

Research article

Size matching between fruits and bill gapes differentially affects gulper and masher frugivorous birds

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Subject Editor: Eliana Cazetta Editor-in-Chief: Pedro Peres-Neto Accepted 8 December 2024 Birds feeding on fruits (frugivores) affect seed dispersal, seedling establishment and, ultimately, plant assemblage composition. Thus, the mechanisms underlying fruit consumption by birds are central to disentangling the assembly dynamics of mutualistic interactions and their effects on ecosystem functioning. In this regard, the sizematching hypothesis states that the bill gape width is an anatomical filter that allows a bird to ingest a fruit. However, handling behaviour could allow birds to overcome anatomical constraints that limit the consumption of certain fruit species. Here we tested how size matching affects consumption rates and probabilities of frugivores that swallow the fruit unprocessed (gulpers) and those that mandibulate the fruits before ingestion (mashers). Gulpers showed a weak augment in both the rate and probability of fruit consumption as bill-gape width increased relative to fruit diameter. On the other hand, mashers did not respond to size matching either in consumption rate or probability. Altogether our results highlight that other factors besides size are affecting the consumption rate and probability of frugivorous birds. Thus, gulpers and mashers fruit consumption could be subject to different mechanisms regardless size matching. In this regard, fruit traits and animal abilities interact leading to consumption by mashing or gulping the fruit highlighting the dynamic nature of handling behaviour. Altogether, our results warn about the unevaluated overutilization of size-matching as the main mechanism to test the multiple facets of the ecology and evolution of frugivory and seed dispersal. Thus, including handling behaviour and other factors into the mechanisms underlying fruit-frugivore interactions could greatly improve our understanding of mutualistic interactions.

Keywords: ecosystem functioning, frugivores, fruit traits, mutualistic interactions, seed dispersal, trait matching



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Introduction

Feeding behaviour results in key ecosystem functions performed by animals (Sekercioglu et al. 2016). Specifically, animals that feed on fruits (frugivores) often represent mutualistic interactions that affect plant reproduction and trajectories of plant assemblages (Jordano 2000, Morán-López et al. 2018). In particular, birds maintain plant diversity and influence the carbon storage in forests (Carlo and Morales 2016, Morán-López et al. 2018, Bello et al. 2024). Thus, the mechanisms underlying the consumption of fruits by frugivore birds are central to assemble mutualistic interactions and articulate their effects on ecosystem functioning.

In this regard, the size matching hypothesis states that the bill gape width is the anatomical filter that allows a bird to ingest a fruit. This mechanism was suggested to be one of the main drivers of the occurrence of mutualistic interactions of birds and fruits (Olesen et al. 2011, Dehling et al. 2016, González-Varo et al. 2022). That is, any fruit larger than the bill width has a near zero probability to be eaten (González-Varo and Traveset 2016). Nevertheless, using fruit diameter and bill gape width alone could be an oversimplification of the feeding process of frugivorous birds. Fruit traits like shape and softness could allow non-matching species to interact. For instance, small-gaped birds consume fruits larger than their gape size typically by pecking pieces of mature fruits, due to their soft structure. On the other hand, birds handling behaviour could allow birds to overcome anatomical constraints that limit the consumption of certain fruit species (Moermond and Denslow 1985, Levey 1987). In sum, if birds can cut the fruit into pieces, the gape width-fruit diameter relationship no longer matters.

Two main feeding strategies have been described for frugivorous birds (Moermond and Denslow 1985). Species that usually mandibulate the fruit in the bill before ingestion are classified as mashers (e.g. tanagers, finches, parrots). On the other hand, species that frequently swallow the whole fruit are called gulpers (e.g. robins, tyrants, doves). Despite the importance given to size matching as a mechanism that helped understand fruit-frugivore interactions, feeding strategies are generally overlooked. Nevertheless, feeding strategies could determine how constrained a frugivore is by size matching. Thus, birds that are able to process the fruits in their bills before ingestion could be less constrained by size matching (Fukui 2003). Conversely, frugivores with weaker bills unable to 'work' the fruit before ingestion will be more constrained by size matching. These constraints to fruit consumption could determine whether or not a bird species consumes a plant species, but it is also expected that handling behaviour and size matching affect the fruit consumption rate in pairs of species that actually interact.

Since mashers often process the fruits in the bill before ingestion, the handling time used by mashers is higher than gulpers (Moermond and Denslow 1985, Jordano and Schupp 2000, Palacio et al. 2017). Thus, it is expected for mashers to show lower consumption rate than gulpers when compared at equal, non-limiting, bill gape width and fruit size.

Consequently, size matching between fruits and bill gapes differentially affects gulper and masher frugivorous birds, but also the plant's seed dispersal effectiveness (at least in the quantitative axis; Jordano and Schupp 2000, Blendinger 2017, Schupp et al. 2017) and/or the resource acquisition effectiveness by animals (Blendinger et al. 2022). This differential effect raises doubts about the generality of the anatomical filtering in frugivory and seed dispersal interactions. Given the central role that frugivorous birds play sustaining plant communities and the consequent ecosystem functions (Schleuning et al. 2020, Marjakangas et al. 2022), assessing the interplay between feeding strategies and size matching is key to amplify our understanding on the assemblage of frugivory interactions.

Using a large dataset of fruits consumed by frugivorous birds, we analysed how size matching controls the fruit consumption rate and consumption probability of birds with contrasting handling behaviour, namely mashers and gulpers. We analysed how the consumption rate and probability vary as a function of the difference between bill gape width and fruit diameter for each foraging behaviour separately. We expect both mashers and gulpers to show higher consumption rate and probability of fruits smaller than their bills (Fig. 1). However, as mashers are expected to be less sensitive to size matching, we expect their consumption rate and probability to increase smoothly as bill gape width increases in relation to fruit diameter (Fig. 1). Conversely, we expect gulpers to increase the consumption rate and probability markedly as fruit diameter shifts from slightly larger to slightly smaller than their bills. Moreover, we expect gulpers

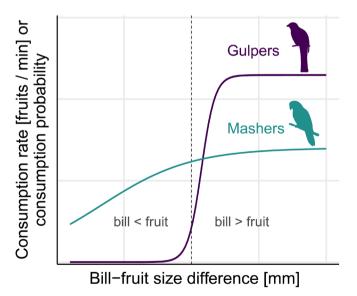


Figure 1. Expected consumption rate as a function of the bill gape width—fruit diameter difference for mashers and gulpers. Mashers mandibulate and process the fruit in the bill before ingestion whereas gulpers swallow the fruits unprocessed. The dashed vertical line indicates no difference between bill gape width and fruit diameter. We expect consumption probabilities to behave similarly for gulpers and mashers, but we have no hypothesis about the values of the upper asymptotes.

to reach a maximum consumption rate higher than mashers, as the latter require longer handling time (Fig. 1). In relation to consumption probability, we expect a similar pattern for mashers and gulpers regarding the contrasting steepness of the curves (Fig. 1), but we have no hypothesis about the values of the upper asymptotes.

Material and methods

Data gathering

We gathered data from diverse bibliographic sources. We conducted a systematic search of articles with information on the number of fruits of a plant species consumed per time unit by bird species across the globe. The search combined the terms 'bird foraging', 'fruit', 'seed dispersal', 'fruit removal', 'fruit consumption', 'feeding rate'. We used the terms with '+', 'and' and 'or' in all possible combinations. We used the search engine Google Scholar and reviewed the first 15 pages given by the search (or all available when less). We made our main search in 2019; thus, novel articles are not included for analysis here. Additionally, we only included studies published in Spanish, English or Portuguese and excluded thesis or non-indexed publications letting out all articles that may contain valuable information but published in other languages or in other platforms. Articles that provided data on the number of fruits consumed by birds per unit time were selected. The interaction data were used when both the bill gape width of the bird species and the fruit diameter of the plant species were available in the literature (either in the same article or in other source). If the data were from the same article, we preferentially used those values. If the trait data were missing we searched for it in McFadden et al. (2022) and Atlantic Birds Traits (Rodrigues et al. 2019) databases for the birds, or obtained from our own measurements of museum vouchers or living birds collected through years of fieldwork. For absent fruit data, we searched in Google Scholar using the species name and synonyms. Unpublished data from PGB and GM were also included. Here observations were taken counting the number of fruits consumed by a frugivore bird species and the time spent by each bird consuming fruits in the plant. Altogether, and after cleaning based on the completeness of the data available, we had a total of 41 sources for further analysis. We obtained measurements of fruit consumption rate from 819 interactions, corresponding to 738 unique pairs of bird-plant species from 94 plant species and 158 bird species (107 gulpers and 51 mashers). The gulper and masher classification was made based on the most frequently observed feeding behaviour, according to information from the studies used, Birds of the World web site (https://www.birdsoftheworld.org), WikiAves (https:// www.wikiaves.com.br) and our personal observations. Of the 819 bird-plant interactions, 549 corresponded to gulpers, and 270 to mashers. Most pairs of species were from the Neotropics, mainly the Yungas cloud forests and the Atlantic forests. The bill size and fruit size distribution of our dataset

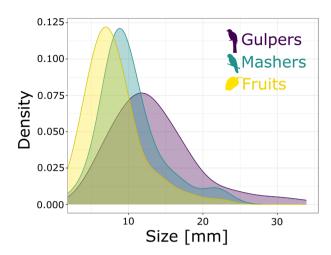


Figure 2. Distribution density of bill gape width of gulpers (purple) and mashers (green) and fruit diameter (yellow) of species used in this study.

is shown in Fig. 2. A general overview on data and references can be found in the Supporting information.

To evaluate how the bill-fruit size difference (i.e. size matching) affects the probability of bird species consuming a plant species, we created pseudo-absences of species interactions. Within each source study we identified all the possible bird-plant species pairs, and considered as non-interacting the pairs for which the consumption rate was not recorded. As the source studies were carried out in relatively small areas or in the same biome, it is safe to assume that the non-recorded pairs of species have overlapping distributions. Despite some pairs of species for which the consumption rate was not recorded and may actually interact, the source studies aimed to measure the consumption rate in most pairs of species that do interact, so most of our pseudo-absences likely reflect real absences and interactions that occur at very low frequency. Thus, the use of pseudo-absences precludes the estimation of an unbiased consumption probability, but it is expected to recover probabilities proportional to the real ones, likely underestimated. Nevertheless, our aim was to assess how the consumption probability varies as a function of the bill-fruit size difference, which effect is not expected to be biased (i.e. the shape of the curve is not affected by the underestimation, only its scale). With this procedure we obtained a total of 1931 pseudo-absences, but 96% (1860) were derived from the three studies with the largest number of bird and plant species (Correia 1997, Gondim 2002 and unpublished data from PGB). Hence, this analysis relies mostly on a small subset of studies and results should be interpreted accordingly. These three studies contained 83 bird species and 61 plant species, resulting in 382 interactions.

Data analysis

To evaluate how the consumption rate and consumption probability vary as a function of the bill–fruit size difference in gulpers and mashers, we fitted two non-linear models.

We assumed a Gamma distribution for the consumption rate, and a Bernoulli distribution for the consumption occurrence {pseudo-absence=0, consumption rate recorded=1}. Their conditional means were modelled as four-parameter logistic functions of the bill–fruit size difference, estimating the upper asymptote and fixing the lower one at zero. All the parameters were allowed to vary among gulpers and mashers. We included random effects over the intercept at the logit scale of the bird and plant species, and in the consumption rate model we also included a random effect of the study source. We did not include this term in the consumption probability model because it assigned too much weight to many studies having too few observations. Hence, we preferred to remove this factor and base our results mostly on the three sources with many observations.

We fitted the models with a Bayesian approach, sampling the posterior distributions with Stan (Stan Development Team 2024). We used weakly informative prior based on simulations. For the consumption rate model, we ran eight Markov chain Monte Carlo (MCMC) chains for 3400 iterations each, leaving 1000 for warm-up and saving one every three iterations, yielding 6400 samples in total. For the consumption probability model we ran six chains for 4000

iterations, leaving 1000 for warm-up and saving one every two iterations, yielding 9000 samples in total. Both models converged based on Rhat values, with large effective sample sizes (Table 1), and showed adequate fit to data (Supporting information). Models are fully specified in the Supporting information. Effect of both plant and bird phylogenies were tested resulting in no evidence of correlation between the response variables and the evolutionary history of both interacting parties (Supporting information). All the analyses were performed in R ver. 4.2.0 (www.r-project.org). The data and code to reproduce our analyses are hosted on GitHub (https://github.com/barberaivan/redoto_birdo_sama.git).

Results

We gathered a dataset that included 94 plant species (81 genera and 43 families) and 158 bird species (from 101 genera and 26 families). Most represented plant families were Lauracea, Melastomataceae and Rubiaceae. Most represented bird families were Turdidae, Tyranidae and Thraupidae. Data sources were mainly from South America (Atlantic Forest and Yungas Forest) and Europe (Mediterranean shrubland)

Table 1. Summaries of the marginal posterior distribution of parameters from the consumption rate and consumption probability models, along with Markov chain Monte Carlo (MCMC) metrics. The 95% credible intervals (CI) are highest density intervals. Rhat values < 1.01 indicate convergence of the MCMC algorithm (Vehtari et al. 2021). The effective sample size is the number of independent-equivalent samples obtained through MCMC, corresponding to the central part of the distribution (bulk) or the tails (Vehtari et al. 2021). Symbols: α =intercept at the logit scale; β =slope at logit scale; κ =upper asymptote for logistic function; ϕ =dispersion parameter of the Gamma distribution; σ =standard deviation of random effects; R^2 =Bayesian R^2 , as percentage (Gelman et al. 2019). Suffixes g and m indicate whether each parameter corresponds to gulpers or mashers, respectively. Suffixes bird, plant and source identify the standard deviation of random effects for these factors. See the Supporting information for further modelling details.

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Parameter-metric	Mean	Mode	95 % CI	Rhat	Effective sample size (bulk, tail)
Consumption rate model					
$lpha_{ m g}$	-1.673	-1.825	-2.324, -0.940	1.001	4457, 5360
$lpha_{ m m}^{\circ}$	-1.676	-1.965	-2.468, -0.738	1.001	4310, 5771
$oldsymbol{eta_{\mathrm{g}}}$	0.030	0.031	0.013, 0.051	1.000	6736, 6305
$\hat{\beta_{m}}$	0.011	0.011	-0.023, 0.044	1.000	6622, 5819
$\mathbf{\kappa}_{\mathrm{g}}^{-}$	19.952	18.338	12.156, 29.775	1.001	4552, 5595
$\overset{\circ}{\kappa_{\mathrm{m}}}$	17.526	12.759	8.708, 29.331	1.000	4211, 5057
Φ_{g}	0.469	0.469	0.416, 0.527	1.000	6298, 5740
Φ_{m}	0.388	0.381	0.315, 0.462	1.000	5980, 6187
σ_{plant}	0.519	0.499	0.368, 0.666	1.002	4344, 5407
$\sigma_{\mathrm{bird,g}}$	0.094	0.040	0.000, 0.221	1.000	3978, 5535
$\sigma_{\mathrm{bird,m}}$	0.136	0.108	0.000, 0.301	1.000	3707, 4613
σ_{source}	0.649	0.593	0.397, 0.935	1.001	3842, 5104
R_{ϱ}^{2}	2.260	1.710	0.099, 4.838	1.000	6550, 6265
R_{g}^{2} R_{m}^{2}	0.686	0.007	0.000, 2.531	1.000	6145, 5926
Consumption probability model					
$lpha_{ m g}$	-0.854	-0.794	-1.554, -0.091	1.003	1310, 3259
α_{m}°	-0.559	-0.591	-1.347, 0.220	1.003	1322, 3033
$eta_{ m g}$	0.052	0.050	-0.008, 0.110	1.002	3988, 6356
$\mathring{\beta_{m}}$	0.005	0.004	-0.075, 0.086	1.001	4217, 7019
\mathbf{K}_{g}	0.992	0.999	0.975, 1.000	1.000	7259, 6681
κ_{m}°	0.989	0.999	0.966, 1.000	1.002	6600, 5819
σ_{plant}	2.760	2.684	2.194, 3.371	1.001	3198, 5631
$\sigma_{ m bird,g}$	0.911	0.865	0.647, 1.195	1.000	4749, 7033
$\sigma_{\mathrm{bird,m}}$	1.403	1.337	0.965, 1.882	1.001	3659, 6418
R_{ϱ}^{2}	0.578	0.013	0.000, 1.649	1.001	4068, 6398
R_{g}^{2} R_{m}^{2}	0.190	0.003	0.000, 0.738	1.000	7586, 8080

reflecting our language searching bias. Fruit diameter ranged from 1.8 mm Phoradendron selloi to 22.35 mm (Alibertia sesilis). Bird gape width ranged from 3.1 mm Eupsittula aurea to 33.92 mm Ramphastos toco. The distribution of size for fruits and birds are in general left-skewed (Fig. 2). Most interacting bird-plant species pairs had bills larger than fruits, but there were also pairs with bills smaller than fruits. Gulpers had a lower proportion of species pairs with bill gapes smaller than fruit compared to mashers: 7.84% (43/549) versus 18.14% (49/270), respectively. In gulpers, the fruit consumption rate varied mostly between 0.03 and 15.00 fruits min⁻¹, with a mean of 3.61 fruits min⁻¹, and reaching an extreme value of 24.84 fruits min⁻¹ (*Turdus rufiventris* eating *Myrsine coriacea*). In mashers, it varied between 0.07 and 36.6 (Tersina viridis feeding on Schinus terebinthifolius), with a mean of 2.74 fruits min⁻¹.

In both gulpers and mashers, the consumption rate and consumption probability did not show a sharp increase as a function of the bill–fruit size difference, with models showing small R² values (Table 1). The predicted means were always above zero and did not reach an upper asymptote (Fig. 3). However, gulpers showed a small but statistically clear increase in the mean consumption rate with increasing bill gape width relative to fruit diameter, while mashers showed null or negligible effects. In gulpers, the consumption

rate increased from ~ 3 fruits min⁻¹ for bills 10 mm smaller than the fruits to ~ 6 fruits min⁻¹ for bills 25 mm larger than the fruits, with a posterior probability of 1 for the slope at the logit scale (β) being positive (Fig. 3a, Table 1). In mashers, the overall consumption rate was lower than in gulpers, and was almost not affected by the bill-fruit size matching [Pr(β > 0) = 0.0.743; Fig. 3b, Table 1]. The consumption probability showed a similar pattern, but in gulpers the bill–fruit size difference showed a larger effect compared to its effect on consumption rate: it increased from ~0.3 for bills 16 mm smaller than fruits to ~0.6 for bills 25 mm larger than fruits [Pr(β > 0) = 0.956; Fig. 3c, Table 1]. In mashers, the bill gape-fruit width difference had no effect on consumption probability [Pr(β > 0) = 0.547; Fig. 3d, Table 1].

Discussion

Using an extensive dataset, we tested how size matching of frugivores and fruits affects the consumption rate and consumption probability of birds with contrasting handling behaviour: gulpers and mashers. Contrary to our expectations, we found that the size difference between bills and fruits has a small or null effect on consumption rate and consumption probability. Indeed, consumption occurred in pairs

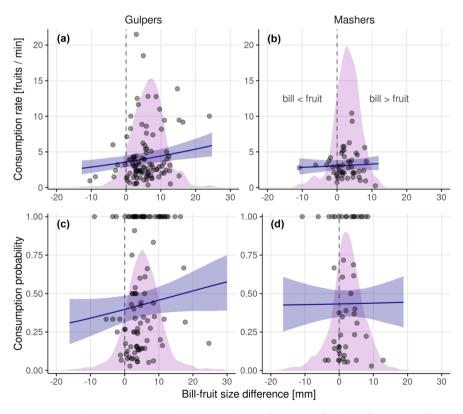


Figure 3. Consumption rate (a–b) and consumption probability (c–d) as a function of the bill-fruit size difference for gulpers (a, c) and mashers (b, d). Lines and ribbons show the predicted mean for average random effects, summarized by the posterior mean and the 95% equal-tailed credible intervals. Points show the mean consumption rate (a–b) or consumption probability (c–d) by bird species. The pink shade shows the distribution of the bill–fruit size difference in each dataset (the density values are not shown in the y-axis, as they are not informative).

of bird-plant species with bill gapes smaller than the fruit width, both in gulpers and mashers. Nevertheless, gulpers showed a small increase in consumption rate with increasing bill size relative to fruit size, and this effect was larger for consumption probability. On the contrary, mashers showed a constant consumption rate as a function of the bill-fruit size difference, and an uncertain consumption probability in relation to size matching. This indicates that size matching does not affect mashers but has a small effect in gulpers, which is more evident in allowing the interactions to occur than in regulating their intensity. Altogether our results suggest that despite the intuitive nature of size matching, other traits are affecting the consumption rate and probability of frugivorous birds. Altogether, our results warn about the unevaluated overutilization of size-matching as the main mechanism to test the multiple facets of the ecology and evolution of frugivory and seed dispersal.

Gulpers consume fruits directly and, as a result, can consume more fruits as long as they are smaller than their bills. That is, size matching appears to be a relevant factor affecting the quantitative component of seed dispersal effectiveness of gulpers. Nevertheless, size is not a categorical constraint on fruit consumption by gulpers. Instead, fruit size acts as a soft filter for gulper fruit consumption. On the other hand, the time used by mashers to handle the fruits before ingestion may be one of the main constraints affecting consumption rates. In this regard, time used by a bird to process and consume a fruit could be affected by fruit softness, the number of seeds or the way in which pulp is attached to seeds (Dumont 1999, Rojas et al. 2021). Feeding strategy classification is based on what is expected of a bird when consuming fruits (Moermond and Denslow 1985), based primarily on bill shape and morphology which are deeply rooted in the evolutionary history of the groups (e.g. at the family level). Nevertheless, bird feeding strategies are not static, but they can switch between one another. Our results support this observation: gulpers consuming fruits bigger than their gape width implies they can mandibulate and process the fruit before ingestion. Additionally, high consumption rates observed in mashers could easily be because they are swallowing small fruits without processing them (e.g. Tersina viridis eating Schinus terebinthifolius; data base used for analysis - see data availability statement). However, the ability to process fruits before ingestion results from the interaction between bill strength and fruit softness. Thus, mashers appear to be more able to process fruits than gulpers. In addition, different intrinsic motivations could determine the decision of birds to exert one behaviour over another ranging from specific needs to personality related decisions (Zwolak and Sih 2020). This can result in mashers swallowing fruits or mandibulating them if they want to. In summary, frugivory interactions are a complex interplay of mechanisms and reducing it to a few factors could obscure our understanding of this ecosystem function.

Size matching was presented as a key mechanism that explains the interaction patterns in frugivory and seed dispersal networks (Olesen et al. 2011, Dehling et al. 2016,

Bender et al. 2018). In addition, size matching was used as well to predict the stability of interacting networks facing species loss and climate change (Donoso et al. 2020, Schleuning et al. 2020, Peña et al. 2023). These studies assume size mismatching as a constraint that strongly limit the links between fruits and frugivorous birds. Nevertheless, the limits of forbidden interactions are fuzzy due to intraspecific variability in size of both plants and animals (González-Varo and Traveset 2016). Here we show that size matching is less prohibitive than previously proposed and is virtually unimportant depending on the handling behaviour of birds (but see Wheelwright 1985). For both bird and fruit size we used the mean values, reducing the variation found in nature. That is, frugivores can select fruits of a certain size within the intra-specific and intra-individual variation (González-Varo and Traveset 2016, Snell et al. 2019). Thus, using means could lead to inaccurate estimations of size matching that may show birds interacting with bigger fruits than their bills and vice versa. Nevertheless, we believe these differences are not big enough to discard the main notions obtained from our results. Despite gulpers and mashers being constrained at some point by fruit size, birds from both handling behaviours included fruits that are larger than their bill gapes. That is, fruit size is just one of the multiple traits that are influencing the interactions between frugivores and fruits (Rojas et al. 2021). Mechanisms that could obscure the influence of size in fruit-frugivore interactions are fruit hardness, chemical composition, seed load and size, frugivore intrinsic preferences and physiology (Levey and Martínez del Rio 2001, Fukui 2003, Nelson and Whitehead 2021, Pizo et al. 2021, Rojas et al. 2021). Moreover, these mechanisms are not mutually exclusive and hierarchically structure frugivores choices (Sallabanks 1993, Rojas et al. 2023). In addition, the specific motivations of individual birds to consume fruits will be linked to the fulfilment of the digestive tract. That is, birds with empty guts will tend to consume more fruits. Finally, consumption rates from gulpers and masher with same body size have contrasting functional responses (Blendinger et al. 2022). In this scenario, using fruit size alone to draw a limit for fruits and birds to interact and understanding fruit consumption could be misleading (as reported for mammals; Ong et al. 2022). Based on the results presented here, seed size-based approaches appear to be better suited to understanding the frugivory process than those based on fruit size (Nunes Martinez and Mistretta Pires 2024).

For years, gulpers-masher dichotomy was an overlooked aspect of frugivory and seed dispersal interactions. Either because mashers were assumed as suboptimal dispersers and gulpers as legitimate dispersers, the handling behaviour (and often mashers too) was left out from the plethora of interconnected mechanisms explaining fruit choices and seed dispersal by birds (Jordano 2000, Jordano and Schupp 2000). Here we showed how handling behaviour modulates size matching, downsizing the importance of it in the fruit consumption process. Consequently, including handling behaviour as part of the mechanisms that explains the interactions could lead to a better understanding of the resultant effects

of frugivore functions in a community. Future work should address the interplay between the multiple factors underlying frugivory interactions enhancing our understanding about ecosystem functioning. Our results invite to rethink how different mechanisms, often tested as isolated parts, dialogue among each other determining frugivory and seed dispersal interactions and their effects on the ecosystem.

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Author contributions

Tobias Nicolas Rojas: Conceptualization (lead); Data curation (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing – original draft (lead); Writing – review and editing (lead). Marco A. Pizo: Data curation (equal); Investigation (equal); Writing – review and editing (equal). Pedro G. Blendinger: Data curation (equal); Investigation (equal); Writing – review and editing (equal); G. Giselle Mangini: Data curation (equal); Investigation (equal); Writing – review and editing (equal). Iván Barberá: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://github.com/barberaivan/redoto_birdo_sama.git (Rojas et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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