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Original article

Title

Frugivorous bird foraging is related to pericarp color and ultraviolet reflectance in fruiting shrub species

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Abstract

Seed dispersal by birds is critical for regeneration and maintenance of plant populations. Birds likely rely on both visible light of human's eyes and ultraviolet (UV) reflectance when foraging for fruit. Fruit color is suggested to be an honest signal that allows birds to assess nutrient status. We assessed UV reflectance and pericarp color as honest indicators of fruit maturity in three fruiting shrubs in Osaka, Japan. We measured sugar content and light spectra in the fruits of *Eurya japonica*, *Ligustrum obtusifolium* and *Ligustrum japonicum* and observed birds foraging on target individuals. We found that a model including fruit color and UV reflection as explanatory variables best explained variation in fruit sugar content in *E. japonica* and *L. obtusifolium*, whereas UV reflection alone best explained variation in *L. japonicum*. Next, we assessed relationships between fruit color and bird foraging behavior and found strong temporal correlation between active foraging and peak sugar content. Bird foraging behavior differed among the three shrub species. This is probably because fruit consumption by birds is not entirely dependent on fruit color or sugar content of the fruits. It must depend on various factors such as presence of fruiting neighbors of conspecific or heterospecific plants and seasonal variation of population-level or community-level fruit abundance.

Keywords: fruit color; mutualism; phenology; reflectance spectrum; seed dispersal

Introduction

Seed dispersal is an important ecological process regulating regeneration and spatial distributions in plants (Takahashi and Kamitani 2003; Masaki 2009). Dispersal conveys three key advantages (Howe and Smallwood 1982). First, dispersal allows seedlings to avoid high density-dependent predation and competition near their parent plants (Nathan 2006). Second, it allows for the colonization of new areas (Amodeo and Zalba 2013; Takano et al. 2019; Silva et al. 2021). Finally, directed dispersal by animals can transport seeds to locations that are more likely to be favorable for germination and establishment (Wenny 2001; Breitbach et al. 2012). Due to these advantages, plants have evolved a stunning array of dispersal structures that aid in abiotic dispersal by wind and water or biotic dispersal by animals (Howe and Smallwood 1982; Wenny et al. 2016). Birds are a particularly dominant dispersal agent for plants (Willson and Whelan 1990; Wenny et al. 2016). Frugivorous birds disperse the seeds of approximately 68,900 plant species, representing more than 1,500 genera from 240 families (Wenny et al. 2016). Collectively, this is representative of roughly 25% of all seed plant species and more than 50% of all plant families. Among bird-dispersed genera, approximately one third include shrub species and 58% include trees. Plants must entice birds to their seeds; this is typically done by reward, usually via sugar or water content (Izhaki et al. 2002; Lei et al. 2021). The advantage for the plant is that the pulp is removed when the bird ingests it, which promotes germination (Yagihashi et al. 2000). For this relationship to function, birds must be able to judge fruit reward status using fruit signals.

Visual detection is critical for foraging birds, in contrast to olfactory reliance in mammals (Debussche and Isenmann 1989). Fruit color is therefore suggested as an honest signal of nutritional content for birds (Lomáscolo et al. 2010; Schaefer et al. 2014) and several studies have provided evidence for the importance of fruit color in diurnal foraging (Debussche and Isenmann 1989; Schaefer et al. 2007). Fruit color typically changes with an increase in sugar content (Koike et al. 2008; Sakurai et al. 2013; Teka 2013). High sugar content is associated with darker colors and low chroma (Cazetta et al. 2012). In one example, fruits with higher lipid content were significantly darker and of lower chroma than congeners with lower lipid content, and two warbler species selected for the less chromatic fruits (Schaefer et al. 2014).

Birds have tetrachromatic color vision and therefore perceive ultraviolet (UV) light. This is below the spectrum visible to humans, which is approximately 400–750 nm (Andersson et al. 1998; Lomáscolo et al. 2010). Burkhardt (1982) reported that many fruits strongly reflect UV light and UV reflectance may be an important attractant for frugivorous birds (Siitari et al. 1999; Altshuler 2001). If birds use UV reflectance as a criterion in foraging, then UV reflectance should be an indicator of fruit maturity. Here, we focused on the mutualistic relationship between frugivorous birds and three shrub species, *Eurya japonica* Thunb. (Pentaphylacaceae), *Ligustrum japonicum* Thunb. (Oleaceae) and *Ligustrum obtusifolium* Sieb. et Zucc.. We first assessed if fruit color and UV reflectance are honest signals of fruit maturity. We further assessed relationships between fruit color and foraging behavior and examined foraging behavior of birds among the three shrub species.

Methods

Study area

Our study took place at the Botanical Garden of Osaka Metropolitan University (34°45′49"N, 135°40′54"E), located in the northwest portion of Mt. Ikoma, Osaka Prefecture, Japan. The Botanical Garden was established in 1950 and is 25.5-ha in size. Average annual temperature and precipitation, taken from the Hirakata Meteorological Observatory located 5 km north of the study site, were 15.6°C and 1,342.8 mm, respectively, for the period of 1981–2010.

The garden is mostly forested, with both native and planted trees. It has a collection of more than 300 species of Japanese woody plants, and is covered by restored representative forest types in Japan, e.g. evergreen broad-leaved forest, deciduous broad-leaved forest and coniferous forest.

Diverse birds and mammals were observed in the garden. During the two-year survey between 2009 and 2011, 74 bird species including 15 summer birds and 19 winter birds were observed (Taira 2014). Resident frugivores, brown-eared bulbul (*Hypsipetes amaurotis*, Pycnonotidae) and Japanese white-eye (*Zosterops japonicus*, Zosteropidae), were the most and the second abundant species of all the observed bird species in the garden. They were observed in all the month of the year. Among the winter birds, Naumann's thrush (*Turdus naumanni*, Muscicapidae) and pale thrush (*Turdus pallidus*) were dominant and seen through November to May. Summer birds such as barn swallow (*Hirundo rustica*, Hirundundae), narcissus flycatcher (*Ficedula narcissina*, Muscicapidae) and Asian stubtail (*Urosphena squameiceps*, Cettidae) were seen around April-October.

In 2022, automatic cameras with an infrared trigger placed near the ground captured red fox (*Vulpes vulpes japonica*), raccoon dog (*Nyctereutes procyonoides viverrinus*), Japanese badger (*Meles anakuma*), Japanese hare (*Lepus brachyurus*), wild boar (*Sus scrofa leucomystax*), and two alien species, Northern American raccoon (*Procyon lotor*) and Masked palm civet (*Paguma larvata*) (S. Nanami, unpublished data). Nomenclature of taxa follows Ohwi (1965) for plants, Ornithological Society of Japan (2012) for birds and Ohdachi et al. (2015) for mammals.

Focal species

To estimate the effects of fruit color including UV reflectance on foraging behavior of birds, we selected as targets three fleshy-fruited shrub species with black-colored fruits, *Eurya* *japonica*, *Ligustrum japonicum* and *Ligustrum obtusifolium*. The first reason was that black-colored fruits are most common in warm-temperate region of Japan (Nakanishi 1996) as well as tropical Asia (Duan et al. 2014). The second point was that the proportion of the canopy area that can be captured by the video camera is relatively larger in shrubs than trees. After selecting the species that satisfied the two conditions, we ordered the species based on the degree of bird preference for the fruits by using the data in Yoshikawa et al. (2009). Yoshikawa et al. (2009) reviewed 80 literatures to examine the interactions between 270 bird-dispersed plants and 14 bird species in Japan. We interpreted that the more literatures a plant species were described in, the more the species was preferred by birds. *Eurya japonica* was described in 25 literatures, and the value was the largest among the shrubs with black-colored fruits. The second-ranked shrub was *Ligustrum japonicum* that was described in 21 literatures. The third and fourth-ranked one was *Ilex crenata* (Aquifoliaceae) and *Fatsia japonica* (Araliaceae). However, the fruit crop of their reproductive individuals was small in our study site. Thus, we selected the fifth-ranked species, *Ligustrum obtusifolium*, described in 12 literatures, as a target of this study.

Eurya japonica is an evergreen shrub native to Japan and the southern Korean Peninsula. Its mature fruits are 4 mm in diameter and contain 10–20 seeds. The fruiting season is October-November (Ohta 2000). *Ligustrum japonicum* is an evergreen shrub typically < 10 m tall that is native to Japan, the Korean Peninsula, Taiwan, and China. The single-seeded fruits are elliptical in shape and 8–10 mm long. *Ligustrum obtusifolium* is a semi-deciduous shrub, typically 2–4 m tall, and is native to Japan and the Korean Peninsula. The fruits are elliptical, 6–7 mm long, and single-seeded. Fruiting season of the two *Ligustrum* species is Octorber-Decemver (Sakio 2010). The fruits of all three species are consumed by birds (Yoshikawa et al. 2009) and are black at maturity (Nakanishi 1996).

For the three shrub species, quantitative estimation of their abundance in the entire garden area was difficult. Instead, we conducted route census along the trails in the garden. We counted the number of individuals ≥ 130 cm height along a total of 4.55 km of the trails in the garden.

We selected eight individuals in total: three of *E. japonica* (*Eja* 1–3), three of *L. japonicum* (*Lja* 1–3), and two of *L. obtusifolium* (*Lob* 1 and 2) (Table 1). The shortest distance between individuals was 8 m that was between *Eja*2 and *Lja*3. The distance between *Eja*1 and *Eja*2 was the largest, being 439 m.

Color assessment

The study was started just before the fruits of each target individual were apparently fully colored. We collected ten fruits from each of the eight individuals every 6–12 days between October 2020 and January 2021. The pericarp of each fruit was irradiated using an Ocean Optics DH-2000-BAL deuterium light source (Ocean Optics, Orlando, FL, USA). The probe holder was placed on the specimen with the probe at a 45° angle to minimize glare (Schaefer et al. 2007; Amao et al. 2012; Anich et al. 2021). The reflectance spectra of each pericarp were measured using a Flame-S-UV-VIS spectrometer and OceanView 1.5.2 software (Ocean Optics) and determined in 1-nm intervals from 300 to 700 nm. Reflectance spectra were expressed relative to a white diffuse reflectance standard (WS-1-SL, Ocean Optics).

Fruit quality and color estimation

We estimated fruit quality as the total soluble solids (TSS) content of each fruit. TSS are a suitable measure of fruit quality because 75–85% of juice TSS are sugar, and higher TSS values therefore correspond with sweeter fruits (Magwaza and Opara 2015; Xu et al. 2019). Because the fruits used in this study were too small to yield adequate juice for measurement, TSS were determined using the following procedure. Following the spectral assessment described above, seeds were removed from each fruit and the pericarp and pulp were placed in a 1.5-mL plastic tube and mashed. We then added 300 μL of sterile water to the mash and mixed thoroughly. Tubes were centrifuged at 15,000 rpm for 15 seconds and the TSS content of the supernatant in each tube was measured using a digital pocket refractometer (PAL-1, ATAGO Co., Ltd., Tokyo, Japan). TSS values were expressed as Brix (%) (Shehata et al. 2021). The effect of dilution was corrected using the equation: Brix (%) = Brix of the supernatant × (total weight of pericarp, pulp, and water/total weight of pericarp and pulp).

We summarized fruit reflectance data using two descriptors obtained from the smoothed reflectance spectra. First, mean brightness (%) (Siefferman and Hill 2005) of the pericarp was calculated as the average of the summed reflectance from 300 to 700 nm, which encompasses the entire visual sensitivity range in birds. Because all three shrubs bear black fruit at maturity, low mean brightness would represent mature fruit. Mean brightness was determined using the ‘summary’ function in the R package ‘pavo’ (Maia et al. 2013). Second, we used darkness (%), represented as 100 minus the brightness value, where larger darkness values indicate more mature fruit. Darkness was used in all further analyses.

To understand how color is perceived and discriminated within the avian visual system, we used the function ‘vismodel’ in ‘pavo’ on the reflectance spectrum data obtained from each fruit. Given that most bird species have UV-sensitive cones (Cuthill 2006), we used the average UV visual system function, ‘avg.uv’. This function is based on the average peak sensitivity found in birds that have a UV visual system (Endler and Mielke 2005). We used ideal settings for the remaining package options of “illum”, “tran” and “bkg”. We used the function ‘vismodel’, which estimates relative cone stimulation values, i.e., normalized to sum to one, of the reflectance spectra of fruit pericarp based on the sensitivity curves of the selected avian visual system. Relative cone stimulations correspond to the relative excitations of the ultraviolet-sensitive, short-wave-length-sensitive (blue), middle-wavelength-sensitive (green), and long-wavelength-sensitive (red) cones caused by the reflectance spectra of fruit pericarps.

We focused on the the relative ultraviolet-sensitive cone stimulation value which is called UCS in this study.

Shrub visitation and foraging by frugivorous birds

Automatic cameras with an infrared trigger (Ltl-Acorn6210MC, Shenzhen Ltl Acorn Electronics Co., Ltd., Shenzhen, China) were used to record video footage of birds visiting the eight target shrubs and consuming fruit. Using a highly sensitive passive infrared sensor, the cameras detect bird presence as a sudden change in ambient temperature within a region of interest. The possible shooting distance was 10 m, the detection angle was 100°, and the shooting angle was 35°. We mounted each camera on a wooden pole approximately 2 m from each target shrub. All cameras were pointed toward shrub sections that were expected to bear large amounts of fruit. The trigger sensitivity of the cameras was set to "High" to avoid missing small bird activities. Upon triggering, video was recorded for 1 minute. Camera footage was downloaded every 6–12 days between October 2020 and January 2021. We identified each bird in the footage, and recorded the date, time, and duration of their visit, and the number of fruits consumed.

Statistical analyses

We used linear mixed models (LMMs) to determine relationships between color signals and

Brix values, where the Brix value was the response variable, and darkness and UCS were the explanatory variables. We tested three model forms: darkness alone, UCS alone, and darkness and UCS in an additive model. The best supported model was determined using Akaike's information criterion (AIC). LMMs were built using the R package 'lme4' (Bates et al. 2020). We used the coefficients from the models to determine predicted Brix values for each species.

Next, we assessed interactions between frugivorous birds and the target species using a bipartite network built using the R package 'bipartite' version 2.16 (Dormann et al. 2021). This weighted interaction network was constructed based on fruit consumption among bird species.

Finally, to determine the accuracy with which birds judge fruit quality based on reflectance spectra, we assessed temporal relationships between predicted Brix values, obtained from models as described above, and bird foraging behavior. We determined the date upon which predicted Brix values peaked by fitting a quadratic function (Radzevičius et al. 2014) to temporal variation in predicted Brix values. The dates of maximum fruit consumption by bird species were determined from camera observations.

Results

Abundance of the target shrubs

Along a total of 4.55 km trail in the garden, the number of individuals ≥ 130 cm height of *E. japonica*, *L. japonicum* and *L. obtusifolium* were 224, 44 and 8, respectively. *Eurya japonica* was a dominant species and *L. japonicum* was a common species in shrub layer at the study site. On the other hand, *L. obtusifolium* was relatively rare.

Color signals and Brix values

Both darkness and UCS were calculated from fruit pericarp reflectance (Fig. 1). For *E. japonica*, Brix values correlated with darkness (R = 0.354, N = 228, P < 0.001, Fig 2a) and UCS (R = 0.338, N = 228, P < 0.001, Fig 2b). Brix values of *L. japonicum* fruit got higher with increasing darkness (R = 0.279, N = 310, P < 0.001, Fig 3a) and UCS (R = 0.481, N = 310, P < 0.001, Fig 3b). For *L. obtusifolium* fruit, Brix values correlated with darkness (R = 0.216, N = 130, P = 0.014, Fig 4a) but not with UCS (R = 0.121, N = 130, P = 0.170, Fig 4b).

LMMs indicated that variability in Brix values was best explained by an additive relationship between darkness and UCS for *E. japonica* and *L. obtusifolium* (Table 2), and by UCS alone for *L. japonicum*.

Frugivorous birds, shrub visitation, and fruit consumption

The eight target individual shrubs were visited by nine bird species: long-tailed tit (*Aegithalos caudatus*, Aegithalidae), hawfinch (*Coccothraustes coccothraustes*, Fringillidae), brown-eared bulbul (*Hypsipetes amaurotis*, Pycnonotidae), Daurian redstart (*Phoenicurus auroreus*, Muscicapidae), red-flanked bluetail (*Tarsiger cyanurus*, Muscicapidae), Naumann's thrush (*Turdus naumanni*, Muscicapidae), pale thrush (*Turdus pallidus*, Muscicapidae), scaly thrush (*Zoothera dauma*, Muscicapidae) and Japanese white-eye (*Zosterops japonicus*, Zosteropidae). Among these, six species, brown-eared bulbul, Daurian redstart, Naumann's thrush, pale thrush, scaly thrush and Japanese white-eye, were observed consuming fruit from the target shrubs (Fig. 5). The most heavily foraged shrub was *Eja* 3, with 2,386 fruits consumed. The main cause of the heavy consumption was visitation of large flock of Naumann's thrush on December 23, 2021. They ate more than 1,500 fruits in one day (Fig. S3). A *L. janonicum* individual, *Lja* 1 was visited by the greatest number of species (n = 5; brown-eared bulbul, Daurian redstart, Naumann's thrush, pale thrush and Japanese white-eye) (Fig. 5). Among the six fruit-consuming species, Japanese white-eye was the most abundant across all target individuals.

Temporal relationships between ripening and foraging

For all three species, temporal change in predicted Brix values were approximated by an upwardly convex quadratic curve (Fig. 6 and Figs S1-S7). The sugar content in un-foraged fruits tended to decline after the peak period of bird foraging.

Temporal order of three kinds of predicted date of maximum fruit sugar content, represented by open, solid and hatched triangles, were inconsistent not only among species but also among individuals of the same species (Fig. 7). However, the number of fruits consumed by all visiting bird species reached its maximum (circled letter, "A", in Fig. 7) exactly on or after the date of one of the three predicted peak sugar contents within 11 days, excluding *Eja* 2. Among the observed bird species, brown-eared bulbul tended to visit the shrubs earlier than other birds. On the other hand, Japanese white-eye and pale thrush were late visitors.

Discussion

Fruit reflectance and sugar content

Fruit ripeness can typically be determined based on pericarp color, given that most fruits change color during the maturation period (Nakanishi 1996; Teka 2013; Radzevičius et al. 2014) and sugar content is usually linked to this change (Koike et al. 2008; Sakurai et al. 2013; Teka 2013). UV reflectance also increases along with fruit maturity (Altshuler 2001). Here, Brix values appeared to be correlated with both darkness and UCS (Figs 2-4). Both variables were included in the best supported models explaining Brix values for *E. japonica* and *L. obtusifolium*, whereas only UCS was included for *L. japonicum* (Table 2). Thus, UV reflectance of the pericarp would be an honest signal of fruit maturity in these three species.

Interaction network of avian frugivores and fleshy-fruited plants

Fruit foraging by animals including birds has been evaluated by visual survey (e.g. Fujitsu et al. 2016), counting pulpless seeds in seed traps (Takahashi and Kamitani 2003) or identification of seeds in feces (Koike et al. 2008; Emura et al. 2012). Recently, automatically triggered cameras taking videos have used as one of the most powerful tools for wildlife research (e.g. Katsuha and Kitamura 2018). In this study, number of fruits that were removed by birds was able to be recorded throughout the entire period by using automatically triggered video cameras.

Japanese white-eye ate fruits from all the eight target shrubs, and brown-eared bulbul and pale thrush consumed fruits from 7 of the 8 shrubs (Fig. 5). These three species were considered important seed-dispersers in Japan (Noma and Yumoto 1997; Takahashi and Kamitani 2003; Yoshikawa et al. 2009), and the observations of this study supported the views of previous studies.

Naumann's thrush fed primarily on the fruits of *E. japonica* (Fig. 5). The situation of Naumann's thrush eating the fruits of certain plant species was similar to that reported by Kominami (1987), who reported that Naumann's thrush removed the fruits of *Vibrunum dilatatum* while co-occurring brown-eared bulbul did not eat them. The reason of this bias is unknown but one possibility might be bird species-specific preferences (Tsujita et al. 2008; Sakurai et al. 2013) for fruits or interspecies competition among bird species for fruits.

However, Yoshikawa et al. (2009) reported that Naumann's thrush consumed fruits of various freshy-fruited species. Thus, the observed biased foraging of Naumann's thrush may be caused by that its large flock visited a *E. japonica* individual, *Eja* 3 (Fig. S3).

Temporal relationships between fruit color and foraging

Previous community-level studies reported the seasonal correspondence between the fruiting phenology of fleshy-fruited plants and the abundance of frugivorous birds. In temperate forests, frugivorous birds were abundant during the fruiting periods of many fleshy-fruited plants (Noma and Yumoto 1997; Takanose and Kamitani 2003). In this study, we examined the correspondence between the fruit maturation phenology and the foraging behavior of birds at finer scale, i.e. plant individual level.

Birds have a poor sense of smell and are believed to rely on their tetrachromatic vision to detect mature fruit (Andersson et al. 1998; Hunt et al. 1999; Siitari et al. 1999). Other studies have confirmed linkages between fruit maturity and frugivorous birds (Noma and Yumoto 1997; Thompson and Willson 1978), with some suggesting that choice by animals has influenced the evolution of fruit color (Breitbach et al. 2010). Here, we sought specific evidence of linkages among foraging behavior, sugar content, and fruit color.

Given the overlap between peak Brix values and peak foraging by birds (Figs 6 and 7), we suggest that birds determine the sugar content of fruits and forage them based on changes in fruit color, which is an honest signal of sugar content (Table 2). Based on behavioral observations, birds appeared to be more reliant on UCS for fruits of *E. japonica* and *L. obtusifolium* and more reliant on darkness for *L. japonicum*. However, the LMMs yielded contrary results, with both UCS and darkness included in the best supported model for *E. japonica* and *L. obtusifolium* and UCS alone for *L. japonicum* (Table 2). This mismatch suggests that birds may be imprecise in their estimation of sugar content. Although we could not directly determine if birds were more reliant on UCS or darkness, we found that the dates with maximum UCS values typically preceded the dates of peak foraging (Fig. 7). This suggests that UCS is a criterion used by birds to judge fruit maturity (Altshuler 2001).

Species-specific differences

We found differences in effective signals of sugar content among the three target shrub species (Table 2). In addition, bird behavior did not correspond to the LMM results (Fig. 7). This suggests that foraging behavior, even within a single bird species, may vary with plant species. However, we also found evidence of commonality in foraging among the three shrubs. First, brown-eared bulbul was the first bird species and Japanese white-eye the last to reach peak foraging, i.e., reach the maximum of fruit consumption, regardless of target species (Fig. 7). Brown-eared bulbul is a large-bodied species about 27 cm in length and may start foraging earlier and more vociferously, i.e., on unripe fruit, to meet their energetic needs. By contrast, Japanese white-eye, a small bird about 12 cm in length, may be a more selective and thus more efficient forager, by selecting fewer, more nutritious fruits.

The timing of fruit ripening differed among the three shrub species and individuals of each species (Fig. 7). The number of consumed fruits and the number of visiting bird species also varied among shrub species and individuals. The most abundant visiting bird species differed for all target shrubs, regardless of species (Fig. 5). Despite these differences, birds consistently foraged fruits only after they had exhibited color change.

For plants, having birds eat the fruit would have a positive effect on population maintenance, because avian gut-passage often facilitates seed germination (Reid and Armesto 2011; Díaz Vélez et al. 2017) by removing pulp that inhibit germination (Yagihashi et al. 2000). However, the removal of pulp from seeds of unripe fruits largely reduced the germination percentage (Yoshikawa and Isagi 2014). Thus, it is important that the fruit be eaten by birds after it matures. In this study, fruits were eaten by birds after they were sufficiently ripe. This indicates that both plants and birds benefit.

We found that both UCS and darkness were honest signals of nutritional value and observed linkages between fruit sugar content and bird foraging behavior. However, there was a discrepancy between the signal representing the sugar content and the predicted sugar content that birds relied upon. This is probably because fruit consumption by birds is not entirely dependent on the UV reflectance or sugar content of the fruits. It must also depend on various factors. Regarding the three shrub species under study, there were fruiting individuals other than the eight targeted individuals in the botanical garden. During the study period, trees and shrubs other than the studied species, e.g. *Photinia glabra* (Rosaceae), *Callicarpa japonica* (Lamiaceae) and *Melia azedarach* (Meliaceae), also bore fruits (S. Nanami, personal observation). The presence of fruiting neighbors of conspecific (Sargent 1990) or heterospecific plants (Carlo 2005) and seasonal variation of population-level (Yamazaki et al. 2016) or community-level fruit abundance (Naoe et al. 2018) should also control the fruit removal patterns by birds.

Furthermore, leaf property may be important in addition to fruit conditions to attract frugivorous birds. Nakayama and Iwashina (2017) discovered that leaves of some woody species including *L. japonicum* showed bright green-blue fluorescence upon exposure to ultraviolet irradiation, and proposed possibility that leaf fluorescence makes it easier for birds to find fruits.

In the field, where diverse conditions are involved, it would be difficult to exactly verify the effects of color and UV reflection of fruits. Therefore, the effects should be tested by experimental methods such as feeding. A more comprehensive assessment of fruit properties and fruiting conditions across a wide range of conditions would improve understanding of the mutualistic relationship between frugivorous birds and fleshy-fruited plants.

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Figure captions

Figure 1. Example of (a) a reflectance spectrum curve, and (b) the relative stimulation of ultraviolet- (U), short-wave- (S), medium-wave- (M) and long-wave- (L) sensitive cones in birds based on ripe fruit of *Ligustrum obtusifolium*. The ultraviolet-sensitive cone is the largest among the four stimulations. In these cases, the reflectance of ultraviolet light, which is imperceptible to humans, is highest.

Nagami et al. Fig. 1

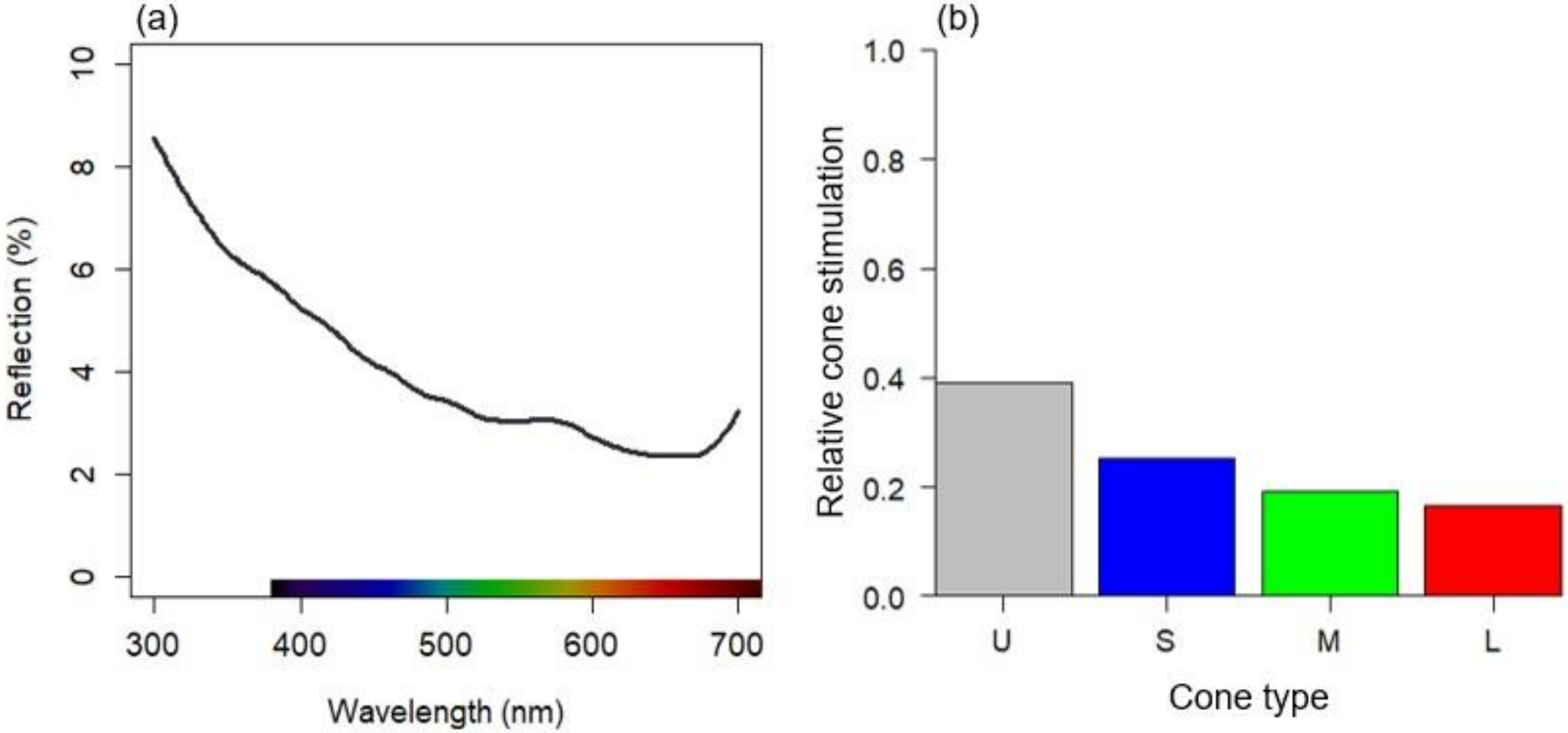

Figure 2. Relationships between (a) fruit darkness or (b) relative ultraviolet-sensitive cone stimulation (UCS) and the Brix value of fruits of three *Eurya japonica* individuals, *Eja* 1, *Eja* 2, and *Eja* 3, collected between October 2020 and January 2021. Circles ($N = 90$), triangles ($N = 48$), and squares ($N = 90$) represent the fruits of *Eja* 1, *Eja* 2, and *Eja* 3, respectively. Pearson's correlation coefficient was (a) 0.354 ($N = 228$, $P < 0.001$) between Brix value and fruit darkness and (b) 0.338 ($N = 228$, $P < 0.001$) between Brix value and relative ultraviolet-sensitive cone stimulation (UCS) of birds based on the reflectance spectrum of fruits.

Nagami et al. Fig. 2

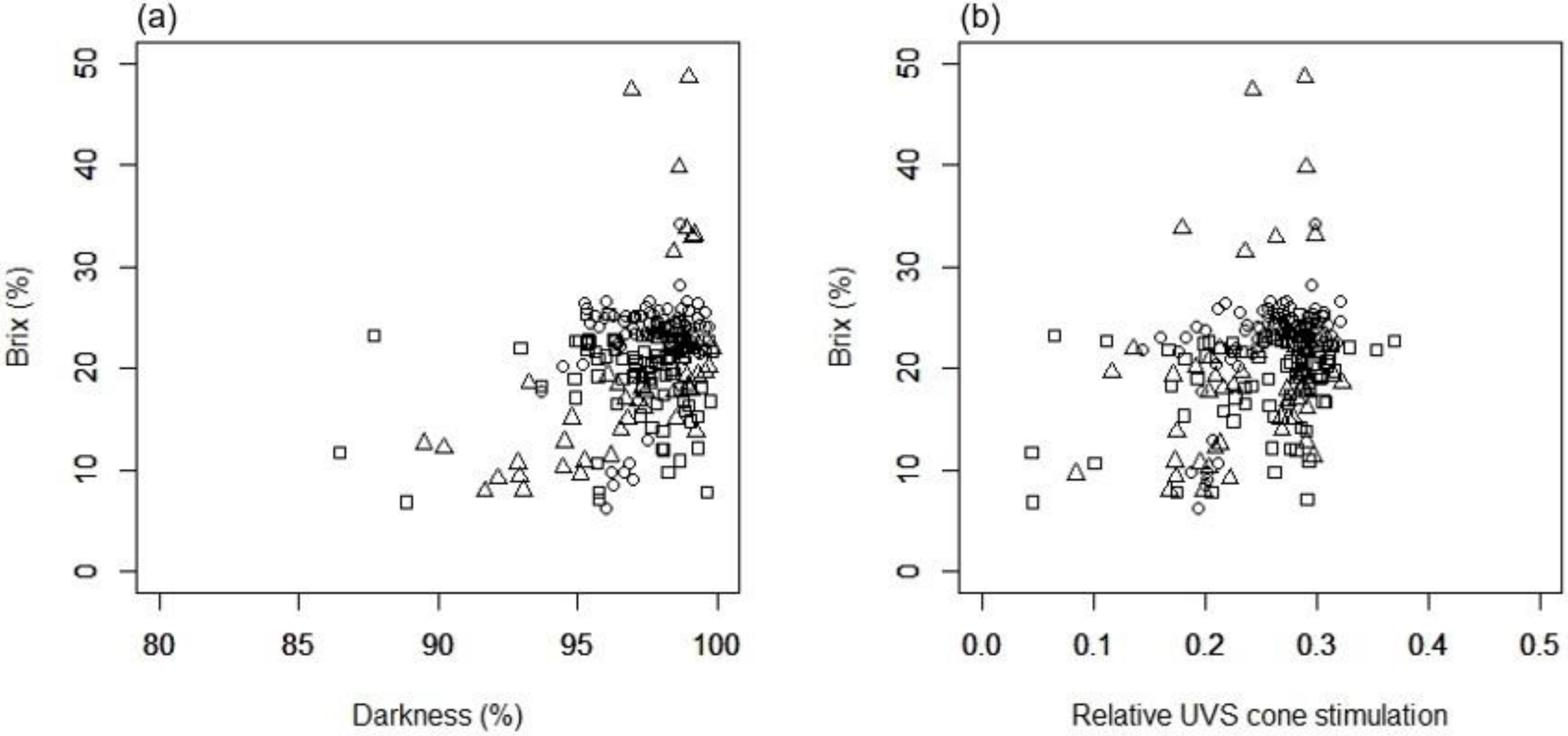

Figure 3. Relationships between (a) fruit darkness or (b) relative ultraviolet-sensitive cone stimulation (UCS) and the Brix value of fruits of three *Ligustrum japonicum* individuals, *Lja* 1, *Lja* 2, and *Lja* 3, collected between October 2020 and January 2021. Circles ($N = 110$), triangles ($N = 110$), and squares ($N = 90$) represent the fruits of *Lja* 1, *Lja* 2, and *Lja* 3, respectively. Pearson's correlation coefficient was (a) 0.279 ($N = 310$, $P < 0.001$) between Brix value and fruit darkness and (b) 0.481 ($N = 310$, $P < 0.001$) between Brix value and relative ultraviolet-sensitive cone stimulation (UCS) of birds based on the reflectance spectrum of fruits.

Nagami et al. Fig. 3

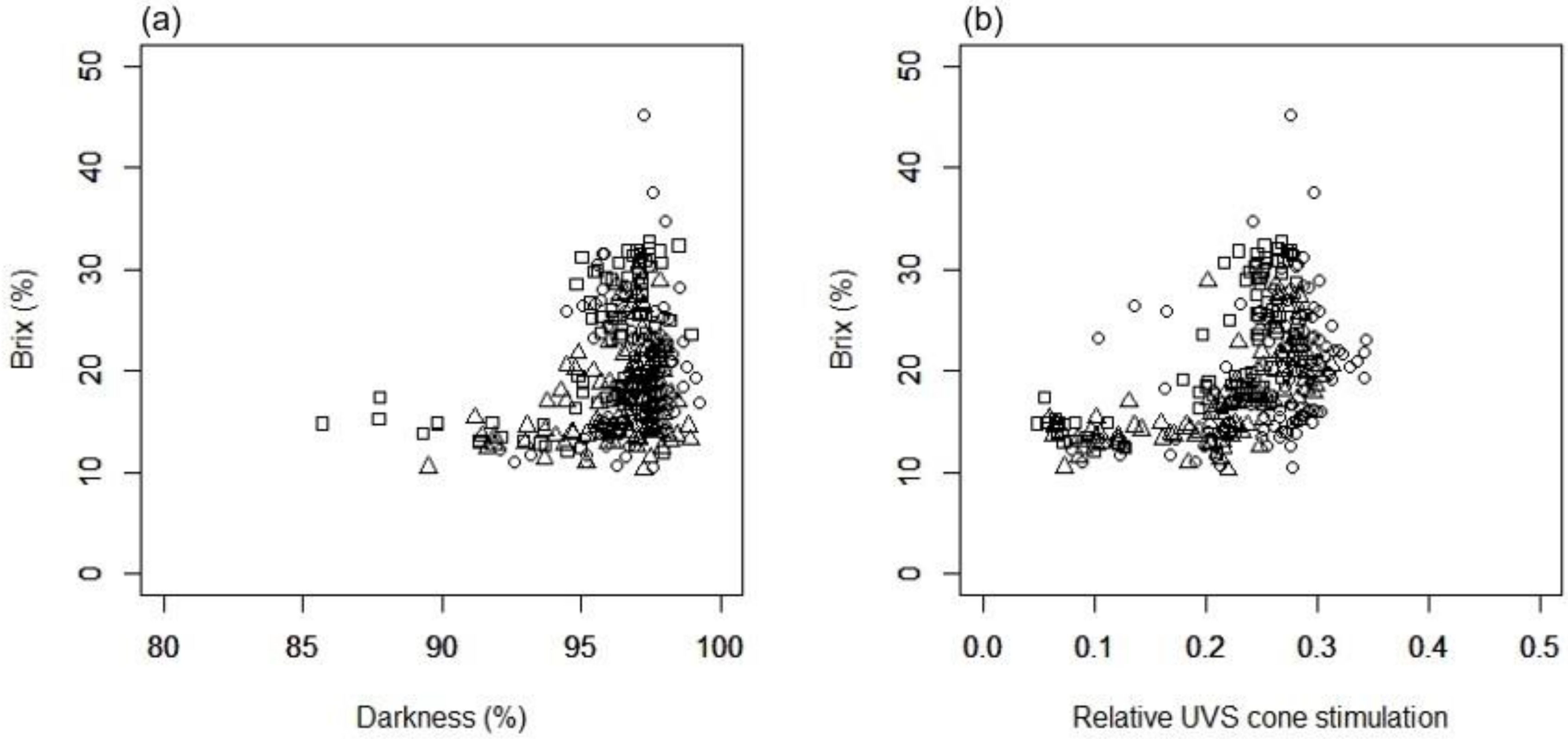

Figure 4. Relationships between (a) fruit darkness or (b) relative ultraviolet-sensitive cone stimulation (UCS) and the Brix value of fruits of two *Ligustrum obtusifolium* individuals, *Lob* 1 and *Lob* 2, collected between October 2020 and January 2021. Circles ($N = 70$) and triangles ($N = 60$) represent the fruits of *Lob* 1 and *Lob* 2, respectively. Pearson's correlation coefficient was (a) 0.216 ($N = 130$, $P = 0.014$) between Brix value and fruit darkness and (b) 0.121 ($N = 130$, $P = 0.170$) between Brix value and relative ultraviolet-sensitive cone stimulation (UCS) of birds based on the reflectance spectrum of fruits.

Nagami et al. Fig. 4

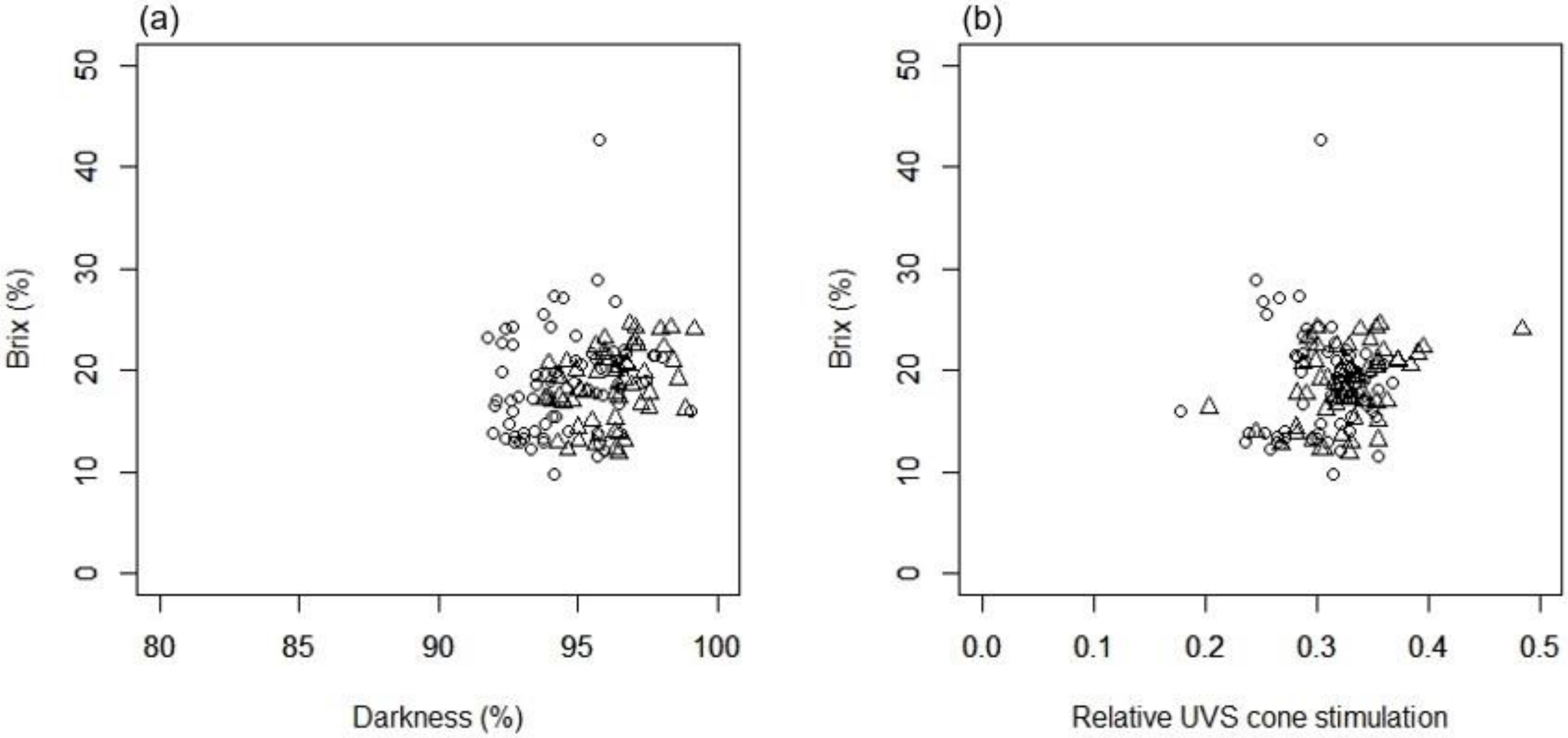

Figure 5. Quantitative seed-dispersal network between the three shrub species and frugivorous birds observed consuming their fruits. The network was determined based on behavior documented using automatic cameras. The width of the bars connecting birds and shrub species are proportional to the number of fruits foraged per hour by a given species. *Eja* 1, 2, and 3 indicate the three individuals of *Eurya japonica*. *Lob* 1 and 2 indicate two individuals of *Ligustrum obtusifolium*. *Lja* 1, 2, and 3 indicate the three individuals of *Ligustrum japonicum*. Six bird species ate the fruits of these eight individual shrubs: brown-eared bulbul (*Hypsipetes amaurotis*), Daurian redstart (*Phoenicurus auroreus*), Naumann's thrush (*Turdus naumanni*), pale thrush (*Turdus pallidus*), scaly thrush (*Zoothera dauma*) and Japanese white-eye (*Zosterops japonicus*). Numbers in parentheses indicate the number of fruits consumed by birds.

Nagami et al. Fig. 5

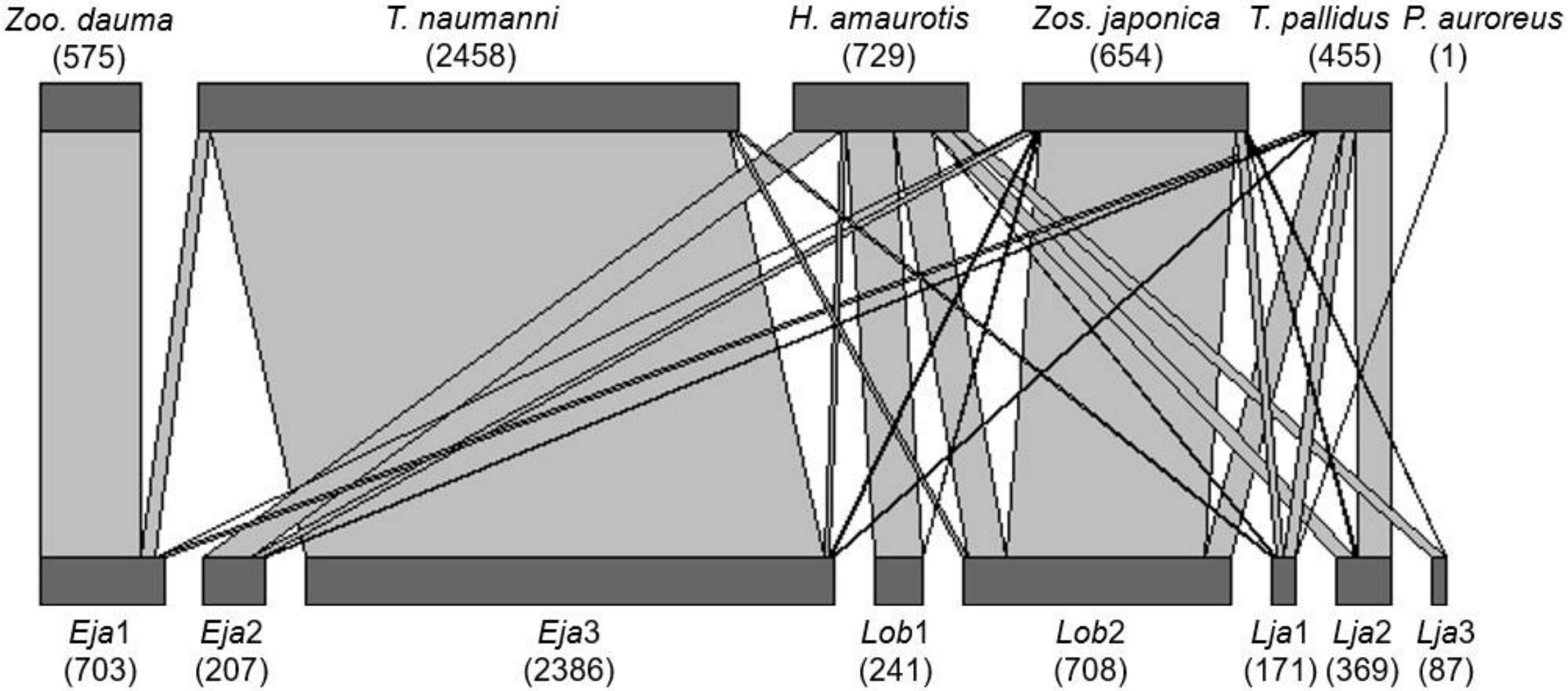

Figure 6. Temporal change in Brix values of fruits predicted based on (a) pericarp darkness, (b) relative ultraviolet-sensitive cone stimulation (UCS), and (c) both parameters, of a *Ligustrum japonicum* individual (*Lja*2) and the number of fruits consumed by birds from October 2020 to January 2021. Dots indicate predicted Brix values. Fitted curves: (a) $Y = -0.001X^2 + 0.107X + 14.790$ ($R^2 = 0.220$), (b) $Y = -0.001X^2 + 0.140X + 13.307$ ($R^2 = 0.382$), and (c) $Y = -0.001X^2 + 0.135X + 13.339$ ($R^2 = 0.356$). Bars indicate daily fruit consumption by birds. Estimated date of the maximum Brix value was December 27, 2020, in (a), January 15, 2021, in (b) and January 18, 2021, in (c). Fruit consumption by birds peaked on January 18, 2021.

Nagami et al. Fig. 6

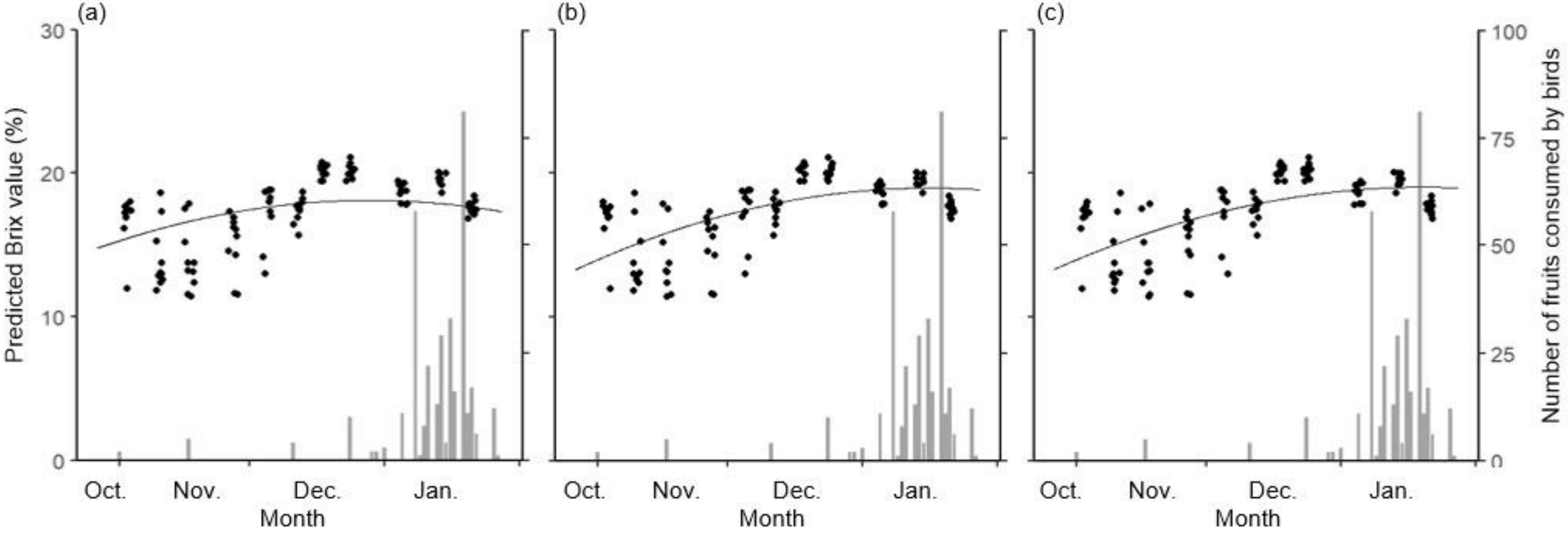

Figure 7. Chronology of the maximum predicted Brix value of three *Eurya japonica* individuals (*Ej*a 1−3), two *Ligustrum obtusifolium* (*Lob* 1−2) and three *Ligustrum japonicum* individuals (*Lja* 1−3) and the dates of maximum fruit consumption by birds for each individual. Open triangles, solid triangles, and hatched triangles represent dates when predicted sugar content peaked based on pericarp darkness, relative UCS stimulation, and both, respectively. Circles represent maximum foraging dates by birds. P: pale thrush (*Turdus pallidus*), N: Naumann's thrush (*Turdus naumanni*), S: scaly thrush (*Zoothera dauma*), B: brown-eared bulbul (*Hypsipetes amaurotis*), W: Japanese white-eye (*Zosterops japonicus*), and A: all bird species.

Nagami et al. Fig. 7

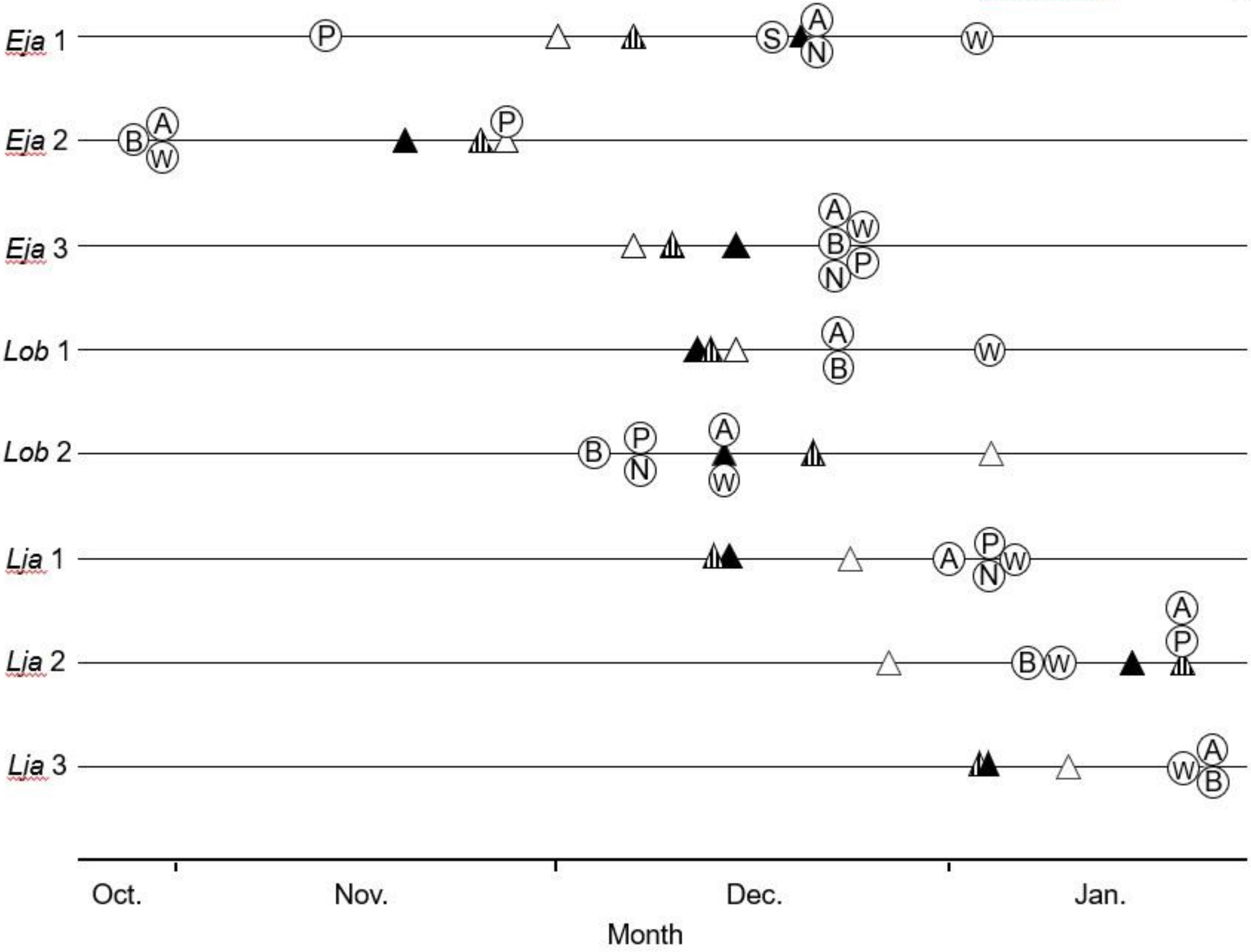

Table 1. Plant height (m) and crown size (m^2) of the eight target individuals of the three fruiting shrub species at the Botanical Garden of Osaka Metropolitan University, Osaka, Japan. Since one camera was set per individual, the effort was equal to the number of days when a camera has been installed. The number of videos was limited to those in which birds were captured.

Species	Individual no.	Plant height (m)	Crown size (m^2)	Location	Observation effort (camera-days)	Number of one-minute videos
Eurya japonica	*Eja* 1	1.8	1.6 × 0.9	34° 45' 45.8" N 135° 40' 45.9" E	80	111
	Eja 2	2.7	2.5 × 1.9	34° 45' 59.6" N 135° 40' 50.0" E	46	51
	Eja 3	3.6	2.8 × 2.4	34° 45' 59.8" N 135° 40' 47.9" E	80	157
Ligstrum japonicum	*Lja* 1	3.5	1.6 × 0.9	34° 45' 52.6" N 135° 40' 43.7" E	94	81
	Lja 2	5.2	2.5 × 1.9	34° 45' 57.0" N 135° 40' 47.0" E	94	37
	Lja 3	4.7	2.8 × 2.4	34° 45' 49.1" N 135° 40' 47.0" E	80	22
Ligstrum obtusifolium	*Lob* 1	4.7	4.0 × 3.8	34° 45' 48.6" N 135° 40' 46.3" E	60	27
	Lob 2	8.5	7.2 × 6.4	34° 45' 59.4" N 135° 40' 49.8" E	45	135

Table 2. Model selection of linear mixed models predicting Brix values. Predictor variables included pericarp darkness and relative ultraviolet-sensitive cone stimulation (UCS) of birds based on the reflectance spectrum of fruits of *Eurya japonica*, *Ligustrum japonicum* and *Ligustrum obtusifolium*. Model 1 includes both explanatory variables, models 2 and 3 include either, and model 4 is a null model. (1|ID) represents a random effect of shrub individual to account for repeated measures, and df represents degrees of freedom. Model selection was based on Akaike's information criterion (AIC) values.

Models	df	AIC		
		E. japonica	*L. japonicum*	*L. obtusifolium*
1. Brix~darkness+UCS+(1|ID)	7	1414.5	1873.0	757.3
2. Brix~darkness+(1|ID)	5	1432.1	1938.8	762.0
3. Brix~UCS+(1|ID)	5	1422.2	1868.5	759.1
4. Brix~1+(1|ID)	3	1452.1	1969.5	763.4

Supplementary Figure S1
Nagami et al.

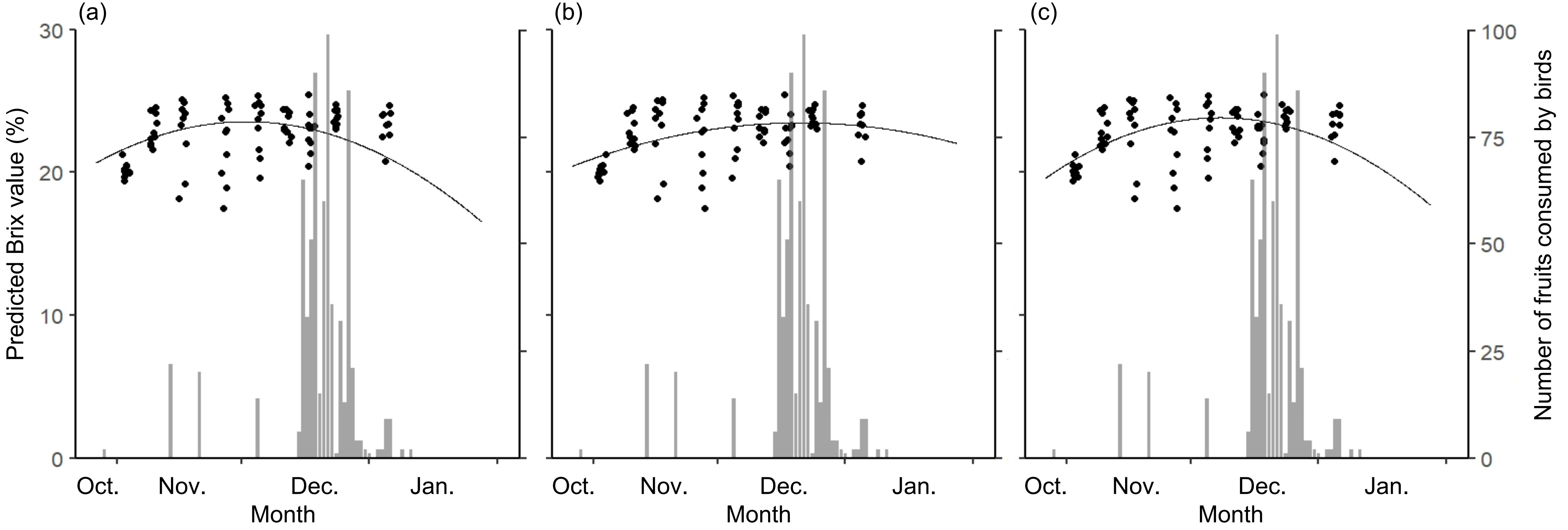

Figure S1. Temporal change in Brix values of fruits predicted based on (a) pericarp darkness, (b) relative ultraviolet-sensitive cone stimulation (UCS), and (c) both parameters, of a *Eurya janonica* individual (*Eja* 1) and the number of fruits consumed by birds from October 2020 to January 2021. Dots indicate predicted Brix values. Fitted curves: (a) $Y = -0.002X^2 + 0.158X + 20.688$ ($R^2 = 0.458$), (b) $Y = -0.001X^2 + 0.110X + 20.460$ ($R^2 = 0.183$), and (c) $Y = -0.002X^2 + 0.200X + 19.627$ ($R^2 = 0.345$). Bars indicate daily fruit consumption by birds. Estimated date of the maximum Brix value was December 1, 2020, in (a), December 19, 2020, in (b) and December 7, 2020, in (c). Fruit consumption by birds peaked on December 21, 2020.

Supplementary Figure S2
Nagami et al.

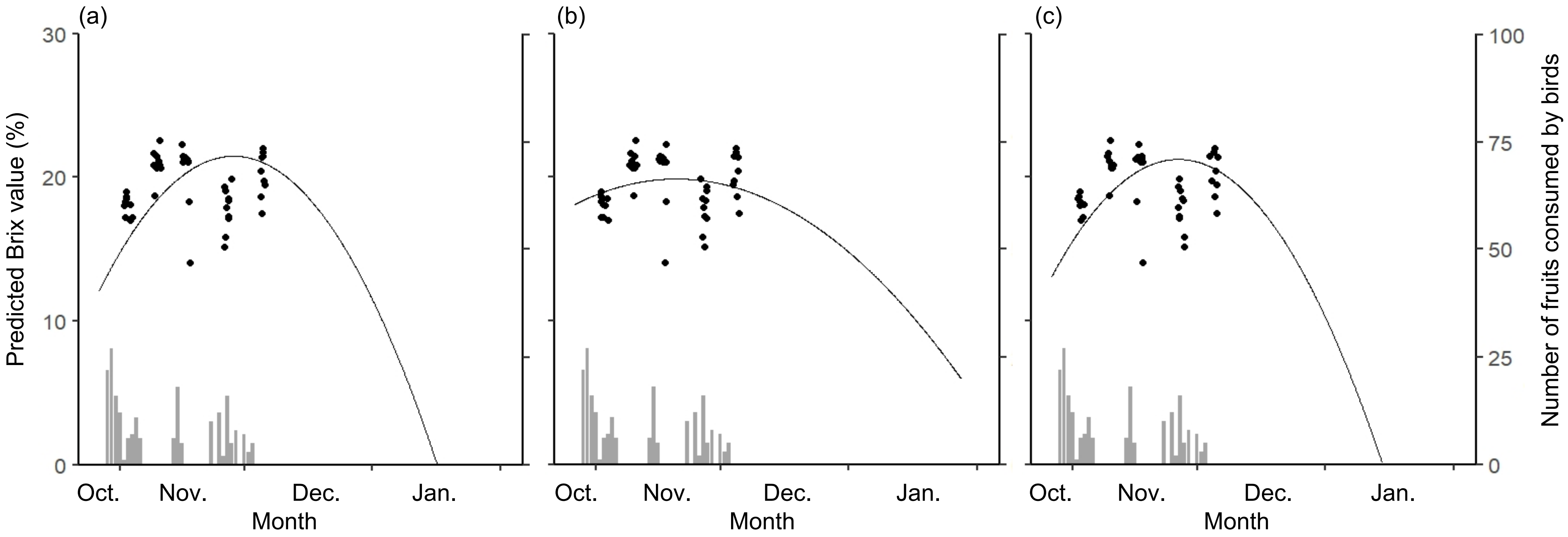

Figure S2. Temporal change in Brix values of fruits predicted based on (a) pericarp darkness, (b) relative ultraviolet-sensitive cone stimulation (UCS), and (c) both parameters, of a *Eurya janonica* individual (*Eja* 2) and the number of fruits consumed by birds from October 2020 to January 2021. Dots indicate predicted Brix values. Fitted curves: (a) $Y = -0.009X^2 + 0.576X + 12.132$ ($R^2 = 0.734$), (b) $Y = -0.003X^2 + 0.114X + 18.119$ ($R^2 = 0.026$), and (c) $Y = -0.009X^2 + 0.535X + 13.100$ ($R^2 = 0.513$). Bars indicate daily fruit consumption by birds. Estimated date of the maximum Brix value was November 27, 2020, in (a), November 19, 2020, in (b) and November 25, 2020, in (c). Fruit consumption by birds peaked on October 29, 2020.

Supplementary Figure S3
Nagami et al.

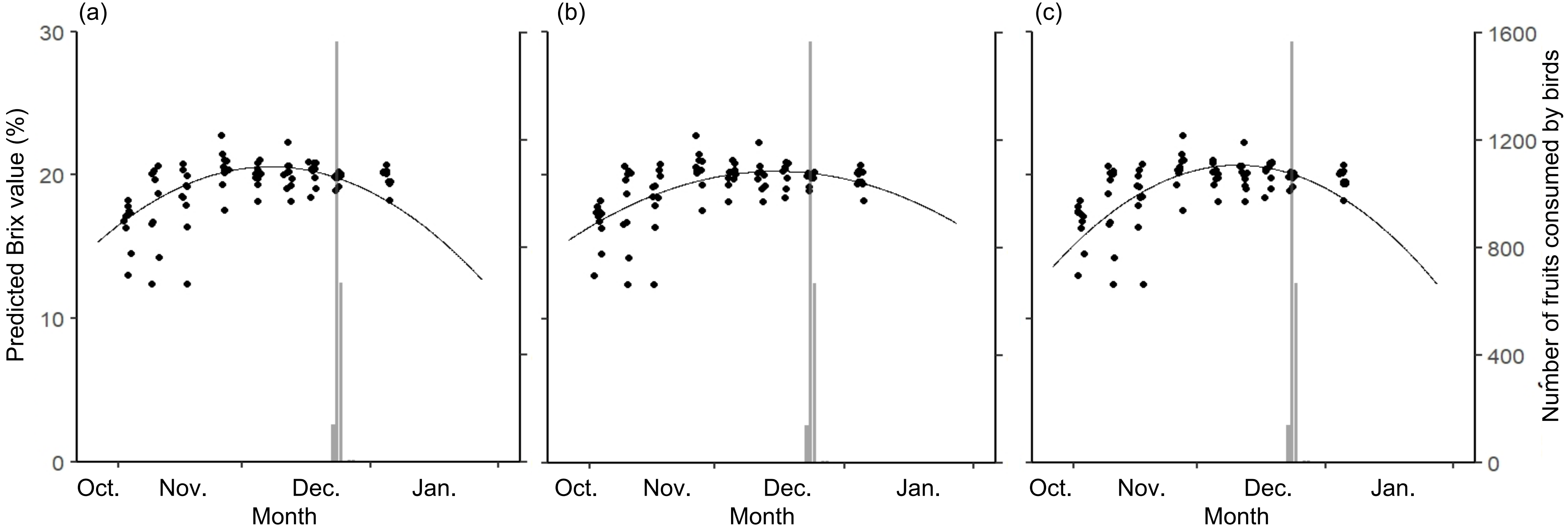

Figure S3. Temporal change in Brix values of fruits predicted based on (a) pericarp darkness, (b) relative ultraviolet-sensitive cone stimulation (UCS), and (c) both parameters, of a *Eurya janonica* individual (*Eja* 3) and the number of fruits consumed by birds from October 2020 to January 2021. Dots indicate predicted Brix values. Fitted curves: (a) $Y = -0.003X^2 + 0.252X + 15.317$ ($R^2 = 0.338$), (b) $Y = -0.002X^2 + 0.193X + 15.494$ ($R^2 = 0.373$), and (c) $Y = -0.004X^2 + 0.317X + 13.632$ ($R^2 = 0.383$). Bars indicate daily fruit consumption by birds. Estimated date of the maximum Brix value was December 6, 2020, in (a), December 14, 2020, in (b) and December 9, 2020, in (c). Fruit consumption by birds peaked on December 23, 2020.

Supplementary Figure S4
Nagami et al.

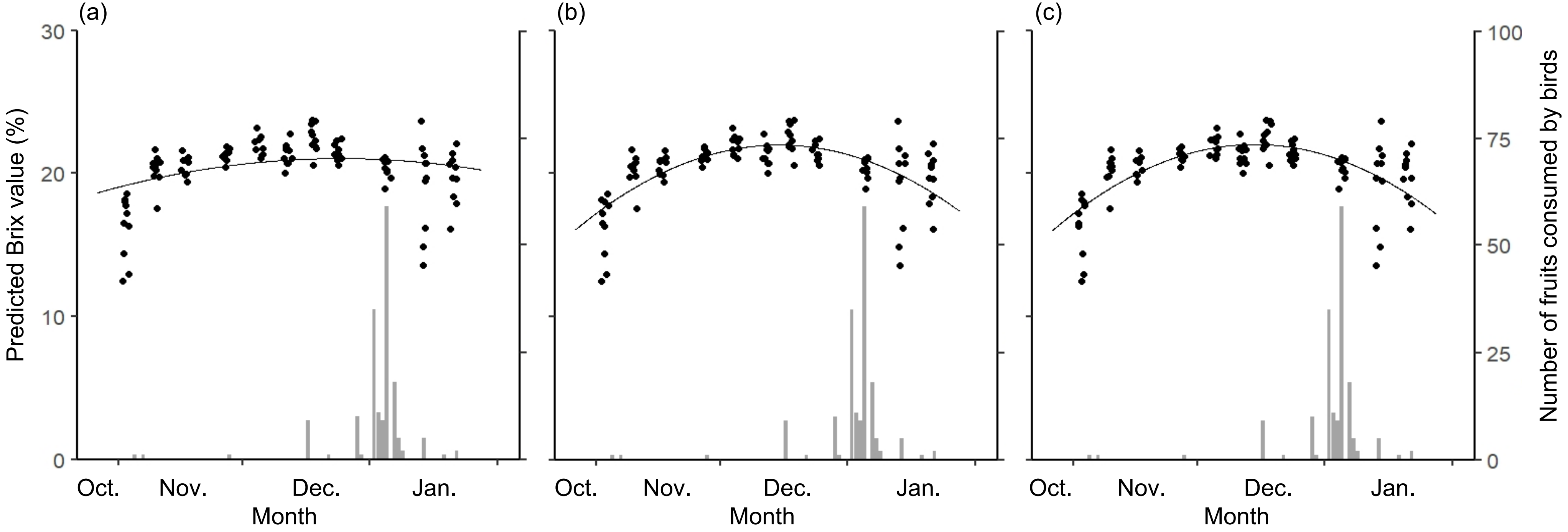

Figure S4. Temporal change in Brix values of fruits predicted based on (a) pericarp darkness, (b) relative ultraviolet-sensitive cone stimulation (UCS), and (c) both parameters, of a *Ligustrum janonicum* individual (*Lja* 1) and the number of fruits consumed by birds from October 2020 to January 2021. Dots indicate predicted Brix values. Fitted curves: (a) $Y = -0.001X^2 + 0.081X + 18.659$ ($R^2 = 0.229$), (b) $Y = -0.002X^2 + 0.240X + 16.083$ ($R^2 = 0.449$), and (c) $Y = -0.003X^2 + 0.246X + 16.037$ ($R^2 = 0.455$). Bars indicate daily fruit consumption by birds. Estimated date of the maximum Brix value was December 23, 2020, in (a), December 14, 2020, in (b) and December 13, 2020, in (c). Fruit consumption by birds peaked on January 4, 2021.

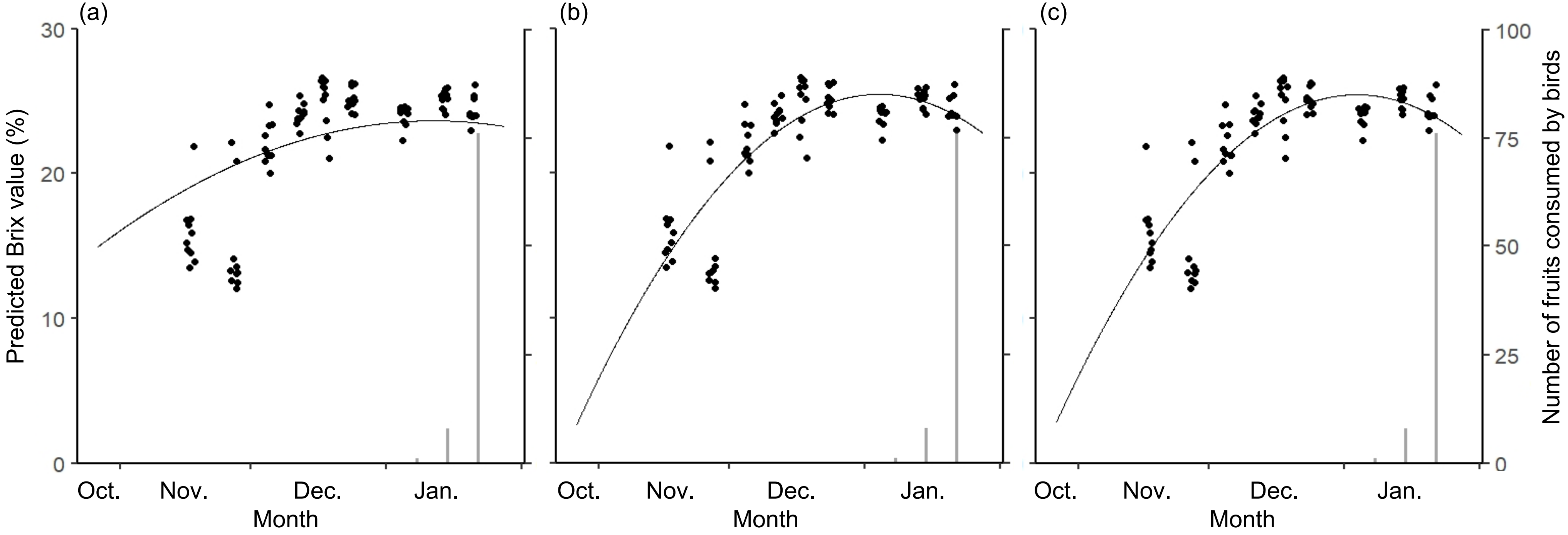

Figure S5. Temporal change in Brix values of fruits predicted based on (a) pericarp darkness, (b) relative ultraviolet-sensitive cone stimulation (UCS), and (c) both parameters, of a *Ligustrum janonicum* individual (*Lja* 3) and the number of fruits consumed by birds from October 2020 to January 2021. Dots indicate predicted Brix values. Fitted curves: (a) $Y = -0.001X^2 + 0.227X + 14.963$ ($R^2 = 0.331$), (b) $Y = -0.005X^2 + 0.659X + 2.663$ ($R^2 = 0.669$), and (c) $Y = -0.005X^2 + 0.657X + 2.854$ ($R^2 = 0.721$). Bars indicate daily fruit consumption by birds. Estimated date of the maximum Brix value was January 10, 2021, in (a), January 3, 2021, in (b) and January 2, 2021, in (c). Fruit consumption by birds peaked on January 21, 2021.

Supplementary Figure S6
Nagami et al.

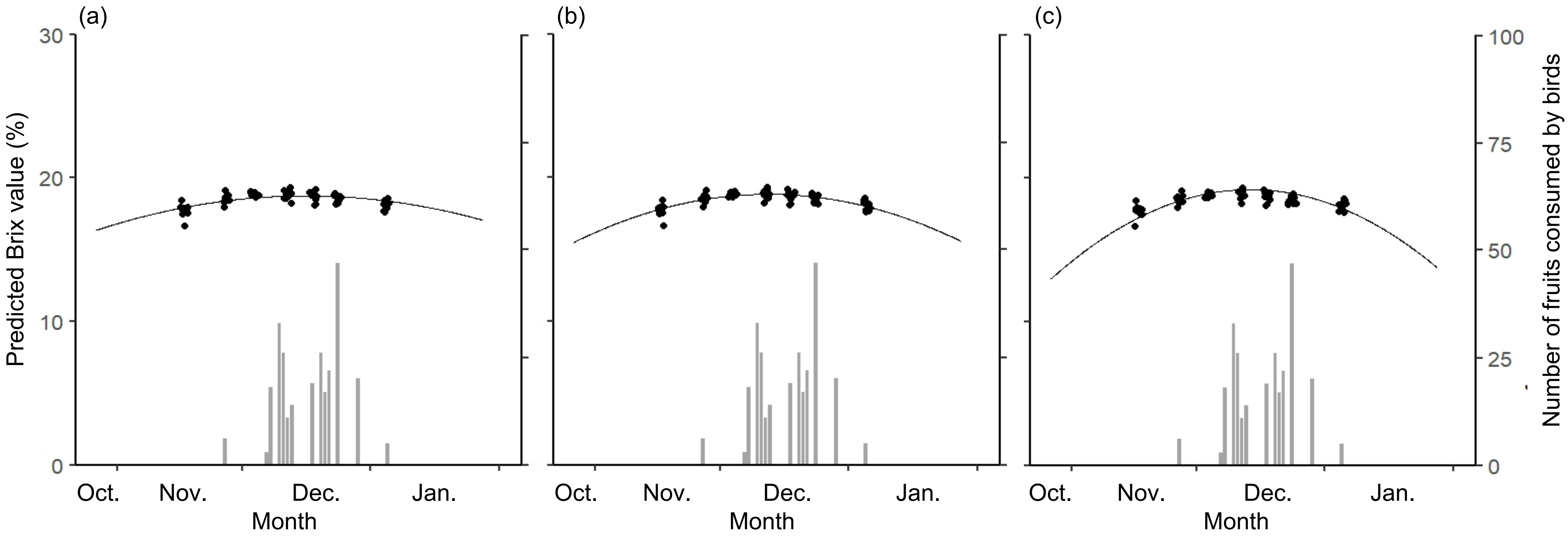

Figure S6. Temporal change in Brix values of fruits predicted based on (a) pericarp darkness, (b) relative ultraviolet-sensitive cone stimulation (UCS), and (c) both parameters, of a *Ligustrum obtusifolium* individual (*Lob* 1) and the number of fruits consumed by birds from October 2020 to January 2021. Dots indicate predicted Brix values. Fitted curves: (a) $Y = -0.001X^2 + 0.095X + 16.363$ ($R^2 = 0.059$), (b) $Y = -0.002X^2 + 0.143X + 15.512$ ($R^2 = 0.572$), and (c) $Y = -0.003X^2 + 0.259X + 12.990$ ($R^2 = 0.294$). Bars indicate daily fruit consumption by birds. Estimated date of the maximum Brix value was December 15, 2020, in (a), December 11, 2020, in (b) and December 13, 2020, in (c). Fruit consumption by birds peaked on December 23, 2020.

Supplementary Figure S7
Nagami et al.

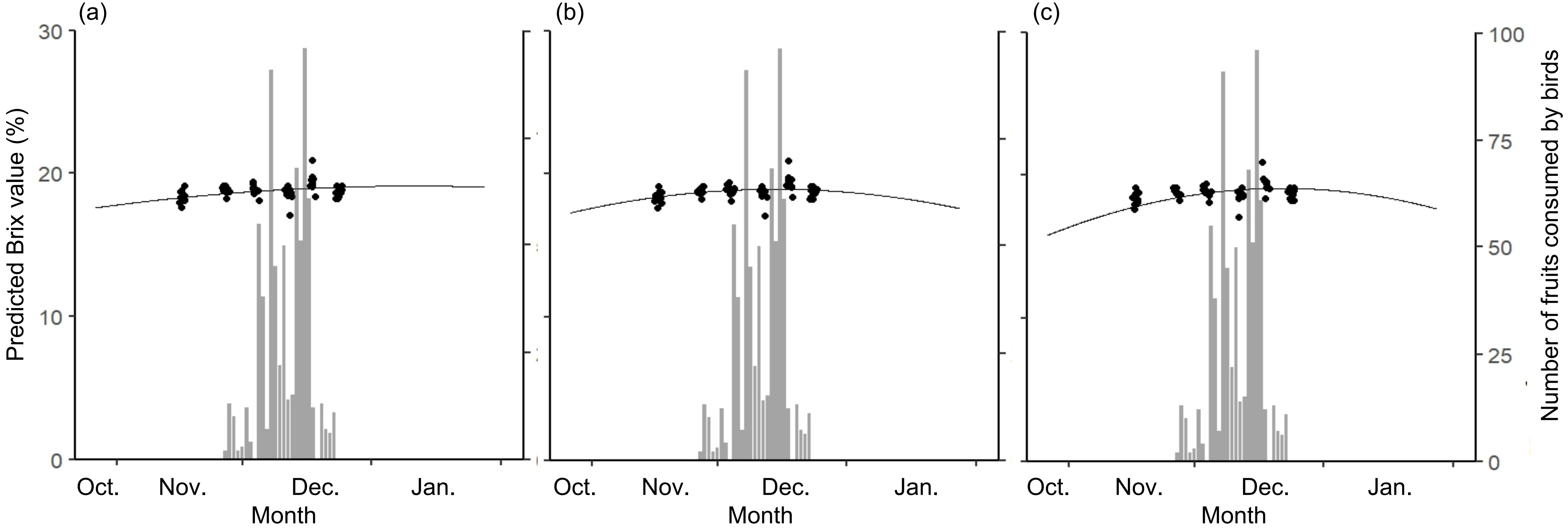

Figure S7. Temporal change in Brix values of fruits predicted based on (a) pericarp darkness, (b) relative ultraviolet-sensitive cone stimulation (UCS), and (c) both parameters, of a *Ligustrum obtusifolium* individual (*Lob* 2) and the number of fruits consumed by birds from October 2020 to January 2021. Dots indicate predicted Brix values. Fitted curves: (a) $Y = -0.0003X^2 + 0.040X + 17.601$ ($R^2 = 0.077$), (b) $Y = -0.001X^2 + 0.067X + 17.298$ ($R^2 = 0.114$), and (c) $Y = -0.001X^2 + 0.117X + 15.817$ ($R^2 = 0.171$). Bars indicate daily fruit consumption by birds. Estimated date of the maximum Brix value was January 9, 2021, in (a), December 13, 2020, in (b) and December 20, 2020, in (c). Fruit consumption by birds peaked on December 15, 2020.