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To cite this article: F.X. Palacio, M. Valoy, F. Bernacki, M.S. Sánchez, M.G. Núñez-Montellano, O. Varela & M. Ordano (2015): Bird fruit consumption results from the interaction between fruit-handling behaviour and fruit crop size, *Ethology Ecology & Evolution*, DOI: [10.1080/03949370.2015.1080195](https://doi.org/10.1080/03949370.2015.1080195)

To link to this article: <http://dx.doi.org/10.1080/03949370.2015.1080195>

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Bird fruit consumption results from the interaction between fruit-handling behaviour and fruit crop size

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Received 18 January 2015, accepted 19 July 2015

Bird foraging behaviour is a major factor involved in mutualistic interactions of fleshy-fruited plants. Despite much research, we still lack quantified demonstrations of how fruit display traits affect fruit removal behaviour. Although the fruit crop size hypothesis proposes a general mechanism for fruit trait selection, it overlooks the fact that distinctive bird behaviours in a bird assemblage would have different effects on fruit crop size. Here, we show that the relevance of fruit crop size for bird fruit consumption is driven by two basic components of fruit foraging behaviour: fruit handling and residence time. We assessed bird fruit-eating behaviour (fruit consumption, fruit handling and residence time) and its relationship with fruit crop size, taking into account body size and spatial focal context (conspecific neighbour density and distance to the forest edge from individual plants) in a population of *Vassobia breviflora* (Solanaceae) in Tucumán, Argentina. At the assemblage level, fruit consumption was positively related to fruit crop size and residence time, and the interaction between fruit crop size and residence time depended on fruit-handling behaviour. At the functional group level, both guplers and pulp consumers showed a positive relationship between fruit consumption and residence time. However, guplers showed a negative interaction between fruit crop

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size and residence time, while pulp consumers showed no interaction. At the species level, fruit consumption by *Turdus rufiventris* (gulper) was positively related to fruit crop size, whereas fruit consumption by *Thraupis sayaca* and *Zonotrichia capensis* (pulp consumers) depended positively on residence time. Essentially, gulpers spent short residence times in plants with larger fruit crops, whereas pulp consumers spent long residence times in plants regardless of fruit crop size. The segregation between fruit-eating behaviours and their relationship with fruit crop size suggests that bird functional groups (i.e. gulpers and pulp consumers) would shape fruit display traits with different intensities.

KEY WORDS: frugivory, gulper, pulp consumer, seed dispersal mutualism, *Thraupis sayaca*, *Turdus rufiventris*, *Vassobia*, *Zonotrichia capensis*.

INTRODUCTION

Bird behaviour plays a key role in the ecology and evolution of seed-dispersal plant–bird mutualisms. On the one hand, animal behaviour affects plant dispersal stages and, subsequently, plant population dynamics (Schupp 1995; Jordano 2000; Morales et al. 2013). On the other hand, fruit display traits such as fruit crop, fruit and seed size, or fruit nutrient content strongly affect animal foraging behaviour, and therefore the rate of energy intake (Jordano 2000; Herrera 2002). In this biological market of reward units supplied by plants to exchange for seed-dispersal services supplied by animals (sensu Noë & Hammerstein 1995), two elements of the exchange, fruit-eating behaviour and fruit display, constitute key pieces in the functioning of the mutualism.

From the bird's perspective, individual fruiting plants represent heterogeneously distributed resource patches (García & Ortiz-Pulido 2004). In an optimal foraging framework (Stephens & Krebs 1986), major aspects of fruit-eating behaviour that affect seed dispersal patterns are patch residence time and fruit consumption rate (as a proxy for energy intake; Martin 1985; Foster 1990). The so-called fruit crop size hypothesis (Snow 1971; Howe & Estabrook 1977; Izhaki 2002) predicts that individual birds should increase fruit removal in plants with larger fruit crop sizes. Consequently, birds should also spend longer periods in these high-quality patches, in order to maximise their long-term average rate of energy intake (Charnov 1976).

However, the typical scenario of the interaction between one plant population and their fruit-eating birds is an assemblage (see Fauth et al. 1996) composed of bird species with distinctive behaviours and consequences for seed dispersal (Schupp 1993; Jordano 2000; Morales et al. 2013; Loayza & Rios 2014). This suggests that the relationship between foraging behaviour type and fruit display traits will also show diverse patterns within a plant population (e.g. Foster 1990; Morales et al. 2013). Altogether, past research has mostly overlooked the relevance of considering and explicitly quantifying the interaction between fruit-handling behaviour and fruit crop size.

In addition, foraging behaviour depends not only on intrinsic plant factors, such as crop size, but also on other behavioural and non-behavioural bird traits (e.g. fruit handling, body size, gape width and physiological processes following fruit consumption; Wheelwright 1985; Levey 1987; Whelan & Schmidt 2007) and spatial context (e.g. habitat type, fruit neighbourhood availability; Saracco et al. 2005; Carlo & Morales 2008;

Blending & Villegas 2011). Therefore, predictions derived from optimal foraging theory are not always straightforward and should be envisioned in light of their multi-factorial context. Among the factors above mentioned, the fruit-handling technique and body size are fundamental to understanding variation in fruit consumption and related behavioural traits (Levey 1987). Bird species that swallow fruits whole (“gulpers”) require less time to handle fruits, and are thus predicted to spend less residence time in a plant and to have higher consumption rates than birds that either mash or peck fruits (“pulp consumers”; Foster 1987; Levey 1987; Schupp 1993). Hence, gulpers should maximise energy intake rate by spending short foraging periods in high-quality patches (i.e. “time minimisation”) and pulp consumers should maximise energy intake rate by spending long foraging periods, regardless of patch quality (i.e. “energy maximisation”; Schoener 1971; Foster 1990). Moreover, large birds are expected to consume more fruits than smaller ones, since they are capable of eating more fruits (Wheelwright 1985), beyond the energetic requirements related to body mass (Martin 1985). Therefore, body size should be considered together with fruit-handling behaviour and fruit crop size. So, the consumption of fruits by birds should be guided by the interaction between factors that include both bird and plant attributes.

Accordingly, we aimed to assess variation in bird fruit consumption and foraging behaviour in a population of the multi-seeded fleshy-fruited tree *Vassobia breviflora* (Solanaceae) in Tucumán province, Argentina. Specifically, we tested the following predictions: (1) frugivorous birds should spend more time and consume more fruits in plants bearing large fruit crop sizes (high patch quality) than in plants with small ones (low patch quality), and (2) fruit consumption patterns by gulpers and pulp consumers should differ based on the interaction between fruit crop size and residence time. In particular, gulpers are expected to prioritise fruit crop size over residence time, whereas pulp consumers are expected to prioritise residence time over fruit crop size. Since variation in fruit consumption is partly explained by body size and spatial context and may cloud the role of fruit display traits in foraging behaviour, we tested these predictions taking into account body size and spatial context (distance to forest edge and neighbourhood effects).

METHODS

Study area

The study was carried out at El Cadillal (26°36'S, 65°10'W, 600 m a.s.l.), between “El Cadillal dam” and “Reserva Provincial Aguas Chiquitas”, Tucumán province, Argentina. The area is located in a transitional zone between the “Chaco Serrano” forest and the Yungas biogeographic province (“Selva Pedemontana”), NW Argentina (Cabrera & Willink 1980). In the study area, vegetation is mainly composed of perennial trees, and dominant species are *Ocotea porphyria*, *Blepharocalyx salicifolius*, *Rapanea laetevirens*, *Juglans australis*, *Myrrhinium atropurpureum*, *Allophylus edulis*, *Cupania vernalis*, *Anadenanthera colubrina* and *Terminalia triflora*. The climate is subtropical and the annual profile shows a dry period (May to September, including austral winter) and a wet period (November to March, including austral summer; Sesma et al. 1998). Mean annual rainfall is 850 mm (Bianchi & Yáñez 1992) and temperatures vary from 20 to 25 °C in summer and 13 to 15 °C in winter (Santillán de Andrés et al. 1967; Minetti et al. 2005).

Study system

Vassobia breviflora (Sendtn.) Hunz. (Solanaceae) is a pioneer shrub or tree up to nearly 15 m in height, native to southern Brazil, Bolivia, Paraguay, Uruguay, and northern and central Argentina (Masetevach Becerra & Barboza 2013). It grows in forest edges, between 200 and 2000 m a.s.l., and in the southern Yungas, it is locally abundant between 900 and 1600 m a.s.l. (Pinazo et al. 2003; Malizia et al. 2012). It produces “inflorescences” with an average of six flowers per inflorescence. Strictly speaking, these inflorescences are constituted by fasciculate brachiblasts (Bernacki 2014). Flowers are hermaphroditic and actinomorphic, and 20–30 mm in diameter (Taura & Laroca 2004; Masetevach Becerra & Barboza 2013). It is characterised as an insect-pollinated self-compatible species in our study population (M. Valoy pers. obs.), and primary pollinators are insects of the families Apidae and Colletidae (Hymenoptera; Taura & Laroca 2004; Bernacki 2014; Bernacki et al. in press). Fruits are depressed-globose berries, orange to red when ripe, 7–9 mm in diameter (Masetevach Becerra & Barboza 2013), and seeds (37.1 ± 12.6 seeds per fruit; Bernacki 2014; Bernacki et al. in press) are dispersed by several vertebrates in its distribution area (birds: Giannini 1999; Capllonch & Lobo 2005; Chatellenaz 2008; bats: Autino & Bárquez 1994; O. Varela pers. obs.; opossums: Cáceres & Monteiro-Filho 2001; Cáceres 2002). In our study area, birds are the main seed dispersers (Giannini 1999; Capllonch & Lobo 2005).

Bird foraging observations and fruit crop size estimation

During December 2012 and January 2013, we observed bird foraging behaviour at 37 focal individual plants for periods of 3 continuous hr per plant. In the following fruiting season (December 2013 and January 2014) we made observations at 106 focal individual plants for periods of 2 continuous hr. Plants were selected according to fruit availability and located along secondary roads and trails, with sufficient surrounding space to carry out field observations. Only five plants were the same during the two reproductive seasons. Observers remained at least 5 m from the focal individual tree, and all observations were made within the first 4 hr after sunrise. During each observation period, bird species, the number of fruits consumed, fruit-handling behaviour and residence time at each individual focal tree were recorded. We considered a visit legitimate if a bird completed its foraging bout by eating at least one fruit. A bird species was considered a gulper if it swallowed the fruit whole, or a pulp consumer if it mashed or pecked the fruit without swallowing it, and discarded remaining parts of the fruit. Since some species were observed to consume fruits with different handling techniques, we classified species as gulpers or pulp consumers according to their most frequent fruit-handling behaviour. Fruit-handling behaviour could not be recorded in the field for Orange-headed Tanager *Thlypopsis sordida* and Tropical Kingbird *Tyrannus melancholicus*, and data were obtained from the literature. This categorisation assumes that behaviour remains constant among individuals of the same species (see Foster 1987; Levey 1987). Body mass data were also obtained from published data.

The number of ripe fruits (i.e. fruit crop size) was considered a surrogate of patch quality (Snow 1971; Foster 1990) and was estimated as follows. *Vassobia breviflora* is a gangly species with several main branches arising from the ground, and their corresponding subsequent branches decreasing in size. A portion of the crown constituted by a main branch and its corresponding subsequent branches (hereafter “main branch”) was randomly chosen from the overall crown, and then 10 infructescences were chosen within the main branch. This procedure was a practical solution in the field as an alternative to other techniques constrained by time, such as total fruit crop counting. The number of ripe fruits per infructescence, the number of ripe fruits within the main branch, and the number of main branches were counted. Fruit crop size was estimated as $FC = F \times I \times B$, where FC is fruit crop size, F is the average number of ripe fruits per infructescence within a main branch, I is the number of infructescences within a main branch and B is the number of main branches per plant. In addition, the distances to the forest edge and to the nearest reproductive neighbour were measured to account for the effect of these factors.

Data analysis

We considered that the bird assemblage of the *V. breviflora* population was adequately represented, given that richness accumulation curves of frugivorous birds species approached an asymptote in the two fruiting seasons, and curves did not differ between seasons (Fig. S1, available as Supplemental online material). To assess the effect of bird residence time and fruit crop (patch quality) on fruit consumption (number of fruits removed in each foraging bout), we used generalised linear mixed models (GLMM; Zuur et al. 2009). GLMM extend generalised linear models by including two types of parameters: fixed and random effects (Bolker et al. 2009). Fixed effects are the effects that predictor variables have on the mean of response variables, whereas random effects are the effects that variation within and among levels of a factor have on response variables (Dingemanse & Dochtermann 2013). We modelled variation in fruit consumption by birds with a hierarchical approach. We first built a model for the whole assemblage, in which we included fruit handling (gulpers and pulp consumers), residence time, fruit crop size, body size and their interactions. Additionally, we built another model with the main factors and their interactions, and the effects of distance to the nearest neighbour and to the forest edge as covariates. Then, we fitted the same two models separately for each functional group (without fruit handling) and for the three most abundant species in our study system (without fruit handling and body size): *Turdus rufiventris* (gulper), *Thraupis sayaca* (pulp consumer; Fig. S2) and *Zonotrichia capensis* (pulp consumer). For all models, we used complete observations (i.e. foraging bouts with data on the response and all explanatory variables). To account for the effects of individual focal plant and year on the variation in fruit consumption, we included these two random factors, with plant nested within year. In all models, we used Poisson error structure and log link function.

To visualise variation in fruit consumption by birds, we used nonparametric thin-plate smoothing splines (Wahba & Wendelberger 1980), with response surfaces between residence time, fruit crop and number of fruits consumed. All analyses and graphs were run in R 3.1.2 (R Development Core Team 2014), using the packages lme4 (Bates et al. 2014) and fields (Nychka et al. 2014). The database is available as Supplemental online material (Table S1).

RESULTS

Frugivore assemblage

We recorded 12 species of birds that visited individual focal trees of *V. breviflora* (111 and 212 accumulated hr of focal observations in the first and second fruiting season, respectively; Table S2). In the first season (2012–2013), we recorded 88 visits (mean = 0.79 ± 1.47 individual birds per hr) and 244 consumption events (mean = 2.20 ± 6.50 fruits per hr) in 16 out of 37 individual focal plants. Gulpers were represented by *Turdus rufiventris*, *Elaenia parvirostris*, *Myiodynastes maculatus* and *Tyrannus melancholicus*, and accounted for 53.41% of the visits and 76.64% of the fruits consumed. Pulp consumers were represented by *Thraupis sayaca*, *Zonotrichia capensis*, *Pipraeidea bonariensis*, *Saltator coerulescens* and *Thlypopsis sordida*. In the second season (2013–2014), we recorded 122 visits (mean = 0.58 ± 0.95 individual birds per hr) and 338 consumption events (mean = 1.59 ± 2.77 fruits per hr) in 51 out of 106 focal individual plants. Pulp consumers, represented by *T. sayaca*, *Z. capensis*, *P. bonariensis*, *S. coerulescens*, *S. aurantirostris* and *Arremon flavirostris*, accounted for most of the visits and fruits consumed (81.15% and 82.54%, respectively). Gulpers were represented by *T. rufiventris*, *E. parvirostris* and *Catharus ustulatus*. We did not observe any antagonistic interactions in either season.

Table 1.

Summary of the generalised linear mixed model of the effect of patch quality (fruit crop size), residence time and body size on the number of fruits consumed by the frugivore assemblage ($n = 126$ foraging bouts) feeding on *Vassobia breviflora* fruits (El Cadillal, Tucumán province, Argentina). RT: residence time, FH: fruit handling (pulp consumers), FC: fruit crop size, B: body size.

Parameter	Estimate	SE	z	P
Intercept	- 0.011	0.232	- 0.049	0.961
RT	0.009	0.002	5.604	< 0.0001
FH	0.400	0.197	2.029	0.042
FC	0.001	0.0002	4.541	< 0.0001
B	0.014	0.004	3.839	< 0.001
RT \times FH	- 0.003	0.002	- 1.738	0.082
RT \times FC	- 0.00001	0.000001	- 4.255	< 0.0001
FH \times FC	- 0.001	0.000	- 4.121	< 0.0001
RT \times FC \times FH	0.00001	0.000002	3.697	< 0.001

Variance components of random factors: plant nested within year = $7.3 \times 10^{-12} \pm$ standard deviation = 2.7×10^{-6} ; year = $5.4 \times 10^{-12} \pm 2.3 \times 10^{-6}$.

Foraging behaviour: factors affecting fruit consumption

We found a significant positive effect of residence time and crop size on fruit consumption when analysed at the level of the complete assemblage, and fruit consumption also depended on fruit handling and body size (Table 1). There was also a significant interaction between fruit handling, residence time and crop size (Table 1). This indicates that the interaction between fruit crop size and residence time affects gulpers and pulp consumers differently (Table 1; Fig. 1). The inclusion of distance to the forest edge and nearest neighbour in the model showed the same patterns on fruit

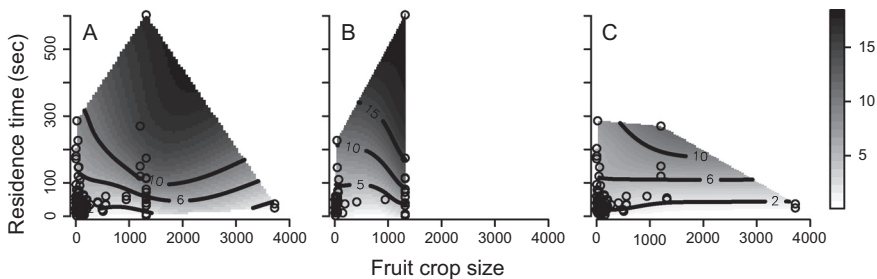


Fig. 1. — Non-parametric thin-plate spline response surfaces for residence time and fruit crop size for A: the frugivore assemblage. B: gulpers and C: pulp consumers in a *Vassobia breviflora* population (El Cadillal, Tucumán province, Argentina). The response variable is number of fruits consumed (vertical bar), and circles represent observed values.

consumption, and had little effect on the main effects (Table S3). Finally, the exclusion of body size showed similar results (Table S4).

Foraging behaviour: gulpers

Fruit consumption by gulpers was positively related to residence time, fruit crop size and body size (Table 2). In addition, a significant negative interaction between residence time and fruit crop was found (Table 2), revealed by the fact that birds increased fruit removal by spending longer periods in plants with small fruit crops (Fig. 1B). The inclusion of covariates showed similar patterns, although the effect of body size was non-significant (Table S3B). In the case of *T. rufiventris*, we also found a significant positive relationship between fruit consumption and crop size (Table 3; Fig. 2A). The inclusion of distance to the forest edge and nearest neighbour in the model showed the same patterns on fruit consumption, and had little effect on the main effects (Table S3).

Foraging behaviour: pulp consumers

Fruit consumption by pulp consumers was positively related to residence time and body size, but not to crop size (Table 2). In contrast to gulpers, this result suggests that pulp consumers increased fruit consumption by foraging for long periods irrespective of fruit crop size (Table 2; Fig. 1C). Similarly, fruit consumption by *T. sayaca* and *Z. capensis* was positively related to residence time (Fig. 2B–C; Table 3). The inclusion of covariates did not change the patterns observed (Table S3B–C).

DISCUSSION

Although the fruit crop size hypothesis establishes a general pattern of fruit trait selection by birds irrespective of species identity, we found that variation in fruit consumption on fruit crop size depends on fruit-handling behaviour and residence time on the plant. This interaction effect between fruit crop size and residence time has not been previously quantified and explicitly included in the description of fruit consumption patterns. Both gulpers and pulp consumers showed a positive relationship between fruit consumption and residence time. These findings held when the effects of body size and spatial context were considered. Our results support the idea that birds use different fruit consumption strategies depending on the synergistic effects of both fruit-handling behaviour and fruit crop size.

Factors affecting fruit consumption

Essentially, pulp consumers spent long residence times in plants regardless of fruit crop size, whereas gulpers spent short residence times in plants with larger fruit crops. Gulpers swallow fruits whole since their flattened bills are quite restricted to crush fruits, and are thus much more gape-limited than those of pulp consumers of the same size (Wheelwright 1985; Levey 1987). As a result, they require much less

Table 2.

Summary of the generalised linear mixed models of the effect of patch quality (fruit crop size), patch residence time and body size on the number of fruits consumed by gulpers ($n = 42$ foraging bouts) and pulp consumers ($n = 84$ foraging bouts) feeding on *Vassobia breviflora* fruits (El Cadillal, Tucumán province, Argentina). RT: residence time, FC: fruit crop size, B: body size.

Parameter	Gulpers			Pulp consumers			
	Estimate	SE	z	Estimate	SE	z	P
Intercept	0.008	0.279	0.030	0.976	0.200	1.863	0.062
RT	0.009	0.002	5.586	< 0.0001	0.001	5.859	< 0.0001
FC	0.001	0.0002	4.400	< 0.0001	0.0002	- 1.446	0.148
B	0.014	0.005	2.639	0.008	0.005	2.803	0.005
RT × FC	- 0.00001	0.000001	- 4.234	< 0.0001	0.000001	0.928	0.353

Variance components of random factors: gulpers, plant nested within year = $1.4 \times 10^{-12} \pm$ standard deviation = 1.2×10^{-6} ; year = $3.9 \times 10^{-12} \pm 2.0 \times 10^{-6}$; pulp consumers, plant nested within year = $8.5 \times 10^{-11} \pm 9.2 \times 10^{-6}$; year = $2.3 \times 10^{-12} \pm 1.5 \times 10^{-6}$.

Table 3.

Summary of the generalised linear mixed models of the effect of patch quality (fruit crop size) and patch residence time on the number of fruits consumed by *Turdus rufiventris* ($n = 19$ foraging bouts), *Thraupis sayaca* ($n = 30$ foraging bouts) and *Zonotrichia capensis* ($n = 27$ foraging bouts) feeding on *Vassobia breviflora* fruits (El Cadillal, Tucumán province, Argentina). RT: residence time, FC: fruit crop size.

Parameter	<i>Turdus rufiventris</i>				<i>Thraupis sayaca</i>				<i>Zonotrichia capensis</i>			
	Estimate	SE	z	P	Estimate	SE	z	P	Estimate	SE	z	P
Intercept	0.891	0.422	2.111	0.035	0.641	0.170	3.778	0.0002	0.733	0.185	3.964	0.0001
RT	0.008	0.006	1.297	0.195	0.009	0.002	4.156	0.00002	0.004	0.002	2.878	0.004
FC	0.001	0.0003	2.438	0.015	-0.0003	0.0003	-0.902	0.367	-0.001	0.002	-0.571	0.568
RT × FC	-0.000005	0.000005	-1.013	0.311	0.000004	0.000004	1.008	0.314	0.00002	0.00004	0.441	0.659

Variance components of random factors: *T. rufiventris*, plant nested within year = 6.0×10^{-12} ± standard deviation = 2.5×10^{-6} ; year = 3.1×10^{-12} ± 1.8×10^{-6} ; *T. sayaca*, plant nested within year = 3.0×10^{-15} ± 5.4×10^{-8} ; year = 2.9×10^{-11} ± 5.4×10^{-6} ; *Z. capensis*, plant nested in year = 4.8×10^{-14} ± 2.2×10^{-7} ; year = 0.

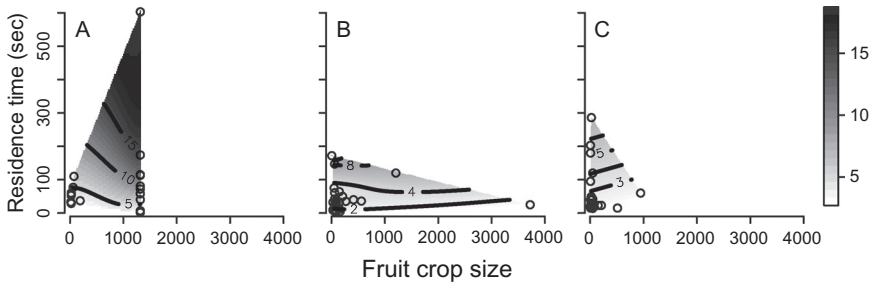


Fig. 2. — Non-parametric thin-plate spline response surfaces for residence time and fruit crop size for A: *Turdus rufiventris*. B: *Thraupis sayaca* and C: *Zonotrichia capensis* in a *Vassobia breviflora* population (El Cadillal, Tucumán province, Argentina). The response variable is number of fruits consumed (vertical bar), and circles represent observed values.

time to handle fruits, and the appropriate strategy to maximise energy intake rate should be minimisation of foraging periods in high-quality patches (Schoener 1971; Foster 1990). In contrast, pulp consumers require more time to handle fruits, so the appropriate strategy should be maximisation of fruit consumption, regardless of patch quality (Schoener 1971; Foster 1990). In this sense, a morphological trait (beak type) partly determines the variation of a behavioural trait (fruit handling). In the case of guppers, fruit-handling behaviour would be more limited than in the case of pulp consumers due to beak morphological restrictions.

Fruit consumption was also related to body size at both the assemblage level and the functional group level. Larger bird species are expected to have higher fruit consumption rates and spend more time in plants than smaller ones (Howe 1979; Pratt & Stiles 1983; Martin 1985; Wheelwright 1991; Wotton & Kelly 2012). Energetic requirements are basic components of foraging models, and body size thus needs to be taken into account when considering the role of fruit-handling behaviour in fruit consumption patterns of different species.

Ecological context also plays a role in fruit-eating behaviour. In our study system, both fruit neighbourhood and distance to the forest edge had a weak effect at the plant individual scale. The presence of heterospecific and conspecific nearby plants fruiting synchronously and sharing the same dispersers might lead to an increase or decrease in the number of fruits removed per plant, as a consequence of facilitation or competition for dispersers, respectively, which are attracted to habitat patches with higher fruit availability (Jordano & Schupp 2000; Saracco et al. 2005; Carlo & Morales 2008). The low responses of bird species to fruit availability in the neighbourhood could have been the result of fruit abundance tracking at other scales different from the individual focal scale (Blendinger & Villegas 2011; Blendinger et al. 2012). Several authors have stressed the importance of considering scale effects at different temporal and spatial scales (Sallabanks 1993; García & Ortiz-Pulido 2004). As long as they are subjected by ecological contingency, optimal foraging predictions based on individual plant patches would become affected by the fruit-bearing plant neighbourhood and their landscape features.

Fruit handling and consequences for seed dispersal

Fruit handling, together with body size and gape width, defines the functional role of species of the assemblage in a seed-dispersal system. Hence, both species composition and functional diversity of the frugivore assemblage could have implications for mutualistic interaction (e.g. Fedriani & Delibes 2009; Escribano-Ávila et al. 2013; Plein et al. 2013; Dehling et al. 2014). From the bird's perspective, this scenario allows birds to share the same fruit resources, which would promote mechanisms of segregation between bird species and therefore facilitate coexistence. From the plant's perspective, different bird functional roles have implications for disperser effectiveness (sensu Levey 1987; Schupp 1993). Pulp consumers are traditionally considered to have a detrimental effect on plant fitness by ingesting fruit rewards without dispersing seeds (Schupp 1993). However, multi-seeded plants such as those in our study system experience high variation in the number of seeds ingested by pulp consumers (Levey 1987; Valburg 1992). In the case of *V. breviflora*, seeds (diameter ~ 0.2 mm; Bernacki 2014; Bernacki et al. in press) are swallowed by several pulp consumers (*T. sayaca*, *A. flavirostris*, *Atlapetes citrinellus*, *Pipraeidea melanonota*, *Poospiza erythrophrys*; Giannini 1999; see Supplemental material). This suggests that seed size does not impose limits to seed ingestion, and both gulpers and pulp consumers might be effective seed dispersers of *V. breviflora* seeds. This prediction needs further testing in the light of the number of ingested seeds, and seed viability after gut passage.

CONCLUSION

As Moermond and Denslow (1983) and Levey (1987) established, the functional partition between gulpers and pulp consumers would result in ecological and evolutionary consequences for the interaction. Differences in fruit-eating behaviour among species might lead to different patterns of natural selection on fruit crop size. The explicit demonstration of such divergence in the shape and intensity of frugivore-mediated selection has not yet been made. In this sense, bird-mediated natural selection on fruit display could be understood if species composition and functional diversity of frugivore assemblages are taken into account (Palacio et al. 2014). Overall, the partitioning of foraging strategies suggests that bird functional groups might be driving, under different directions and magnitudes, fruit display traits.

ACKNOWLEDGEMENTS

We thank M. Portal and Plásticos La Rioja for logistical support, and S.S. Santistevé, A. Montero and O.R. Delgado for field assistance. We specially thank H. Ayarde for field assistance and kindly providing information on the study area. E. Schupp, P. Blendinger, A. Giraudo, S. Benítez-Vieyra, J. Fornoni and an anonymous reviewer provided valuable comments on the manuscript. Fieldwork was authorised by Dirección de Flora, Fauna Silvestre y Suelos, Tucumán province, Argentina (Number 69/13 given to M. Ordano).

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

FUNDING

This study was partially supported by Fundación Miguel Lillo and Consejo Nacional de Investigaciones Científicas y Técnicas [CONICET, PIP 11420110100395 to M. Ordano]. The authors declare no conflicts of interest.

SUPPLEMENTAL DATA

Supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/03949370.2015.1080195>

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