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EXPLORING FRUGIVOROUS BIRDS' ABILITY TO ADAPT TO ARTIFICIAL FRUIT COLOURS

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Abstract: Alteration of fruit traits for domestication purposes is expanding globally, yet its impact on the adaptability of frugivores, especially birds, remains unclear. Fruit traits have been known to evolve in response to interaction with frugivores. However, technology-driven alterations to fruit traits deviate from these natural processes. We investigated the influence of changing natural fruit colour on the behaviour of birds via frugivory rate on natural and alternative fruit colours. Modelling clay was used to create three different colours of fake fruits (natural, red, and blue) by mimicking the fleshy fruit of *Ficus microcarpa* L.f., 1782 and the field experiment was conducted in EcoHub, Universiti Sains Malaysia. We measured the spectral reflectance of each fruit colour and accessed their conspicuousness level through the avian eye model. We also analysed the peck marks on the fruits. A statistically significant result showed that birds' preference was the highest for natural fruit colour. Our findings reflect the inadaptability of frugivorous birds to changes in natural fruit colour and we believe that exercising caution when pursuing agricultural advancements is essential to prevent unintended disruptions to ecosystems.

Keywords: Natural fruit colour, frugivorous birds, colour preference, behaviour, avian eye model.

Introduction

Fruit traits are pivotal in determining their attractiveness and accessibility to consumers. Throughout evolution, fruit traits have been known to coevolve with frugivores as these traits are essential for the dispersal of fruit and survival of frugivores (Gautier-Hion *et al*., 1985; Fleming & John Kress, 2011; Onstein *et al*., 2017; Bender *et al*., 2018; Valenta & Nevo, 2020). Fruit traits have evolved in a way that best suits the needs of frugivores to increase reproduction success. For example, they tend to develop colours contrasting with background foliage, enhancing their conspicuousness to existing frugivores (Burns & Dalen, 2002; Melo *et al*., 2011; Nevo *et al*., 2018).

Fruit colouration is significant for attracting frugivores, especially birds which possess remarkable abilities to perceive a broad spectrum of hues through their tetrachromatic vision (Wheelwright & Janson, 1985; Schaefer *et al*., 2006; Cazetta *et al*., 2007; Nevo *et al*., 2018; Pires *et al*., 2018; Osorio, 2019). The complex interplay between the evolutionary pressures exerted by frugivorous birds and their colour preferences has been the subject of research. Several studies showed that birds could learn to select fruits based on memory, palatability, social learning, and nutritional value, indicating the critical role of colour in their foraging behaviour (Ham *et al*., 2006; Schaefer *et al*., 2008; Slagsvold & Wiebe, 2011; Slagsvold, 2019; Hämäläinen *et al*., 2021).

However, expanding the human population has continuously altered food crops to meet diverse market demands, including improved crop quality and consumer appeal (Chapotin & Wolt, 2007; O'Sullivan *et al*., 2019). In this process, fruit traits are sometimes altered in ways that deviate from their natural state. One example is the transformation of red tomatoes into purple, achieved by regulating anthocyanin levels, which prolongs shelf life and enhances storability (Sharma *et al*., 2022). Given that frugivores are presumably accustomed to the current fruit traits, it is possible that they may fail to recognise these altered fruits and perceive them as distinct fruit species. Unlike natural evolution processes, which occur over relatively long timescales, modern agrotechnology can lead to rapid and drastic changes in fruit traits (Kolisnyk *et al*., 2020; Nascimento *et al*., 2020), where frugivorous birds may struggle to adapt to the altered fruit trait.

There have been limited studies on the influence of fruit trait changes on frugivores, and whether they can adapt to the changes remains unclear (Rodriguez-Saona *et al*., 2019; Chabaane *et al.,* 2021). This study aims to fill this research gap by investigating the adaptability of frugivorous birds to changes in fruit colour from the perspective of colour preferences. We employed modelling clay to mimic fig fruits with three different colourations, representing scenarios where fruit colour is altered through technological means. We addressed the following question: Do changes in natural fruit colour influence the frugivory rate of birds? Our objective is to assess the influence of altering fruit colour on the behaviour of frugivorous birds.

Material and Methods

The experiment was held at EcoHub, Universiti Sains Malaysia, on Penang Island with coordinates of 5°21'40.1" N100°18'18.2" E (Figure 1). As a small secondary forest, the site provided an optimum setting with various fruiting trees and more than 100 recorded bird species (Muin *et al.,* 2019).

We selected *Ficus microcarpa* L.f., 1782, a fleshy fruit species naturally occurring within the study site, as the model fruit. Our choice was based on extensive field observation, consistently documenting its frequent visitation by various bird species (Muin *et al*., 2019). From the family Moraceae, *F. microcarpa* acts as a keystone species for frugivorous birds (Lambert & Marshall, 1991; Mackay *et al*., 2018). As a native plant distributed widely across Malaysia (MyBIS, 2023), it is a familiar and ecologically relevant fruit model for the avian inhabitants of the study area. We also excluded transition colours (unripe and ripening stage) such as green and pink as alternative fruit colours to avoid potential bias of frugivores. Non-toxic modelling clay (Polar, Malaysia) was shaped into a spherical model with a 0.5-

Figure 1: (A) The location of Penang Island in Malaysia, and (B) experimental site in EcoHub, Universiti Sains Malaysia
Source: Google Map (2023)

0.8 cm diameter, mimicking the figure. Three distinct colours were used: Natural (to replicate the fruit's typical purple-black colouration), red, and blue.

Regarding odour, neither real figs nor fake fruit emit distinct scents detectable by the human olfactory system. However, we acknowledged the potential influence of odour on birds' foraging behaviour while emphasising that our study primarily focused on fruit colouration. Thus, we considered the factor of odour negligible. To produce natural fruit colour (purple-black), food colouring (Star Brand, Malaysia) with a ratio of four red: One blue was kneaded along red modelling clay. Alternative colours are used directly from clay, where the manufacturer has produced the colour. Additionally, we added black watercolour dots (Buncho, Malaysia) to simulate the numerous black spots observed on the surface of real fig fruits during the observation period, thereby enhancing the authenticity of the fake fruits.

We randomly took five samples of ripe fig fruits from the same plant within reachable height at EcoHub to measure reflectance values using Colour Meter Pro (CHNSpec, 2021). The device was auto-calibrated with a built-in standardised black and white colour index, following industry-standard methods, including ASTM E313-00, ASTM E313-73, CIE/ISO, AATCC, Hunter, and Taube Berger Stensby. Measurement was taken with an integrated full-band balanced LED light source by placing the device on the fruit surface at 90° to exclude ambient light (CHNSpec, 2021). We measured three reflectance values for five fruit samples for each fake fruit colour and averaged using ColorExpert Software (ColorExpert, c.2021). Due to the device's limited sensitivity, we could only assess the reflectance range of 400-700 nm at intervals of 10 nm. This means we could not measure the UV wavelength (10-400 nm). However, we assume the fake fruit does not reflect UV and the main colour comparison would only be associated with visible wavelengths.

To model the conspicuousness of fruit colours through bird vision (UVS visual system), spectral sensitivities and receptor noises of cones u, s, m, and one by blue tits, *Cyanistes caeruleus* Linnaeus, 1758 were used to visualise the position of each colour in tetrahedral colour space. Blue tits were used to represent visual perception as frugivorous birds in the area also commonly come from the order Passeriformes (Muin *et al.,* 2019). Relative cone outputs were calculated using formulas by Endler and Mielke andorobyev and colleagues (Vorobyev *et al*., 1998; Endler & Mielke, 2005). The values were then transformed into coordinates x, y, and z within tetrahedral colour space with a height of one in MatLab (2023), using the code developed by Stoddard and Prum (2008). The conspicuousness of each fruit colour against foliage (fig leaves) was calculated via Euclidean distance, considering the differences in coordinates between fruit and leaf colour (Burns *et al*., 2009).

We held the experiment weekly for a month with a three-day break (Sunday to Tuesday) between four days of continuous observation (Wednesday to Saturday) in November and December 2022. Experimental procedures were modified by referencing previous research and unpublished protocol from M. Galetti (Alves-Costa & Lopes, 2001) to ensure the relevance and effectiveness of the methods in the context of our study. For each colour, 30 replicas of fake fruit were used (N = 90). Each colour had six experimental trees, with five fake fruits attached to each tree using flexible wire circling the branch, which acts as a base for support. Due to the variability of trees on the experiment site, each tree was chosen under two conditions: Exclude fruiting trees (to avoid confusion of different fruit species on trees) and the lowest branch height of the tree must be within reachable distance (2 m). The colour of the fake fruit was selected randomly for the first tree, followed by its closest experimental tree (2-3 m), where the determination of fake fruit colour was done by coin tossing, excluding the fruit colour of the first tree. The same process was applied to the remaining experimental trees. Fake fruits were placed near terminal branches to mimic the fruiting tree. All fake fruits were placed above leaves on the same branch whenever possible, with heights ranging from 1.5-2 m. A camera trap was set up randomly on an experimental tree of each fruit colour to capture bird feeding behaviour. Due to limited footage during the initial phase, the camera trap settings were extended for an additional two months and the number of fake fruits was increased to 15 to ensure comprehensive data collection.

All fake fruits were collected and replaced carefully using latex gloves for each observation day between 15:00 and 17:00 to avoid interrupting bird active hours at 17:30 (Jaafar & Anuar, 2003). We observed all fake fruits under a table lamp and magnifying scope to ensure no peck marks were missed in the data recording.

As data normality could not be archived, we used the Kruskal Wallis test to determine whether there is a significant difference in preference among three fruit colours. Subsequently, we conducted Mann-Whitney U tests with Bonferroni correction to examine differences between each pair of fruit colours.

Results

All fruit colours reflected light throughout the visible spectrum, ranging from 400-700 nm (Figure 2). The fruit of *F. microcarpa* and fake fruits with natural colour have similar average reflectance spectra with black colour, displaying relatively low intensity without a specific peak region. Red fake fruit showed the highest reflectance intensity, peaking around 620-700 nm. Blue fake fruit showed moderate intensity, peaking at 460-500 nm. All colours were described according to human perception.

All fruit colours were aligned with their respective colour regions in tetrahedral space, indicating that birds perceived them as the same colour as described (Figure 3). The similarity of colour coordinates between real fruit and fake fruit with natural colour also reflected the reliability of the fruit colour produced. Results from Euclidean distance revealed that red has the highest conspicuousness level against foliage (0.660), followed by blue (0.403), and natural fruit colour (0.316). This model has a caveat since no UV values were recorded; however, it does not affect the overall calculation as the points within the tetrahedral are still correctly positioned in relation to their edge nomination.

Birds selected Natural fruit colour the most with the highest mean number of marked fake fruits (0.323) while blue showed a slightly higher mean value of 0.140 than red with 0.113 (Figure 4). On the other hand, results from the Kruskal Wallis test showed a significant difference in at

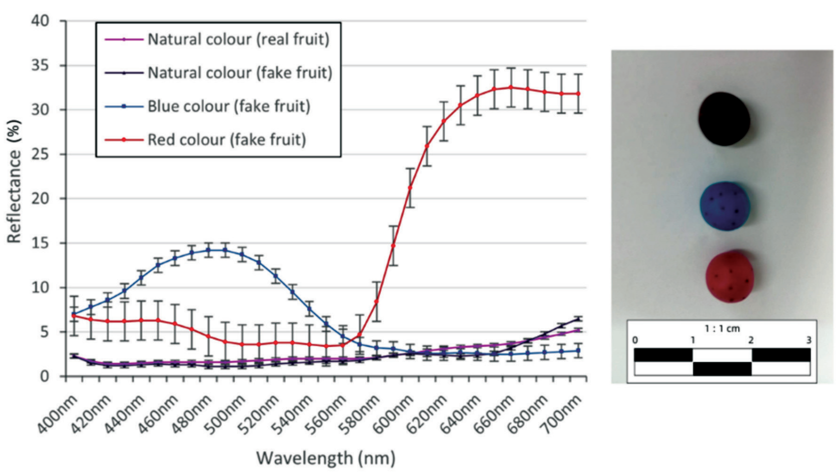

Figure 2: Reflectance spectra of natural *F. microcarpa* fruit (diamond), natural colour fake fruit (triangle), blue colour fake fruit (square), and red colour fake fruit (circle). Error lines represent standard error (inset picture). Fake fruit model for each of the colour

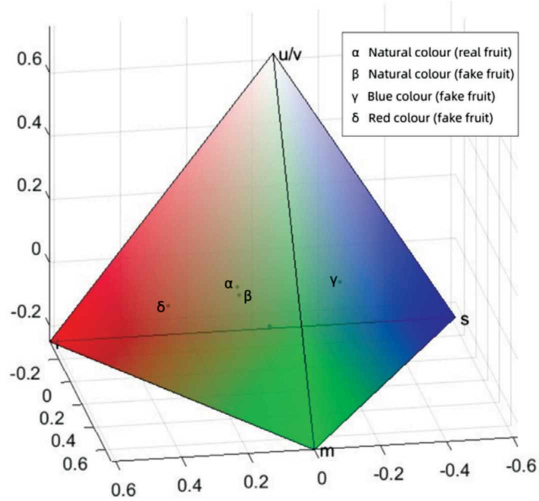

Figure 3: The coordinate of each fruit colour in tetrahedral colour space using the model UVS bird visual system by blue tits (*Cyanistes caeruleus*)

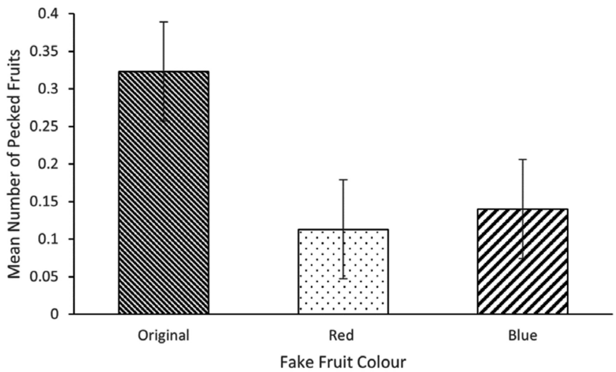

Figure 4: Mean number of pecked fruits of each fruit colour. Same letter above bar indicates statistically significant differences ($p < 0.05$) of pairwise comparison (Mann-Whitney U test with Bonferroni correction)

least one of the frugivorous bird rates among three fruit colours, $\chi 2$ (2, N = 288) = 41.008, $p < 0.001$. Post hoc analysis used the Mann-Whitney U test with Bonferroni correction to reduce Type I error. Results showed a significant difference was found between the two groups with a p-value lower than alpha 0.017, which includes natural versus red colour (U = 2491.000, z = -5.817, p = 0) and natural versus blue colour (U = 2789.000, z = -4.957, p = 0). No significant difference was found between bird frugivory rate of red and blue colour fake fruit (U = 4232.500, z = -1.102, p = 0.271).

Discussion

We demonstrated that tropical frugivorous birds strongly prefer natural over alternative fruit colours despite all fake fruits sharing similar morphological characteristics. Due to the proximity of natural fruit colour to black in spectral reflectance, natural fruit colour is classified as “dark” in the following discussion. Our results align with previous studies where birds preferred darker fruit colours (Schaefer *et al*., 2008; Schaefer, 2011).

Conspicuousness plays a pivotal role in fruit selection by birds (Schmidt *et al*., 2004; Cazetta *et al*., 2007; Duan *et al*., 2014). Red fruit generally yields a higher contrast against foliage, making them more conspicuous in avian vision (Burns & Dalen, 2002; Melo *et al*., 2011; Camargo *et al*., 2013). Interestingly, results showed that red fruits were the least consumed. Frugivorous birds did not consistently select the most conspicuous colour (red) but rather preferred dark, less conspicuous colours. The finding supported recent research showing that the conspicuousness of fruit does not influence bird preferences (Lim & Burns, 2021).

The phenomenon might be explained by the role of colour in reflecting fruit content (Schaefer & Schmidt, 2004). The bright colouration is often associated with aposematism as it serves as a warning signal that reflects the unripe status or the presence of toxic compounds in fruits, potentially deterring frugivores (Lev-Yadun *et al*., 2009; Caro, 2017; Lev-Yadun, 2021). Results from the spectrographic analysis indicated that red and blue colours were much brighter than natural ones. While birds may easily detect these bright colours, they might also signify unripe or highly toxic fruits (Schaefer *et al.*, 2007), leading to their avoidance of consumption.

The theory was supported by footage from camera traps where birds only observed red and blue fruits from a distance and did not approach them, contrary to natural-coloured fruit, where birds showed interest and approach behaviour (Figure 5). Furthermore, an aposematic fruit in the experimental site, *Phaleria macrocarpa* (Scheff.) Boerl (Figure 6) may provide further justification. The plant contains brightly coloured red fruit, which proved toxic to animals (Ilyas *et al*., 2019; Simanjuntak & Rumahorbo, 2022). Previous encounters with this plant

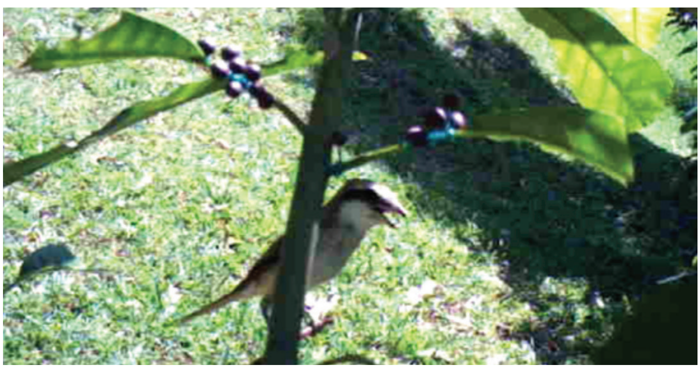

Figure 5: Sighting of bird on natural colour fake fruits through camera trap

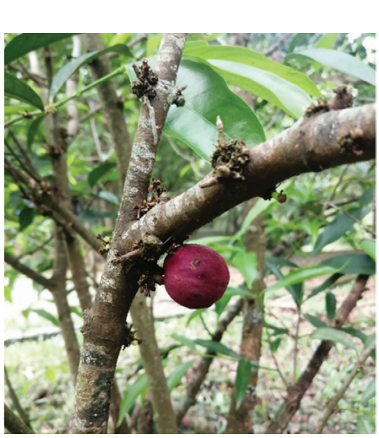

Figure 6: God's crown (*Phaleria macrocarpa*) on experimental site

species might contribute to birds associating red with unpalatable or toxic foods and avoiding approaching red fruits. In this regard, aposematism may have been a dominant factor in shaping frugivorous bird preferences, superseding the influence of conspicuousness. However, the speculations remain anecdotal due to the limited footage.

Despite the abundance of fruit trees in the experimental site, frugivorous birds preferred to consume dark-coloured fruits, which are uncommon in the immediate vicinity. This behaviour can be attributed to the learned behaviour of frugivorous birds (Honkavaara *et al.,* 2004). Over three decades, the fig tree model has consistently attracted bird visits (Muin, personal communication, 2023), establishing a learned preference for natural-coloured fruits. Birds consumed fake fruits with natural colours more frequently due to their resemblance to real fig fruits, which they were naturally accustomed to consuming. Furthermore, unlike migratory species, tropical birds rely on long-distance movements for food resources (Boyle, 2010; Sekercioglu, 2010). Limited seasonality in tropical countries contributes to the less defined fruiting season, allowing fruits to be available throughout the year (Newell *et al.*, 2002; Jansen *et al*., 2020). As a result, they tend to develop a strong knowledge of their local food availability (Ward & Zahavi, 2008), thus, exhibiting a preference for fruits that they are familiar with.

In addition, colour can be used to encourage learning and memory of food palatability (Ham *et al*., 2006; Hämäläinen *et al*., 2021). In tropical (Wheelwright & Janson, 1985) and subarctic regions (Willson & Comet, 1993), birds favour black are linked with high palatability. Since most birds were previously seen to feed on the actual fig fruits, it would be reasonable to suggest that birds associated the palatability of dark fig fruits with natural colour fake fruit (Honkavaara *et al.,* 2004). Black fruits or fruits with high UV reflectance also reflect a higher content of anthocyanins (Altshuler, 2001; Schaefer *et al*., 2008; Schaefer, 2011), which play an important role in maintaining birds' health due to their antioxidant properties (Frawley *et al*., 2021; Mounir *et al*., 2022). Although all fake fruits are assumed not to have UV, dark-coloured fake fruits may be perceived by birds as having high anthocyanin content, thus, contributing to the highest frugivory rate.

The lower consumption rate of red and blue fake fruits may be explained by the development of neophobia in birds. Neophobia is a form of avoidance of things that an individual has never experienced or that are dissimilar from previous experiences and it is often associated with a feeling of fear (Greenberg & Mettke-hofmann, 2001). The aversion to novelty was also evident in camera trap footage, where birds approached natural colour fruits more confidently but hesitated and observed red and blue fruits from a distance. The results were also consistent with previous studies, where familiar food results in faster approaching times (Marples *et al*., 2007; McMahon & Marples, 2017). Furthermore, camera footage revealed the visitation of a bird species known to commonly feed on fig fruits, yellow-vented bulbul (*Pycnonotus goiavier*) (Nurqamareena *et al*., 2018). This bird species is presumably accustomed to natural fruit colour, which might explain its weariness behaviour towards red fake fruits that they have not seen before. The familiarity and recognition of natural fruit colour likely drive the birds' preference as they represent a known food source, however, this assumption is based on anecdotal evidence from camera traps. It is also worth noting that despite our best efforts to find similar experimental trees, the orientation of fake fruits might differ due to the different tree branching systems, which birds might perceive differently.

The limitation of our research is that the black spots displayed on the fake fruits might have influenced the feeding behaviour of frugivorous birds due to their higher visibility in red and blue fruits compared to natural dark fruit colour. This also presented a possible caveat as we intended to mimic the real figs at the experimental site to achieve a complete resemblance between fake fruits and actual fruits. We acknowledged that the presence of black spots might potentially lead to the perception of frugivorous birds as indicative of ants crawling on the surface of fruits or other potential threats. While we disregarded the possibility of fungal infection in the figs due to their healthy appearance and absence of rotting signs (Sardella *et al*., 2016), other possibilities such as environmental or visual cues could have played a role in bird behaviours.

The presence of black spots might also be an indication of ant mimicry. In previous studies, ant mimicry has been discussed in the context of herbivory in other parts of the plant such as flower and stem (Lev-Yadun, 2009; Liu *et al*., 2017). The possibility should not be ruled out despite the lack of findings on ant mimicry on fruits. As of now, we suggest that the factors we discussed above would be more of the dominant forces that contributed to the differences in the frugivory rate of each fruit colour. From another perspective, our study demonstrated how differences in fruit colour could influence other fruit traits (such as the visibility of black spots), potentially influencing feeding behaviours. Further research should see whether the existence of black spots on fruits could impact the choices of frugivorous birds. It is important to acknowledge that our study is geographically limited to the site and may yield different results when conducted elsewhere.

While our results cannot shed light on the implications of technology usage in agriculture, it is clear that frugivorous birds strongly preferred the natural fruit colour to the altered one. This preference raises concerns about their adaptability in the face of drastic changes in food resources due to human-induced alterations in fruit colour. Given the vital role of frugivorous birds in seed dispersal, their inability to recognise altered fruit colours may result in ecological consequences. This study also showed that the conspicuousness of fruit colour did not influence fruit colour preferences of tropical frugivorous birds but was possibly related to the factors associated with their environment and previous foraging experiences. Based on the findings, we hypothesised that they would not be able to adapt when encountering drastic colour changes in their food resources. Therefore, we advise caution in altering fruit colouration and recommend avoiding colours that frugivores may perceive as aposematic. Agriculture sectors should consider the impact on frugivorous birds before implementing large-scale technological changes on food crops. Nevertheless, it should be noted that fruit colour is not the sole factor contributing to the adaptability of frugivorous birds, other fruit traits should also be investigated.

Conclusions

This study provides a general framework for future research to investigate the possible impact of alternating fruit traits on frugivores. Future studies should also examine the influences of alternating other fruit traits on the adaptability of frugivores. Comprehensive knowledge of the relationship between frugivores and their food resources can help inform strategies, balancing the needs of human and conservation efforts while maximising mutual benefits.

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Conflict of Interest Statement

The authors declare that they have no conflict of interest.

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