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THE EFFECT OF COLOR ON FRUIT SELECTION IN SIX TROPICAL ASIAN BIRDS

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Abstract. The preferences of frugivorous birds for certain colors have been proposed to explain the evolution of fruit color, but evidence supporting this hypothesis is weak. Furthermore, evidence from tropical Asia is lacking, although in tropical Asia birds are more important seed dispersers than are their counterparts in other regions. We experimented with artificial fruit of five colors to evaluate the color preferences of six bird species (33 individuals, 2 families) from tropical Asia. We also checked whether contrast affects color detection by displaying red and green artificial fruits against green and red backgrounds. We found that five species had a consistent and strong preference for red, and one species preferred blue, with a low degree of variation among individuals. Species that preferred a certain color also consumed a small portion of fruit of different colors. Contrast increased the rate of consumption of green and red fruit in comparison with that against a monochrome background. Because all the species in this experiment showed a strong preference for a fruit color, we conclude that the interaction between frugivorous birds and fruit color may be tighter in tropical Asia than in other regions. Although contrast mediated the rate of consumption of red and green fruit to some degree, red was still the most preferred and green the least consumed.

Key words: *artificial fruit, color contrast, color preference, frugivorous bird, frugivore–plant interaction.*

Efecto del Color en la Selección de Frutos por Seis Aves Tropicales Asiáticas

Resumen. Las preferencias de las aves frugívoras por ciertos colores han sido propuestas para explicar la evolución del color del fruto, pero hay poca evidencia que respalde esta hipótesis. Más aún, no existe evidencia de Asia tropical, aunque en el trópico asiático las aves son dispersores de semillas más importantes que sus contrapartes en otras regiones. Experimentamos con frutos artificiales de cinco colores para evaluar las preferencias de color de seis especies de aves (33 individuos, 2 familias) de Asia tropical. También evaluamos si el contraste afecta la detección del color mediante el despliegue de frutos artificiales rojos y verdes contra fondos verde y rojo. Encontramos que cinco especies tuvieron una preferencia consistente y fuerte por el rojo, y una especie prefirió el azul, con un bajo grado de variación entre individuos. Las especies que prefirieron un cierto color también consumieron una pequeña proporción de frutos de colores diferentes. El contraste aumentó la tasa de consumo de frutos rojos y verdes en comparación con aquellos contra un fondo monocromático. Debido a que todas las especies en el experimento mostraron una fuerte preferencia para un color de fruto, concluimos que la interacción entre aves frugívoras y color del fruto puede ser más estrecha en Asia tropical que en otras regiones. Aunque el contraste condicionó hasta cierto punto la tasa de consumo de frutos rojos y verdes, el rojo fue el más preferido y el verde el menos consumido.

INTRODUCTION

Most terrestrial plants are immobile and depend on mobile animals as agents of dispersal. Brightly colored flowers and fruits are often considered an adaptation that increases the detectability of flowers and fruits by diurnal pollinating insects (Campbell et al. 2010, Hirota et al. 2012, Newman et al. 2012) and seed-dispersing birds (Willson and Whelan 1990, Schaefer et al. 2004, Lomascolo et al. 2010), respectively. Experiments during the 1980s and 90s testing the influence of seed-dispersing birds on the evolution of fruit color used as subjects mainly wild-caught birds. For example, some studies have reported some seed-dispersing birds to prefer certain colors (Puckey et al. 1996, Siitari et al. 1999, Hartley et al. 2000), but others have found only weak and transient color choices and strong variability between and within species (Willson and Whelan 1990, Willson and Comet 1993, Willson 1994). Field observations have provided little evidence for strong color preferences in seed-dispersing birds (Willson and Melampy 1983, Traveset and Willson 1998).

In addition to color, a fruit's conspicuousness (color contrast against background) is also reported to be a signal affecting birds' food-searching behavior (Burns and Dalen 2002, Schmidt et al. 2004, Burns et al. 2009). Some studies

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suggest that frugivorous birds do use fruit color when selecting fruit (Schaefer et al. 2008), but it appears that most of these patterns can be explained by the conspicuousness of fruit resulting from the spectral contrast between fruit and leaves, capsules, bracts, stems (Burns and Dalen 2002, Schmidt et al. 2004, Burns et al. 2009). The stronger the contrast between fruit and background, the more conspicuous the fruit and the more frugivorous birds will detect or consume it (Schaefer et al. 2006, Cazetta et al. 2007).

Red and black are the most common fruit colors found in nature (Wheelwright and Janson 1985, Willson and Whelan 1990) and are also the most conspicuous against natural backgrounds (Lee et al. 1994, Schmidt et al. 2004). If fruit color and conspicuousness serve as a signal to attract seed dispersers, red and black fruit should have a greater chance of being dispersed via animals' feeding on them and excreting them. Tropical Asia has the largest number of species of frugivorous birds globally (Corlett 1998), and these birds also have been found to be of greater importance dispersing early successional species than are their neotropical counterparts (Ingle 2003, Muscarella and Fleming 2007). However, the ecological relationship between fruit color and consumers and seed-dispersing birds in Asia is still being investigated, and few studies have addressed whether frugivorous birds preferentially select black and red fruit in this region.

Centered at 21° 55′ N, 101° 16′ E, Xishuangbanna, Yunnan Province, southwestern China, is located at the northern edge of tropical Asia. The region is renowned for its especially high biodiversity, which includes 16% of the higher plant and 36% of wild bird species found in China (Zhang and Cao 1995). Of the region's 412 species of plants bearing fleshy fruit, approximately 40% produce black fruit, 19% red, 13% brown, 13% yellow, 8% bicolor, 4% green, 2% white, and 1% blue (Chen et al. 2004). To explain the patterns of colors of natural fruit, many studies have focused on birds as selective agents because of their excellent color vision (Goldsmith 1990, Schmidt et al. 2004). However, direct evidence for the relationship between the distribution of fruit color and birds' preference for food color is scant from tropical Asia. Here we address the influence of color on birds' food selection by hypothesizing that when selecting food seed-dispersing birds have a strong preference for certain colors. We hypothesized that the prevalence of black and red fruit means these colors are the most preferred, and that other colors of lower frequency are consistently less selected. Last, we hypothesized that bird's color preferences should change with a fruit's conspicuousness and that greater conspicuousness should lead to increased selection.

MATERIALS AND METHODS

STUDY SITE AND MATERIALS

At Xishuangbanna, in January 2011, before the breeding season, we mist-netted 10 individuals of *Pycnonotus jocosus*, 8 of *P. melanicterus*, 2 of *Iole propinqua* (three species of the Pycnonotidae), and 2 of *Alcippe poioicephala* (Timaliidae), after the breeding season in December 2011 we netted 5 individuals of *P. aurigaster* (Pycnonotidae) and 6 of *Zosterops japonicus* (Timaliidae, Jønsson and Fjeldså 2006) . We selected these species because they are the most common frugivorous birds at our study site. As have other related studies (Gervais et al. 1999), we attempted to minimize the effect of small sample sizes on data interpretation, using in our experiments a total of 33 individuals and 6 species. Birds were held individually in cages 30 × 30 × 40 cm. The maintenance diet of all birds consisted of apple, pear, banana, and mealworms; water was available ad libitum. After our experiments, we retained the birds in captivity for other studies, and we plan to release them all in 2013. This study was approved by the Administrative Panel on the Ethics of Animal Experiments of Xishuangbanna Tropical Botanical Garden (2011-003).

The artificial fruit used in our experiments was composed of apple, pear, banana, wheat flour, and corn flour (1:1:1:1:1). We dyed the artificial fruit with 0.01% tasteless food colorants (black, red, yellow, green, or blue); all the food colorants are artificially synthesized commercial products (Haitian food coloring, Shanghai Singular Industrial Co., Ltd.). We chose these colors as they represent the gradient of colors of natural fruit at our study site (e.g., Chen et al. 2004). We shaped the artificial fruit into spheres of diameter 5–7 mm, similar to the size of natural food of bulbuls and white-eyes at our study site. All the fruits were similar in shape and size; they differed only in color.

EXPERIMENTAL DESIGN

We ran two experiments to test for the effects of fruit color and conspicuousness on the birds' rate of fruit consumption. The first food-choice experiment, in March and April 2011 and February 2012, tested whether the birds selected food on the basis of color. Experiments took place from 09:00 to 11:00 and from 13:00 to 15:00 under similar light conditions. Before the experiment, we removed maintenance food from the cage for 1–1.5 hr; water was still available ad libitum. In the experiment, we placed a total of 40 artificial fruits, eight of each of the five colors, evenly in a transparent Petri dish to avoid the effect of position on fruit selection. The total is greater than the number of fruits these birds could possibly consume within the exposure time. Each experiment lasted 15 min, then we counted the number of unconsumed food to determine the number of fruits pecked or removed. We tested each individual separately to avoid one birds influencing another's color selection. We repeated the experiment 6–8 times for each bird.

Our second experiment evaluated the effect of conspicuousness (color contrast against background) on fruit selection. We decorated the Petri dishes with red or green stickers to create a red or green background. We selected green and red as background colors since green (e.g., leaves) and red (e.g., bracts) are the main background colors in nature

(Wheelwright and Janson 1985). The diameter of the background was about 12 cm, considerably larger than the 5- to 7-mm diameter of the artificial fruits; this large background allowed birds to view and detect fruits consistently against a background. Since the experiment took place in a laboratory with a controlled light environment, we also ignored the influence of ambient light on the conspicuousness of a color (e.g., Endler 1993, Endler and Théry 1996). Following the same method described above, we displayed the artificial fruit on a red or green background over 15 min, then counted the number of fruit consumed. We repeated this experiment 6–8 times for each bird and each background. In this experiment we evaluated only the effect of contrast on selection of red and green artificial food because these combinations represented the maximum (red fruit vs. green background, green fruit vs. red background) and minimum (red fruit vs. red background, green fruit vs. green background) potential color contrast.

COLOR MEASUREMENT AND CONTRAST CALCULATIONS

We measured the reflectance spectra of six artificial fruits of each color, then calculated the mean as an approximation of the reflectance of each color. We also measured the reflectance of the two backgrounds (the stickers) against which artificial fruits were displayed. Because variability in the reflectance spectra of the stickers was very small, we calculated mean reflectance on the basis of only three. For all measurements we used an Ocean Optics USB4000 spectrometer and an Ocean Optics Deuterium–Halogen DT-MINI-2-GS as a standardized light source; we measured reflectance in relation to a standard white reference tile (Top Sensor Systems WS-1-SS). For color measurements, we used a coaxial fiber cable (QR400-2-UV-BX, Ocean Optics) mounted inside a matt-black plastic tube to exclude ambient light (Schaefer et al. 2007) and fixed the angle of illumination and reflection at 45°. We processed the spectra with SigmaPlot and calculated them in 20-nm intervals from 300 to 700 nm.

We calculated the color locus of each color of fruit and background as seen by a tetrachromatic bird (Goldsmith 1990), taking into account absorbance of visual pigments, transmittance of the oil droplet, and transmittance of the ocular media (Hart et al. 2000, Hart 2001), following Théry et al. (2005) as well as Théry and Casas (2002). Therefore, we computed the sensitivity factor R for each photoreceptor as

$$R = 1/\int_{330}^{700} I_B(\lambda)S(\lambda)D(\lambda)d(\lambda) \qquad (1)$$

where, $I_B(\lambda)$ is the spectral-reflection function (the percentage of incident light reflected at each wavelength by the measured surface) of the backgrounds and $S(\lambda)$ is the spectral-sensitivity function of the receptor (the relative sensitivity of the photoreceptor to each wavelength). Because passerines are the most common frugivorous birds at our study site, we used the model of the eye of the Blue Tit (*Cyanistes caeruleus*) as the template for the spectral-sensitivity function. $D(\lambda)$ is the spectrum of illuminating daylight (the number of photons present in daylight at each wavelength) CIE D65, since frugivorous birds are active in normal daylight. We then computed the effective quantum flux P (the fraction of the total number of photons present in the incident light at each wavelength that are reflected by the measured surface and perceived by the photoreceptor) for each spectrum in the respective photoreceptor as follows:

$$P = R\int_{330}^{700} I_s(\lambda)S(\lambda)D(\lambda)d(\lambda) \qquad (2)$$

where $I_S(\lambda)$ is the spectral-reflection function of the fruit. We assumed that photoreceptors respond at half their maximum when stimulated by the light reflected from the adaptation background. We normalized the maximum excitation $E_{\max}$ of each photoreceptor to unity and calculated the physiological signals of the receptor's voltage E_{UV}, E_{B}, E_{G}, and E_{R} as

$$E = P/(P + 1) \qquad (3)$$

We then calculated coordinates of each spectrum in the color space, which for birds has the shape of a tetrahedron (Goldsmith 1990), as follows:

$$x = \frac{2\sqrt{2}}{3} \cos 30°(E_{\mathrm{G}} - E_{\mathrm{R}}) \qquad (4)$$

$$y = E_{\mathrm{UV}} - \frac{1}{3}(E_{\mathrm{B}} + E_{\mathrm{G}} + E_{\mathrm{R}}) \qquad (5)$$

$$z = \frac{2\sqrt{2}}{3}[\sin 30°(E_{\mathrm{G}} + E_{\mathrm{R}}) - E_{\mathrm{B}}] \qquad (6)$$

Finally, we estimated the chromatic contrast between each pair of fruit and background as the Euclidean distance ΔS_t

$$\Delta S_t = \sqrt{x^2 + y^2 + z^2} \qquad (7)$$

STATISTICAL ANALYSES

We used Kruskal–Wallis tests to assess whether a species preferred a certain color, Mann–Whitney *U*-tests to check which color among the five colors was the most preferred. To test the effect of contrast on fruit selection we also used Mann–Whitney *U*-tests to identity differences in the number of red or green fruit consumed when displayed against a contrasting or concolor background.

RESULTS

REFLECTANCE SPECTRA AND CONSPICUOUSNESS OF FRUIT COLORS

Reflectance spectra of fruits and backgrounds are shown in Appendix 1. Fruit colors differed in their contrast against red and green backgrounds (one-way ANOVA, red background, $F_{4,25} = 7.22$, $P = 0.000$; green background, $F_{4,25} = 61.42$,

TABLE 1. Chromatic contrast (mean values) of five colors of artificial fruit against a green or red background.

	Fruit color				
Background	Black	Red	Yellow	Green	Blue
Green	0.34	0.24	0.18	0.17	0.23
Red	0.14	0.08	0.14	0.15	0.13

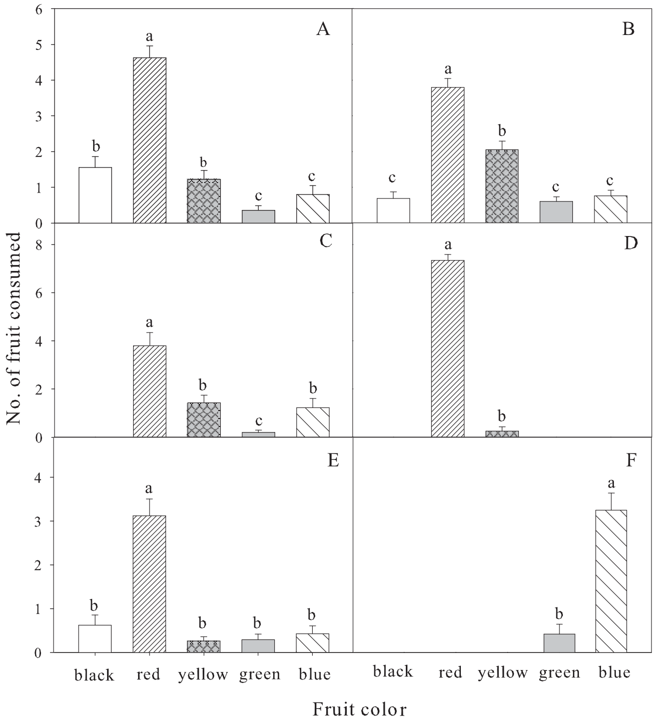

FIGURE 1. Preference of six species of birds for five colors of artificial fruit. *Pycnonotus jocosus* (A), *P. melanicterus* (B), *P. aurigaster* (C), *Iole propinqua* (D), and *Zosterops japonicus* (E) strongly preferred red, whereas *Alcippe poioicephala* (F) strongly preferred blue. Different letters above each bar indicate statistical significance at $P < 0.01$ (Mann–Whitney U-test). Comparisons are made within each panel.

$P = 0.000$). Black is the most conspicuous, red and blue less so, and yellow and green are least conspicuous against a green background (Tables 1 and 2). Red fruit was the least conspicuous against a red background (Tables 1 and 2).

EXPERIMENTS ON FRUIT-COLOR SELECTION

All the species preferred a particular fruit color (Kruskal–Wallis test, χ^2 = 139.0, 101.2, 54.5, 52.6, 78.2, and 49.6 for *P. jocosus*, *P. melanicterus*, *P. aurigaster*, *I. propinqua*, *Z. japonicus*, and *A. poioicephala*, respectively; df = 4, $P < 0.001$ for all) (Fig. 1). *Pycnonotus jocosus* (10 individuals), *P. melanicterus* (8 individuals), *P. aurigaster* (5 individuals), *I. propinqua* (2 individuals), and *Z. japonicus* (6 individuals) showed a strong preference for red artificial fruit (Fig. 1A–E), whereas *A. poioicephala* (2 individuals) preferred blue artificial fruit (Fig. 1F).

Although five species preferred red fruits strongly and consistently (Fig. 1A–E), a few individuals' color choice was weak (Appendix 2). For example, 28 of the total of 31 individuals of these 5 species preferred red (including 8 individuals that preferred both red and one another color). Of the remaining 3 individuals, one (*P. aurigaster*) preferred blue and yellow and two (*P. melanicterus*) weakly preferred yellow. Both individuals of *A. poioicephala* were consistent in preferring blue fruit (Appendix 2).

Because we tested only two individuals of *I. propinqua* and *A. poioicephala*, in order to make the comparison of species consistent, we recalculated the pattern of color selection by *P. jocosus*, *P. melanicterus*, *P. aurigaster* and *Z. japonicus* with two randomly selected individuals. There was a total of 45 possible combinations for *P. jocosus* (10 individuals); each of the combinations was consistent in preferring red fruit. There were 28 possible combinations for *P. melanicterus* (8 individuals), and 25 of the 28 combinations preferred red; 2 combinations showed a preference for both red and yellow, and 1 combination preferred yellow. There were 15 possible combinations for *Z. japonicus* (6 individuals), and 14 of the 15 combinations preferred red; 1 combination preferred both red and black. There were 10 possible combinations for *P. aurigaster* (5 individuals), and 7 of the 10 combinations preferred red; 1 combination preferred both red and yellow, 1 combination preferred blue, and 1 combination preferred yellow. It is therefore clear from this analysis that, almost all the possible combinations of two individuals consistently preferred red fruit.

EXPERIMENTS ON CONSPICUOUSNESS

For species that were found to prefer red fruit we presented artificial red fruit against a red or green background. All species

TABLE 2. Results of the post hoc test (P-values) following ANOVA of multiple comparisons between fruit colors against green and red backgrounds.

	P-values of multiple comparisons									
	Black				Red			Yellow		Green
Background	Red	Yellow	Green	Blue	Yellow	Green	Blue	Green	Blue	Blue
Green	0.001	0.001	0.001	0.001	0.001	0.001	0.58	0.44	0.001	0.001
Red	0.001	0.79	0.60	0.40	0.001	0.001	0.002	0.79	0.27	0.17

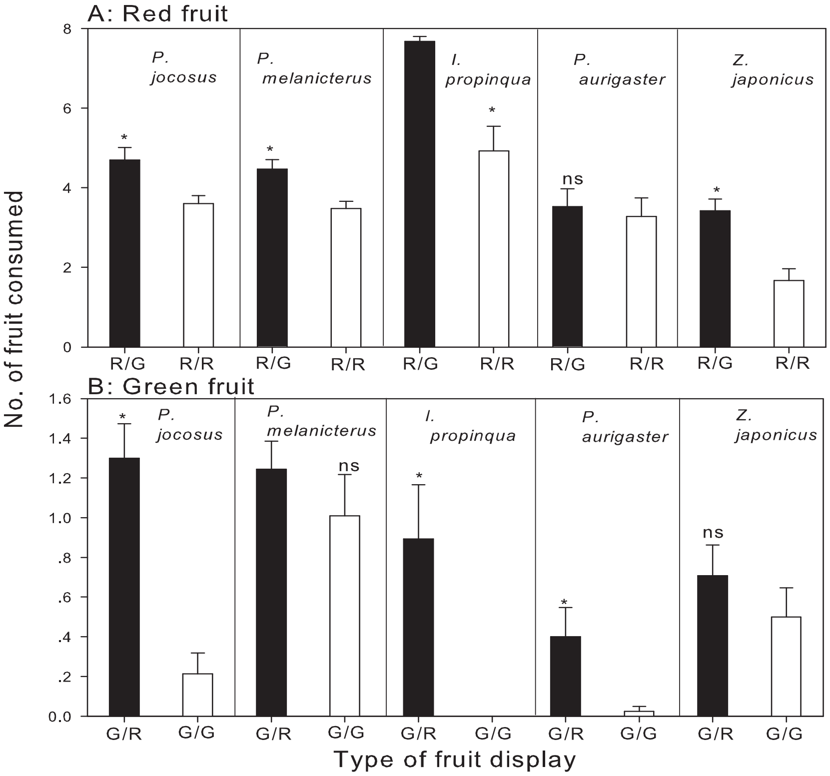

FIGURE 2. Preference of six species of birds for red (A) and green (B) artificial fruit displayed against a contrasting (black bars) or concolor (white bars) background. Note the different scales of the *y* axes.

significantly preferred the contrastingly displayed food (Mann–Whitney *U*-test, U = 2874.1, 2234.0, 65.5, and 119.0 for *P. jocosus*, *P. melanicterus*, *I. propinqua*, and *Z. japonicus*, respectively; $P < 0.01$ for all) (Fig. 2A), except for *P. aurigaster* ($U = 759.5$, $P = 0.69$). The experiment with green fruit yielded a similar preference for contrasting display ($U = 2482.3$, 126.0, and 677.0 for *P. jocosus*, *I. propinqua*, and *P. aurigaster*, respectively; $P < 0.05$ for all) except for *Z. japonicus* ($U = 241.5$, $P = 0.29$) and *P. melanicterus* ($U = 2746.2$, $P = 0.18$) (Fig. 2B). Although the food-removal rate changed with the background color, the rate of consumption of red fruits on a green background was always higher than that of green fruits on a red background (Fig. 2)

DISCUSSION

Birds' selection of food is often invoked to explain the distribution of colors of natural fruit. Tropical Asia might be a region important to understanding the interaction between fruit color and birds' food selection since forest succession in tropical Asia is more dependent on birds (Ingle 2003, Muscarella and Fleming 2007). Using six species of frugivorous birds (33 individuals) of two families, our study is the first experimental assessment of fruit color and frugivorous birds in tropical Asia. Our results are inconsistent with previous reports that found birds' color preferences to be weak and transient (Willson and Whelan 1990, Willson and Comet 1993, Willson 1994, Schmidt et al. 2004) but consistent with others that also found a preference for red (Puckey et al. 1996, Borgia and Keagy 2006). The pattern was the same even when we analyzed preferences of two randomly selected individuals of each species. Red reflects more light and looks more conspicuous against the natural green background, possibly explaining why birds choose this color (Cazetta et al. 2007, Schaefer et al. 2008). This preference for reflective fruit might increase birds' efficiency in foraging, by allowing them to select more easily detectable food items. Interestingly, of the five species in our experiment that preferred red fruit, the color choice of only a few individuals was weak, and most individuals preferred red consistently (Appendix 2)

Increasing conspicuousness might not be the only means that plants use to attract seed-dispersing birds to their fruits (Schaefer and Schmidt 2004). It is possible that the color of preferred food items is correlated with some nutritional signals (e.g., carbohydrates). In this case, birds would use color as a reliable indicator of the nutritional rewards of fleshy fruits (Schaefer et al. 2008, Valido et al. 2011). However, further information on selection of natural fruit in this region is needed for this hypothesis to be tested. Although five of the six species in our experiment preferred red fruit consistently, we found that *Z. japonicus*, *P. jocosus*, and *P. melanicterus* consumed food of all other colors to some extent. This pattern may indicate that food-color preferences in these species function to prioritize food consumption rather than to dictate the rejection of fruit of other than the preferred color.

Black is also a signal of palatability and contrasts strongly with the forest background (Schmidt et al. 2004), yet no species in our experiment preferred black fruit. This could be explained by the fact that the artificially colored black fruit used in our experiment was not the same black as real fruit, as indicated by its reflectance spectrum (Appendix A). In fact, the artificial "black" had a reflectance peak in the blue range, so it may have appeared blue to birds. A comparison of the spectra of natural and the artificial fruits is also needed to facilitate the interpretation of this pattern of preference. For example, Schmidt et al. (2004) tested the spectra of some natural black fruits whose reflectance is lower than that of the artificial black fruit in our study. Also, the natural black fruits of Schmidt et al. (2004) were highly contrasting, and birds used the contrast, not the color, as their signal for foraging. Besides selection by frugivorous birds, phylogenetic inertia could also be a factor influencing fruit color at our study site (Chen et al. 2004).

Although our experiments tested only two individuals of *A. poioicephala*, both consistently and strongly preferred blue fruit (Appendix 2). This preference was very different from that of the other species tested and may be attributable to different habitats and light conditions that the species experiences in nature, as the apparent color of a fruit is often affected by the interaction between the spectral composition of ambient light and the fruit's reflectance spectrum (Endler 1990, Endler and Théry 1996). For example, *P. jocosus* and *P. melanicterus* are mainly active in the forest canopy and open areas (Malmborg and Willson 1988, Loiselle and Blake 1990), while *A. poioicephala* inhabits the mid- and understory. Light conditions are more stable in the canopy than in the understory, and the chromatic contrast of fruits of the understory is often greater (Cazetta et al. 2007). Consistent with Cazetta et al. (2007), we also suggest that birds of the understory, such as *A. poioicephala*, depend more on contrast to detect blue fruit, which contrast strongly against a green background (Table 1). Furthermore, *A. poioicephala* is omnivorous, and red insects appear to signal unpalatability (Roper and Cook 1989, Schuler and Roper 1992), so the color selection of *A. poioicephala* in our experiment might also have been influenced by the birds' previous experiences.

The influence of conspicuousness on fruit selection has received some attention. Burns and Dalen (2002) reported that red fruit displayed against a contrasting background was removed at higher rates. Similarly, Schmidt et al. (2004) reported that seed-dispersing birds consumed more green and red artificial fruit when that fruit presented against a contrasting background than when it was presented against a concolor background. We too found that presenting red fruit against a contrasting green background significantly improved its rate of consumption by *P. jocosus*, *P. melanicterus*, *Z. japonicus*, and *I. propinqua* but not by P. aurigaster. Contrast also increased rates of removal of green fruit by *P. jocosus*, *P. aurigaster*, and *I. propinqua* but not those by *P. melanicterus* and *Z. japonicus* (Fig. 2). Although contrast influenced the fruit-removal rate, the total number of green fruits consumed was always smaller than the number of red fruits consumed, regardless of background. In other words, the general pattern of fruit removal was not influenced by the presence of an artificial background. This can be explained because the contrast between the artificial fruit and the background was still high enough to allow the food to be detected.

In summary, our study is the first to our knowledge to report an interaction between fruit color and birds' food selection in tropical Asia. All six species tested strongly preferred a certain color, and five of these preferred red fruit; only a few individuals' preferences were weak. Most species still consumed a small proportion of fruit of other than the preferred color. We conclude that the interaction between frugivorous birds and fruit color is tighter in tropical Asia than elsewhere in the world. Although changes in contrast mediated the detectability of red and green food to some degree, they did not fundamentally change the general pattern of selection, because red was always preferred over green, whether presented against a contrasting or a concolor background.

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