

# Preference for an invasive fruit trumps fruit abundance in selection by an introduced bird in the Society Islands, French Polynesia

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Received: 21 June 2012 / Accepted: 5 March 2013  
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**Abstract** Introduced plants with fleshy fruit can alter the dietary decisions of frugivorous birds in their novel ranges by producing fruit of higher quality or by producing fruit in greater abundance. We used fruit choice experiments with wild-caught captive Red-vented Bulbuls (*Pycnonotus cafer*) on the tropical Pacific island of Moorea, French Polynesia, to determine whether this bird prefers the fruit of a highly invasive tree (*Miconia calvescens*) over three other fruit (one alien, two native) and to determine whether birds would eat less preferred fruit when it was more abundant than preferred fruit. Birds showed consistent preferences, and chose *M. calvescens* more than any other species. Birds selected more abundant fruit first when a single species was presented. However, when

both fruit species and abundance were modified simultaneously, patterns of preference for particular species remained intact while the response to abundance disappeared. Results imply that dietary preferences are more important than small-scale variations in abundance for fruit selection. The strong preference for *M. calvescens* suggests that Bulbuls will select the fruit even in habitats where it is rare.

**Keywords** Frugivory · *Miconia calvescens* · *Pycnonotus cafer* · Feeding preference · Invasive plants

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**Electronic supplementary material** The online version of this article (doi:10.1007/s10530-013-0441-z) contains supplementary material, which is available to authorized users.

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## Introduction

Species invasions by fruit-bearing plants alter patterns of both relative availability and quality of fruiting resources in a plant community, and thus have the potential to influence the dietary choices of frugivorous birds (Aslan and Rejmanek 2012). Dietary shifts in frugivores may modify the invasion process by facilitating the spread of invasive plants and can affect the dispersal of native seeds if changes lead to less reliable dispersal (Richardson et al. 2000). Increased consumption of fruit by frugivores in the early stages of invasion can accelerate the rate of spread of invasive species and can lead to more rapid establishment of remote satellite populations (Clark 2001). Understanding what mechanism leads to integration of

introduced fruit into the diets of frugivores is therefore key to predicting how frugivores may modify the dynamics of invasion.

Birds show preferences for some fruits over others in both laboratory and field experiments (Carlo et al. 2003; Levey et al. 1984). Studies of frugivore preference for native and invasive fruit have found mixed results with some showing preference for natives while others show opportunistic choice (Aslan and Rejmanek 2012). According to optimal foraging theory, birds are also expected to adjust their foraging strategies based on the abundance of available fruit (Stephens and Krebs 1986). At a small scale, birds use fruit crop size to select between fruiting trees (Carlo et al. 2003) and between fruit clusters on the same plant which can vary in size (Amsberry and Steffen 2008). Preferences for native fruit over introduced fruit may be overridden if invasive species have larger fruit clusters. Thus, avian choices between fruit are likely to depend on both the strength of dietary preferences and the magnitude of responses to small-scale variations in fruit abundance.

On remote oceanic islands, the invasion of introduced species is an important driver of population declines and species extinctions in both flora and fauna (Reaser et al. 2007). In French Polynesia, multiple fruit bearing plants and frugivorous birds have been introduced and current ecosystems are highly modified by the presence of numerous alien birds (Monnet et al. 1993) and plants (Fourdrigniez and Meyer 2008). At the same time, avian extinction has left the islands with only a subset of original avifauna. The existing community of frugivores is extremely small relative to tropical continental regions, consisting of one surviving endemic pigeon and three recent passerine introductions (Spotswood et al. 2012) including the Red-vented Bulbul (*Pycnonotus cafer* L. 1766, Passeriformes, Pycnonotidae, Bulbul hereafter). In 1937, the introduction of the fruit bearing tree *Miconia calvescens* DC. (Melastomataceae) resulted in the catastrophic invasion of 75 % of the land surface on the island of Tahiti and 25 % on the nearby island of Moorea (Meyer 2010). The fruit of *M. calvescens* is consumed by all avian frugivores on these islands, and birds respond to changes in the local abundance of *M. calvescens* by increasing consumption of *M. calvescens* fruit at sites where it is most abundant (Spotswood et al. 2012). Compared to Moorea, seed dispersal networks are altered on Tahiti where alien

species (both birds and plants) account for the majority of interactions between frugivores and plants (Spotswood et al. 2012). *M. calvescens* spread across Tahiti in ca. 30 years and authors have speculated that its invasion was facilitated by the consumption and dispersal of fleshy fruits by avian frugivores (Meyer 1996).

In this study, we used choice experiments conducted in aviaries to uncover how preference and small-scale abundance variation influence decisions to consume native and alien fruits in one common introduced frugivorous bird. Specifically, our objectives were to examine whether (1) birds prefer fruit of the invasive tree, *M. calvescens*, to other fruit of similar size, color and shape, (2) whether birds can respond to changes in abundance of fruit and (3) whether patterns of preference can be overridden when preferred fruit are presented at low abundance.

## Materials and methods

### Study site

This study was conducted on the island of Moorea in the Society Archipelago of French Polynesia (17°38'S 149°30'W and 17°32'S 149°50'W). An estimated 30 % of native species, 20 % of introduced naturalized plants (591 species), and as many as 40–50 % of naturalized plants considered invasive contain fleshy fruit adapted for dispersal by vertebrates in French Polynesia (Fourdrigniez and Meyer 2008). For a more comprehensive site description, see Spotswood et al. (2012).

### Study species

The introduced Bulbul is a medium sized passerine (mean mass  $\pm$  SD = 36.65  $\pm$  3.49 g) native to India and Pakistan. First seen naturalized on Tahiti in the late 1970s (Bruner 1979) where it was probably introduced as a cage bird, it spread rapidly across Tahiti in low and mid-elevation valleys (Monnet et al. 1993) and is now found up to 2,200 m. It spread to the neighboring island of Moorea at 17 km north-west from Tahiti sometime during the 1980s and is now one of the most common birds on this island where it is present at all elevations.

We used four species of fruit (Table 1) in choice trials including two alien invasive plants; *M. calvescens* and *Lantana camara* (L., Verbenaceae), and two common native species; *Rhus taitensis* (Guillemin, Anacardiaceae) and *Tarennia sambucina* ((Forst.) Durand ex. Drake, Rubiaceae). All four species are readily available in the wild during our study period. Additionally, fruit are all blue to purple-black when ripe and similar in size and external shape (Fig. 1), which allowed for control of these variables. We collected branches from the wild containing fully developed fruit which were allowed to ripen in water for several days until use in trials. All species are consumed in the wild by Bulbuls, and in a study of the diets of frugivores on Moorea and Tahiti, *M. calvescens* was found in 14.29 % of fecal samples collected from Bulbuls on Moorea whereas *L. camara* was found in 16.33 %, *T. sambucina* in 38.78 % and *R. taitensis* in 5.44 % of fecal samples (Spotswood et al. 2012).

### Fruit choice experiments

We captured 11 wild Bulbuls at the Richard B. Gump South Pacific field station using a walk-in trap baited with fresh mango, banana and papaya. Birds were held

in pairs in three aviaries  $3 \times 3 \times 2$  m each located outdoors for between three and 7 days before trials began. All birds were fed daily with a mixture of fresh bananas (*Musa x paradisiaca*), papayas (*Carica papaya*) and mango (*Mangifera indica*) and whey protein powder supplemented with maggots. Food was removed from aviaries on the evening before experiments and birds were not fed again until trials were completed the following morning. Each aviary contained an experimental perch made of round wooden dowels 45 cm long supported by a pole at a height of 130 cm. Fruiting structures were attached to perch ends (Fig. 1), and were constructed with chicken wire and six sharpened plastic cable ties, each of which held a single fruit. A window on the outside of each aviary allowed fruit to be placed at the beginning of each trial without entry, and a black dividing cloth allowed birds to be separated at the beginning of trials each morning. Observers remained in a hide roughly three meters from the aviary for the duration of each trial which was completed either when all fruit had been consumed or when 15 min had elapsed. To minimize stress to birds, a maximum of four trials were conducted per bird per morning between 6:00 a.m. and 9:30 a.m. complete sets of 22 trials were conducted with all birds between August 4th and August 15th, 2010. Data recorded

**Table 1** Fruit traits for four species used in fruit preference trials with Bulbuls on the island of Moorea, French Polynesia

Species	Origin and habitat	Status	Growth form	Fruit color <sup>a</sup>	Fruit type	Seeds/fruit ( $\pm$ 1SD)	Fruit diameter (mm), ( $\pm$ 1SD) n = 20 <sup>a</sup>
<i>Miconia calvescens</i>	Central/South America, tropical wet forest <sup>f</sup>	Invasive <sup>g</sup>	Tree (5–10 m) <sup>g</sup>	Purple/black	Berry	194.7 (36.7), n = 80 <sup>c</sup>	4.95 (0.59)
<i>Lantana camara</i>	Central/South America, disturbed open habitats <sup>b</sup>	Invasive <sup>g</sup>	Shrub <sup>g</sup>	Blue/black	Drupe	1 <sup>a</sup>	5.1 (0.59)
<i>Tarennia sambucina</i>	South Pacific Mariana islands to French Polynesia <sup>d</sup>	Native <sup>d</sup>	Tree (5–13 m) <sup>d</sup>	Black	Berry	~20–50 <sup>a</sup>	6.95 (1.24)
<i>Rhus taitensis</i>	Indonesia to French Polynesia <sup>c</sup>	Native <sup>c</sup>	Tree (30 m) <sup>c</sup>	Black	Drupe	1 <sup>a</sup>	4.7 (0.46)

Traits include species origin, status in French Polynesia, and characteristics of fruit. Fruit diameters are taken from measurements of 20 individual fruit for each species, published elsewhere in Spotswood (2011). Other information is taken from various sources cited above

<sup>a</sup> Spotswood (2011)

<sup>b</sup> Duggin and Gentle (1998), Fourdrigniez and Meyer (2008), Gosper and Vivian-Smith (2006)

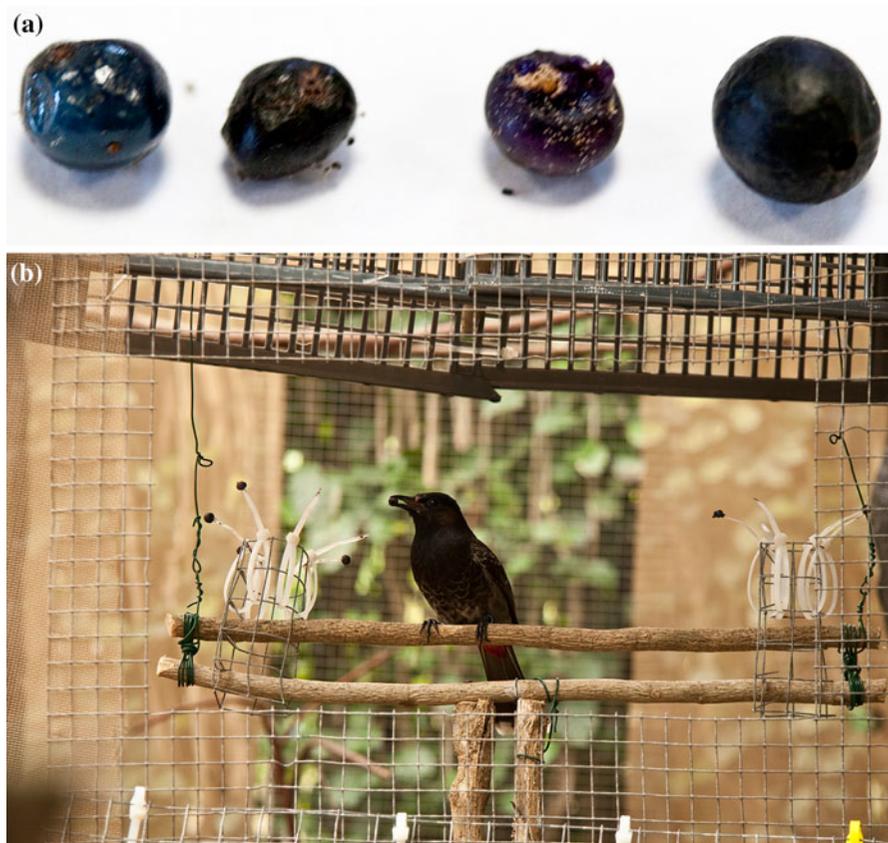
<sup>c</sup> Hou (1978)

<sup>d</sup> Smith (1988)

<sup>e</sup> Meyer (1998)

<sup>f</sup> Meyer (1996)

<sup>g</sup> Fourdrigniez and Meyer (2008)



**Fig. 1** Fruit choice trials conducted with Bulbuls on Moorea, French Polynesia, in aviaries at the Richard B. Gump South Pacific Field Station. Figure shows **(a)** four species of fruit used in trials from *left to right* *L. camara*, *R. taitensis*, *M. calvescens*

and *T. sambucina*, and **(b)** experimental setup with fruiting structures and perch where Bulbuls make a choice between one or two species of fruit presented at equal or varied abundance

included the time, position and order of consumption of every fruit as well as the handling of each fruit (consumed, pecked or dropped).

We conducted three types of pairwise trials for a total of 22 trials per individual. The order of trials was randomized for each bird and the position of each fruit species was rotated from trial to trial so that no one species was consistently on either the right or the left fruiting structure for multiple trials in a row.

1. *Equal abundance* To test whether birds preferred exotic over native fruit, we paired all possible combinations of species together in equal abundance with six fruit on each fruiting structure. Each fruit species was paired once with every other species for a total of six trials per bird.
2. *Single species* To test the effect of abundance on fruit choice, we tested each species with itself at high (six fruit) and low (two fruit) abundance.

Each species was tested only once for a total of four single species trials per bird.

3. *Varied abundance* To test whether preferences can be overridden by abundance, we repeated trials for all species pairs with one species at high abundance (six fruit) and the other at low abundance (two fruit). Each species pair was tested twice to include both possible combinations of high and low abundance. Trials were conducted only once with each bird for a total of 12 trials per bird.

We used the results of the equal abundance trials to determine which species is preferred for each possible pair in order to predict the outcome of varied abundance trials. We expected that if abundance can override species preferences, then abundant fruit should be consumed earlier in all cases, no matter which species is preferred for a given species pair.

Alternatively, if preferences cannot be overridden by abundance, then more preferred food items should be consumed earlier no matter how abundant. We used two variables to quantify fruit selection patterns. First, we calculated the percent of total fruit consumed in each trial. Second, we used the order of consumption of fruit to determine which types of fruit were consumed first in each trial. Accessibility has been shown to be an important factor influencing fruit choice in birds (Moermond and Denslow 1983). Using this fact, we generated an expected order of consumption for each fruiting position in which more accessible fruit pointing inward toward the middle of the perch were predicted to be consumed earlier than less accessible fruit pointing outward (Fig. 1). We validated the expected order of consumption by calculating the mean order for each position across all trials and all individuals.

We calculated deviations from expected order of consumption by subtracting the expected rank from the observed rank for each fruit in each trial. Rank shifts for each fruit were either zero, negative or positive (hereafter designated as zero, negative or positive ‘selectivity’). Zero represented no shift from expected rank of consumption, indicating that fruit were consumed on basis of accessibility alone. Negative numbers indicated later consumption than expected by accessibility and positive numbers indicated earlier consumption. Rank shifts were normalized by the ratio of fruit consumed to fruit presented for each species in each trial. Normalization was necessary because not all fruit were consumed in each trial, which biased rank shifts towards earlier consumption in trials where fruit were not completely consumed. Rank shifts were only comparable for fruiting structures with the same numbers of fruits; therefore equal abundance trials (12 fruit total) were analyzed separately from trials with abundance differences.

We analyzed single species trials for each species separately using a model including the fixed factors time since sunrise, side of the experimental perch (right or left—included to account for wariness birds might possess for a specific side of the aviary), and the abundance of fruit. We conducted two analyses to quantify preferences using the equal abundance trials. First, we considered whether the proportion of total fruit consumed varied by species. We then used rank shifts quantified as selectivity to determine which

species was preferred for each species pair. We analyzed varied abundance trials by separating each species pair and each abundance level so that fruit were compared only to clusters of the same size (e.g. high or low abundance) during the analysis. For example, high abundance fruit for the *M. calvescens*/*L. camara* pair represents data from two separate trials in which *M. calvescens* was presented at high abundance (with *L. camara* at low abundance), and the reverse. Fixed factors for equal and varied abundance trials included species, side of the experimental perch, and the time since sunrise.

### Statistical analysis

We used generalized linear mixed modeling with a binomial error distribution and maximum likelihood estimation to analyze the proportion of total fruit consumed in the equal abundance trials. All other analyses used linear mixed modeling with maximum likelihood estimation. For all analyses, the individual bird was included as a random effect in order to account for the lack of independence of repeated trials on the same individual. We compared models with and without the factor of interest (abundance in single species trials, and species in varied and equal abundance trials) using a Likelihood Ratio Test (LRT). All analyses were conducted in R 2.12.2 (Bates and Sarkar 2007; R Development Core Team 2011). Linear mixed modeling was conducted using the nlme package (Pinheiro et al. 2011; R Development Core Team 2011) and generalized linear mixed modeling using lme4 (Bates and Sarkar 2007).

## Results

### Single species

When a single species was presented with itself at high and low abundance, fruit at high abundance were consumed earlier than expected based on accessibility and low abundance were consumed later than expected for two out of four species. Consumption was earlier in *L. camara* ( $n = 90$  fruit, Likelihood Ratio = 14.41,  $P < 0.001$ ) and *T. sambucina* ( $n = 94$  fruit, Likelihood Ratio = 12.95,  $P < 0.001$ ), but similar to expectations of accessibility in *R. taitensis* ( $n = 114$  fruit, Likelihood Ratio = 0.98,  $P = 0.322$ )

and *M. calvescens* ( $n = 88$  fruit, Likelihood Ratio = 1.79,  $P = 0.18$ , Fig. 2, Online Resource 2).

### Equal abundance

The proportion of total fruit consumed depended on the species (Likelihood ratio using Chi square approximation = 2,541.9,  $df$  difference = 3,  $P < 0.0001$ ) and was close to 100 % for the invasive species, *M. calvescens* and *L. camara*, over 90 % for the native *T. sambucina*, and between 20 and 40 % for the native *R. taitensis* depending on the time of day. When presented at equal abundance, Bulbuls showed clear preferences that were not entirely consistent with dietary observations from birds captured in the wild. *M. calvescens* was consumed significantly earlier when paired with *L. camara* and *R. taitensis* but not to *T. sambucina* (Fig. 3, Online Resource 1,3). *L. camara* was consumed earlier when paired with *R. taitensis* but not *M. calvescens* or *T. sambucina*. *T. sambucina* was consumed earlier when paired with *R. taitensis*, but similarly when paired with *L. camara* and *M. calvescens*. Finally, *R. taitensis* was consumed

significantly later than expected when paired with all other species.

### Varied abundance

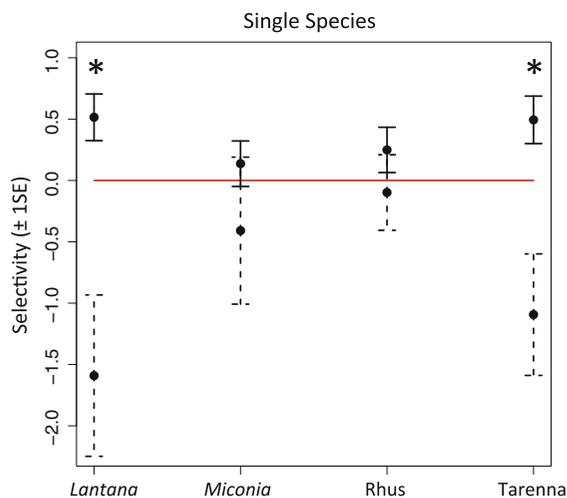
We found little evidence that the preferences identified using selectivity in equal abundance trials could be overridden by abundance in varied abundance trials (Fig. 3, Online Resource 1,3). Patterns of preferences identified in equal abundance trials were retained in varied abundance trials and were remarkably similar for all three types of trials. Fruit with positive selectivity in equal abundance trials were consistently consumed earlier when presented at both high and low abundance. The only exception to this pattern was in trials with *M. calvescens* and *L. camara* for which the significance of the preference for *M. calvescens* disappeared when this species was presented low abundance (Online Resource 3).

## Discussion

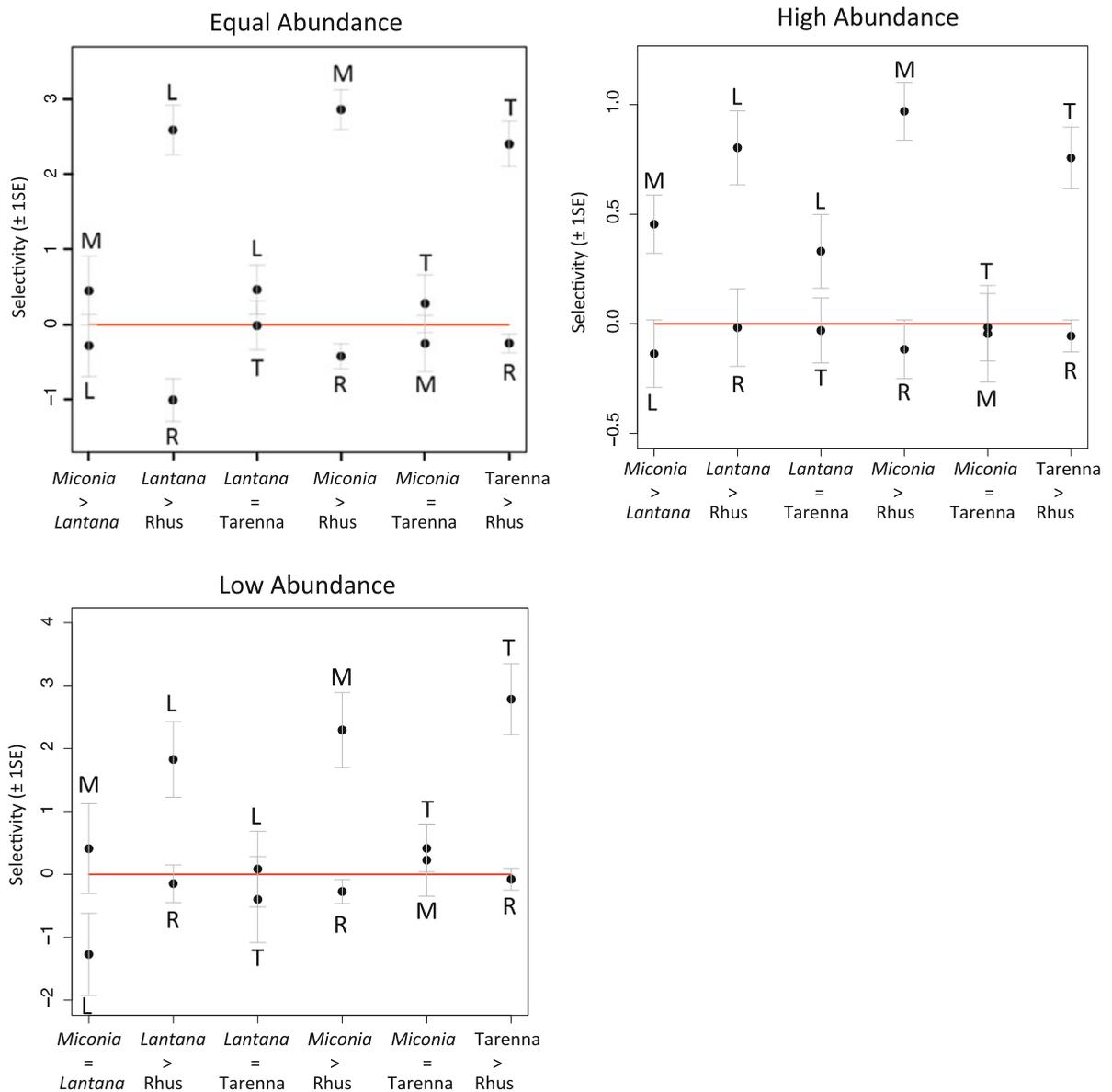
### Do birds prefer alien invasive fruit?

Bulbuls did not consistently prefer invasive fruit over native fruit. Birds showed a preference for *M. calvescens* over two of three of the other species in this study, making it the most preferred of the species in the study. *M. calvescens* was chosen equally often as *T. sambucina*. Bulbuls preferred the invasive *L. camara* and the native *T. sambucina* equally, and never preferred *R. taitensis*. In a recent meta-analysis, Aslan and Rejmánek found that studies that matched native and non-native fruit in terms of similarity of surface characteristics (color, shape and size) were slightly more likely to find a preference for non-native fruit, especially among non-native frugivores (2012). Bulbuls are themselves introduced in French Polynesia, and other studies have also found that non-native frugivores are less likely than native frugivores to prefer native fruit (reviewed in Aslan and Rejmánek 2012).

Other research has noted the importance of members of the genus *M. calvescens* to frugivores in other parts of the world (Blendinger et al. 2008; Carlo et al. 2003), and it is possible that lipids and protein contents make fruit in the genus palatable to a wide range of frugivores. Bulbuls showed a clear distaste for



**Fig. 2** Fruit chosen in single species fruit choice trials with 11 individual Bulbuls. In all trials, each species was paired with itself at high (black lines) and low (dashed lines) abundance. Selectivity was measured as normalized deviations from consumption predicted by chance. Fruit eaten earlier than expected lie above the zero line, while fruit eaten later lie below the zero line. Introduced species are shown in italics. Significant differences are represented with an asterisk, and were derived using a linear mixed model with bird as a random effect and abundance, site and time of day as fixed factors (Online Resource 2)



**Fig. 3** Fruit chosen in equal and varied abundance trials with 11 individual Bulbuls in which each of four species was paired with every other species at equal, high and low abundance. Species included *L. camara* (L), *M. calvenscens* (M), *R. taitensis* (R) and *T. sambucina* (T). Selectivity of fruit was measured as normalized deviations from consumption predicted by accessibility. Fruit selected earlier than expected are *above* the zero line, while fruit selected later lie *below* the zero line. Varied abundance trials were analyzed by separating each species pair and each abundance level so that fruit were compared only to clusters of the same size (e.g. high or low abundance) during the analysis. For example, high abundance fruit for the

*M. calvenscens/L. camara* pair represents data from two separate trials in which *M. calvenscens* was presented at high abundance (with *L. camara* at low abundance), and the reverse. This comparison measures whether birds behaved differently to each abundance level when the species was different. All analyses were performed using linear mixed modeling with individual bird as a random effect and species, perch side (*right or left*) and time of day as fixed factors. *Symbols* indicating which species was consumed earlier (>, <) indicate statistically significant differences from likelihood ratio tests. An = symbol indicates no difference in consumption for a species pair. Introduced species are shown in *italics*

*R. taitensis*; fruit were frequently spat out and left uneaten. In the field, *R. taitensis* was the fifth most common food item of ten species recorded in the diet of Bulbuls on Moorea (Spotswood et al. 2012). Levey and Moermond found that some fruits that were consumed in the wild were consistently rejected by caged birds, and speculated that proximity to less preferred but available fruit might explain why the fruit was sometimes consumed (1984). The large size of the fruit crop and the long fruiting phenology (fruit are present for several months out of the year) are two possible factors that could explain why Bulbuls consume *R. taitensis* in the wild (Spotswood pers. obs.). While similar in size, *T. sambucina* was the largest of the four fruits in this study, which could explain the preference for this fruit by Bulbuls.

#### Do birds choose abundant fruit first?

When a single species was tested at high and low abundance, abundant fruit were consumed earlier for *L. camara* and *T. sambucina* but not *M. calvescens* and *R. taitensis*. The apparent abundance of a fruiting resource may be influenced by fruit size (Sobral et al. 2010), and it is possible that the abundance differences were more obvious to birds in *L. camara* and *T. sambucina* because these species contain slightly larger fruit than *M. calvescens* and *R. taitensis*. Optimal foraging theory predicts that travel time between locations incurs a cost which must be weighed against the benefit of energy gained via foraging (Stephens and Krebs 1986), and the cost of hopping from one fruit cluster to another on a single fruiting bush could deter birds from selecting clusters with very few fruit. Travelling time and energy expended were probably greatest when birds were required to hop from one fruiting structure to the other, and captive Bulbuls avoided doing so by reaching as many fruit as possible while standing on the perch between the two fruiting structures. More abundant fruits were probably chosen earlier in single species trials because the time spent hopping could be delayed until after six fruit had been consumed. The absence of this pattern with *M. calvescens* and *R. taitensis* could be related to preference. For example, *R. taitensis* was often left uneaten at the end of trials, and birds may have chosen only the most accessible fruit to consume, leaving other fruit uneaten.

#### Can abundance override preference?

We found little evidence that differences in abundance could override fruit preferences, suggesting that the costs incurred by consuming a less abundant food item was not as great as the cost of consuming a less preferred food item. These results do not support those found by Levey (1988), in which preferences for certain fruits could be overridden by increasing the distance between fruit, and those of Moermond and Denslow (1983), where preferences could be overridden by making fruit less accessible. Instead, this study suggests that abundance is a less important factor in determining dietary choice than either accessibility or distance. However, it is also possible that abundance differences in this study were too small to override preferences. In the field, the response to abundance may be stronger when fruits of differing preference and abundance are separated by larger distances, or when differences in abundance are greater than we could present in laboratory conditions. Less preferred food items may also be more readily accepted during periods when fruit are scarce (Schaefer and Schaefer 2006). There was a slight increase in the total percent of *R. taitensis* consumed during trials later in the morning, implying that birds are less selective when they are hungry.

The response to abundance and preferences in this study demonstrate that Bulbuls are capable of decision making based on a maximization principle (Moermond and Denslow 1983). When choosing between fruits of the same species, birds chose the most abundant fruit. When choosing between fruit of two species, birds chose the fruit they preferred, even when it was less abundant. Taken together, these results suggest that Bulbuls can balance unlike variables and can make different choices depending on context.

#### Implications for the dispersal of native and alien fruit

*M. calvescens* was the most preferred food item in this study, implying that *M. calvescens* may be integrated into Bulbul diets even when it is not abundant because of its attractiveness as a food item. These findings are particularly relevant for islands with Bulbuls where the extent of invasion by *M. calvescens* remains restricted such as on Moorea, Raiatea and Tahaa (Meyer 2010). Extra caution should also be taken on

islands without *M. calvescens* where the Bulbuls is already present, including several islands in the Society archipelago, the Australs and the Tuamotus (Holyoak and Thibault 1984).

Early integration into the diets of frugivores could accelerate rates of spread in the early stages of invasion, and could lead to the establishment of new remote satellite populations distant from the original source population (Clark 2001). Fruits contain an average of 194 seeds (Table 1), and the consumption of small numbers of berries could lead to the spread of many seeds. Similar preferences for *M. calvescens* by other frugivores could also have influenced the history of invasion of this species on Tahiti where it spread from its point of introduction in 1937 to cover much of the island in less than 40 years (Meyer 2010). The rate of spread, estimated at 400 m per year, as well as the appearance of remote populations distant from the original point of introduction is consistent with frugivore-mediated dispersal (Spotswood 2010). More rapid invasion, and a decrease in the lag time between introduction and invasion can constrain the effectiveness of control and eradication programs, and should be considered during conservation planning. In the tropical Pacific, islands with frugivorous birds with similar preferences should receive priority in the prevention of introduction of *M. calvescens*.

This study provides evidence that birds can respond both to small-scale variations in abundance and to preferences for certain food items, and that they can balance decisions about which to prioritize depending on the context. An important conservation implication of this result is that efforts aimed at conserving populations of rare plants or at controlling the spread of alien fruit-bearing plants depend on adequate knowledge of the preferences of the frugivorous community specific to a given location.

**Acknowledgments** We thank Carol Raydon, Ravahere Taputuarai, Kelly Kaban, Laura Stephenson, Hela Tetanui, Alex Song, Jasper Wu, Stephanie Taing and the staff at the Richard B. Gump Field Station on Moorea for help with fieldwork and logistical support. Helpful comments on the methods and manuscript were provided by Doug Levey, John Battles, Brent Mishler, and the members of Steve Bessinger laboratory at UC Berkeley. Funding was provided by the University of California and US National Science Foundation grant DEB-1011697. The corresponding author was supported during fieldwork with a Fulbright and a fellowship from PEO International. A research permit for this work was provided by the Délégation à la Recherche (French Polynesian government).

This experiment was carried out under a permit from the University of California at Berkeley Animal Care and Use committee (permit #R313-0610).

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