within frugivory
6 levels are also shown. See also Fig. 1.

		Diaspore size	Proportion $\geq 75\%$ gape	Number plant species
<u>ANCOVA</u>				
Gape width				
	F	14.04	1.48	4.36
	p	0.001	0.002	0.045
	r²	0.50	0.50	0.40
	β	0.46	-0.42	0.28
Frugivory level				
	F	12.36	10.49	8.53
	p	<0.0001	<0.0001	0.001
Gape width x Frugivory level				
	F	0.57	2.7	0.83
	p	0.57	0.08	0.44
<u>FRUGIVORY LEVEL</u>				
Major frugivore (n=10)				
	Mean	7.8	0.31	47.0
	r² with gape width	0.36	0.44	0.35
Mixed-diet (n=15)				
	Mean	6.6	0.20	47.9
	r² with gape width	0.42	0.39	0.09
Minor frugivore (n=12)				
	Mean	4.4	0.04	6.1
	r² with gape width	0.16	0.01	0.24

Table 3. *The average number of native plant species from selected plant families (those with >3 species in the dataset) that were potentially dispersed by birds with high, medium and low seed dispersal potential, and by major and mixed-diet frugivores. ‘Number of species’ is the number of native plant species in the data set. ANOVA showed significant differences between the three seed dispersal potential classes in the number of plant species consumed from all families ($p < 0.02$ for all tests); subscript letters next to means show the results of pairwise LSD comparisons. ‘p’ shows the results of t-tests between major and mixed-diet frugivores (shown in bold if $p < 0.05$).*

Average number plant species potentially dispersed							
Plant family	Number of species	Frugivory level versus plants consumed			Seed dispersal potential Vs plants potentially dispersed		
		Mixed	Major	p	Low	Medium	High
		n = 10	n = 8		n = 20	n = 6	n = 12
Araliaceae	4	1.60	1.63	0.38	0.00 _a	1.50 _b	1.67 _b
Arecaceae	5	1.60	1.88	0.25	0.04 _a	0.33 _a	1.50 _b
Celastraceae	4	0.60	0.00	0.005	0.00 _a	1.00 _b	0.08 _a
Ebenaceae	4	1.20	1.25	0.85	0.00 _a	1.00 _b	1.17 _b
Elaeocarpaceae	6	3.20	2.75	0.40	0.00 _a	1.83 _{ab}	3.08 _b
Euphorbiaceae	11	3.20	2.38	0.81	0.17 _a	2.8 _b	1.4 _{ab}
Lamiaceae	5	0.90	0.63	0.47	0.00 _a	0.33 _{ab}	0.83 _b
Lauraceae	21	4.80	9.88	0.04	0.00 _a	1.83 _a	8.17 _b
Meliaceae	7	3.20	1.88	0.16	0.00 _a	1.67 _b	2.50 _b
Menispermaceae	4	0.40	0.38	0.66	0.00 _a	0.33 _b	0.25 _b
Moraceae	13	7.40	7.13	0.49	0.65 _a	6.67 _b	7.83 _b
Myrtaceae	20	5.50	4.13	0.26	0.00 _a	3.50 _b	4.42 _b
Oleaceae	6	1.20	1.75	0.24	0.04 _a	0.67 _{ab}	1.25 _b
Pittosporaceae	4	0.80	0.50	0.17	0.00 _a	0.67 _b	0.50 _b
Rhamnaceae	4	1.70	0.88	0.08	0.04 _a	1.50 _b	0.67 _{ab}

Average number plant species potentially dispersed							
Plant family	Number of species	Frugivory level versus plants consumed			Seed dispersal potential Vs plants potentially dispersed		
		Mixed n = 10	Major n = 8	p	Low n = 20	Medium n = 6	High n = 12
Rosaceae	4	0.90	0.63	0.57	0.00 _a	1.17 _b	0.33 _a
Rubiaceae	10	1.70	1.13	0.45	0.00 _a	0.83 _{ab}	1.25 _b
Rutaceae	11	2.10	2.13	0.90	0.00 _a	1.17 _b	1.92 _b
Sapindaceae	17	5.00	2.13	0.003	0.35 _a	3.17 _b	3.58 _b
Sapotaceae	4	0.30	0.38	0.65	0.00 _a	0.00 _a	0.42 _b
Vitaceae	6	2.50	2.63	0.83	0.00 _a	1.67 _b	2.50 _b

1 **Figure legends**

2 FIGURE 1. The relationship between gape width (mm) and the: (A) average size of diaspores
3 consumed; (B) average proportion (Prop.) of diaspores consumed that were close to the
4 maximum handling capacity ($\geq 75\%$ of gape width); and (C) number of native plant species
5 consumed for major frugivore species (open circle, solid line), mixed-diet species (closed square,
6 dashed line) and minor frugivore species (open triangle, dot-dash line). Gape width is shown on
7 the x axis in all three plots. Lines show the correlation between gape width and dependent
8 variables, calculated separately for each frugivory level.

9

10 FIGURE 2. Classification of frugivore species based on Bray-Curtis similarity in patterns of
11 consumption of native plant species. Seed dispersal potential groups: 1 High, 2 Medium, 3 Low;
12 Frugivory levels: Major (open circle), Mixed (closed square), Minor (open triangle); S small
13 gape (< 10 mm), M medium gape (10 - 15 mm) , L large gape (> 15 mm); D seed disperser, C
14 seed crusher.

15

16 FIGURE 3. Correlation between bird species' gape widths and their body mass for seed
17 dispersers (closed circles; $r^2 = 0.86$, $p < 0.001$) and seed crushers (open circles; $r^2 = 0.62$, $p =$
18 0.03).

19

Figure 1

1
2

Figure 3