Habitat Selection Theory and the Preference for Flowers – Is There Empirical Support?

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Abstract

Although the aesthetic appreciation of flowers is a well-known aspect of human behavior, theories explaining its origin are missing. An exception is the evolutionary theory of Heerwagen and Orians, who suggest that humans emotionally respond to flowers because they signal food availability. However, fruits are stronger and more direct signals of food availability than flowers, therefore fruits should elicit stronger emotional responses than flowers. To test the theory, we performed two online studies in Czechia. The participants ($n = 3354$ and 744 respectively) indicated on a six-point scale their preferences for the photographs of 14 edible Czech plant species (study A) and 20 edible plant species from African savannas (study B), varying in their growth stage (flowering, fruiting). Paired t-tests found no preference for Czech fruiting plants and a strong preference for African flowering plants ($p < 0.0001$, Cohen's $d = 1.24$). Our results show that the theory deserves renewed attention.

Keywords

evolutionary aesthetics, habitat selection, flower preference, evolutionary anthropology

1. Background

Human attraction towards flowers is a phenomenon that is manifested in various ways, from ornamental gardens and flower exhibits to product design and get-well gifts. The volume of the global cut flower trade reaches € 15 billion per year (Mamias, 2018). One can find abundant examples of the aesthetic responses to flowers in many different cultures and historical periods. This fact led some authors to the conclusion that this human *phytophilia* – a term first used by Irenäus Eibl-Eibesfeldt (1989) – is probably common to humans as a species and was inherited from our ancestors (Appleton, 1975; Eibl-Eibesfeldt, 1989; Kellert, 1995; Wilson, 1984). In fact, phytophilia might even be typical for other members of the genus *Homo* (Solecki, 1975). One might ask why this behavior evolved.

In this paper, we use the term *aesthetic response* in the same way as Berlyne (1971) and Ulrich (1983, 1986), i.e., as a preference or a like-dislike effect in association with pleasurable feelings caused by visual exposure to a stimulus. Although measuring the aesthetic response might be

performed using different scales (such as like-dislike or beautiful-ugly), it does not lead to significantly different results, and the scales are highly correlated (Ulrich, 1986; Zube et al., 1975).

The proponents of evolutionary aesthetics link the aesthetic response to function and adaptive value (Volland & Grammer, 2003): Our ancestors evolved to consider environments, objects or situations that increased their chance of survival and reproductive success as beautiful and those that decreased it as ugly (Russo et al., 2003; Ulrich, 1986; Thornhill, 2003). Emotional responses to beauty and ugliness should, therefore, represent an adaptive reaction to potentially beneficial or harmful situations because they are very rapid and strong motivators of human behavior (Heerwagen & Orians, 1995).

The emotional response is stronger for signals that are more important for the receiver (Ulrich, 1983). This is evident, for example, in the Open Affective Standardized Image Set database (Kurdi, Lozano, & Banaji, 2017), where images differ in their valence (positive vs. negative) and arousal (low vs. high). Images showing imminent threats on the one hand and good foraging opportunities and safe spots on the other are highly arousing. Highly arousing positive images depict, for example, landscapes with water, vegetation, and vistas, lowly arousing include images of lawns or monotonous fields. Highly arousing images with negative valence include wildfires or severe drought, whereas lowly arousing ones might display junk or rubbish yards.

Judith Heerwagen and Gordon Orians applied the principles of evolutionary aesthetics in their theory of habitat selection (Orians & Heerwagen, 1992; Heerwagen & Orians, 1995). The theory incorporates environmental cues crucial for the survival of our ancestors – such as the presence of food, fresh water and shelter, and the ability to easily orient themselves in the landscape to avoid predators and other threats – into one conceptual framework.

The theory describes spatial and temporal frames of habitat selection. Different aspects of habitat are central for each of these frames. The spatial frame includes decisions on whether and how profoundly to explore an area and whether it is suitable for various activities. The temporal frame distinguishes environmental cues that require immediate attention (e. g., an incoming storm), cues associated with seasonal changes (e. g., the leafing out of trees), and cues influencing long-term behavior (e. g., the presence of a lake). The authors also argue that because a suitable habitat has to fulfill the needs of many different activities across time, people evolved not only to evaluate the immediate state of the environment, but also to pay attention to features that might help them to predict its probable future states.

Flowers are a typical cue associated with seasonal change. They signal important, positive changes in resource availability and represent a promise of good foraging opportunities in the future. Thanks to their specific appearance, they also help people to distinguish and localize different types of resources. Paying attention to flowers thus had adaptive value because it improved human functioning in natural environments (Orians & Heerwagen, 1992).

In their latter work, the authors emphasize a more straightforward link between flowers and food. They describe flowers as a potential food source, rich in nitrogen compounds and relatively free of toxins (when compared to other plant parts). Furthermore, bees use pollen from flowers to produce honey, which has long been a highly appreciated natural source of sugar (Heerwagen & Orians, 1995). The authors also speculate about a possible human preference for flowers with zygomorphic or otherwise unusual shapes, because on average, they contain more nectar and pollen. However,

our previous results found the opposite: raters disliked zygomorphic and unusual flowers (Hůla & Flegr, 2016).

Heerwagen and Orians state that conceptual theories about human responses to flowers are lacking and that the habitat selection theory offers a potentially powerful approach to this issue (Orians & Heerwagen, 1992). The theory operates with the concept of an ancestral environment that shaped human minds. For hundreds of thousands of years, this environment was located in the African savannas, where humans lived in small groups as hunters and gatherers (Heerwagen & Orians, 1992). The African savanna might be considered as the environment of evolutionary adaptedness (Tooby & Cosmides 1990) for human landscape and habitat preferences (Balling & Falk, 1982).

Although the habitat selection theory offers testable hypotheses and was formulated almost 30 years ago, it has not yet been empirically tested in relation to human aesthetic responses to flowers. This might be due to the fact that the topic of human perception of flowers has long been entirely out of the scope of evolutionary aestheticians and other researchers from related fields (which also explains the lack of current literature in the theoretical part of this paper). However, the renewed interest in the study of phytophilia and related human-plant interactions centered on plant morphology in recent years (Elsner & Wertz, 2018; Hůla & Flegr, 2016; Oberzaucher, 2017; Wertz & Winn, 2014a, 2014b; Włodarczyk et al., 2019) leads us to believe that a reliable theoretical framework might be hugely beneficial for the whole field and that the habitat selection theory of Heerwagen and Orians has the potential to provide such a framework. However, empirical evidence is urgently needed.

We decided to follow the logic of the habitat selection theory and compared two types of stimuli related to seasonal change and resource availability – flowers and fruits. Both signals have a positive valence, but they differ in their importance for the receiver. In contrast to fruits, flowers are only exceptionally eaten by humans and seldom by other African primates. On the other hand, fruits are one of the most important food sources (Peters et al., 1981; Peters, O’Brien, & Box, 1984). Fruits also usually contain large amounts of sugar and are generally nutritionally richer than flowers.

Flowers are ephemeral when compared to fruits. A flower blooming for a week is already considered to be long-lived. A majority of flowers blooming during the day in a hot or dry climate, for example, in the African savanna, do not last more than a single day (Primack, 1985). Flowers thus represent an approximation of possible future resource availability, whereas fruits are an instant, direct, and strong signal of the presence of resources at a given moment and also, thanks to their relatively greater longevity, in the near future. This is why fruits should elicit stronger responses and should be preferred more than flowers.

2. Hypothesis

Our main objective was to determine if there is empirical evidence for the theory of human preference for flowers that was proposed by Gordon Orians and Judith Heerwagen (Heerwagen & Orians, 1993; Orians & Heerwagen, 1995).

We formulated a testable hypothesis:

Plant species with edible fruits will receive a higher score on the preference scale during the fruiting stage than during the flowering stage.

2.1. Exploratory part

In the exploratory part of the study, we first wanted to examine whether women and men differ in their ratings of flowers and fruits. Some authors have speculated that there might be sex differences in the aesthetic preferences of natural environments due to the hypothetically predominant role of women as gatherers and men as hunters in human evolutionary history (Ruso, Renninger, & Antzwanger, 2004). This differentiation of roles between men and women already serves as the explanation for sex differences in other aspects of human behavior and abilities, such as orientation in space - the so-called hunter-gatherer theory of spatial sex differences (Silverman & Eals, 1992; Silverman, Choi, & Peters, 2007).

A considerable number of studies have found differences in general human color preferences (reviewed in Crozier, 1999) and have discussed possible explanations for these differences (Hurlbert & Ling, 2007; Palmer & Schloss, 2010; Sorokowski, Sorokowska, & Witzel, 2014). There is also evidence for differences in color preferences of flowers (Hůla & Flegr, 2016; Yue & Behe, 2010) and trees (Muderrisoglu, Aydin, Yerli, & Kutay, 2009). For these reasons, we wanted to explore whether the color of flowers and fruits in our dataset influences their preferences.

3. Materials and Methods

The Charles University review board approved this research (approval no. 2017/10).

3.1. Study A – Czech plants

Stimuli

In study A, we used photographs of 14 plant species with edible fruits native to or commonly cultivated in the Czech Republic. The discussed theory emphasizes the importance of fruits and flowers in relation to food resources, so we wanted the raters to know that the fruits are indeed edible. There were four herbs, five shrubs, and five trees in the set (see Table 1). Each species was displayed in the flowering stage and the fruiting stage and from three different distances: 1- a close-up of the flowers/fruits, 2- flowers/fruits and a part of the plant (photographs were taken from a distance of 0.5 to 1 meter), 3- the whole plant with flowers/fruits. In total, there were six photographs per species. By using the same species for displaying both flowers and fruits, we tried to minimize a possible bias that might occur if we displayed flowers and fruits of entirely different plants (different leaf shapes, the habitus of the plant, etc.). We also tried to choose a wide range of flower and fruit colors.

We used non-standardized freely available photographs from the internet. In few cases, we used private photographs. Their owners gave us written permissions to use the photographs for this research. We tried to control for the plant-background ratio and also rescaled the images to the same size (600 x 450 px), see Fig. 1. Our data from an independent study show that images from the internet can be used as a substitute for real flowers or standardized images in preference ratings. We already presented these results to an international audience (Hůla, Šámalová, & Flegr, 2018) but have not yet published them. We also asked 12 independent raters to indicate the correct distance

for each photograph. We then replaced a few problematic photographs in cases in which one of the raters judged the distance incorrectly.

All stimuli are available here: <https://figshare.com/s/e124d9ad5a57bde18ce7>

Display

The rating of the photographs was part of a broader anonymous online questionnaire that consisted of several unrelated topics. We created the questionnaire using Qualtrics software. In the part relevant to this study, participants first answered basic demographic questions. They also specified whether they had any sight conditions, such as color blindness. During the rating, there was displayed a photograph of a plant and a question, “How do you like the plant in the photograph?”. Participants then chose a number on a six-point scale where 1 meant “It is very ugly” and 6 meant “it is very beautiful”. We instructed the participants to rate only how they liked the plant itself, not the composition or quality of the photograph. Each rater was randomly assigned to one distance and rated 28 photographs (14 species, 2 growth stages) in random order.

Participants

The questionnaire was in Czech, and it was aimed at the Czech (and partly Slovak) population. However, participation was open to anybody who understood Czech. The majority of participants came from the *Labbunnies* [Pokusní králíci] community, which is grouped around the Facebook and web pages administered by Dr. Flegl’s team. Labbunnies consist of more than 20 thousand Czech and Slovak volunteers willing to take part in experiments in evolutionary psychology. We recruited the participants using a Facebook-based snowball method. Any participant could share the link to the questionnaire. Before proceeding to the questionnaire, each participant had to read information about the research and consent to take part in it. There were no restrictions on participation.

3.2. Study B – plants of the African savannas

The objective of study B was to repeat the study A with an independent set of stimuli and raters.

Ten months after the start of the data collection in the online questionnaire, we replaced the photographs used in study A by a new set of stimuli. The new set contained 20 plant species with edible fruits native to the African savannas (Table 1). There were only close-up images, so each participant rated 40 photographs (20 species, 2 growth stages). Otherwise, the setting was identical to Study A.

We used only close-up photographs because we found no distance-related differences in preference for the flowering and fruiting stages in study A. We also decided to use species generally unknown in the Czech Republic, so that the participants could not connect the images with the taste of the fruits or possible emotional personal memories related to the displayed plants. Since the authors of the habitat selection theory operate on the presumption that human landscape and habitat preferences were shaped in African savannas, we decided to use species that are native to this biome.

The stimuli are available here: <https://figshare.com/s/3c7cb1fa138b8fab6973>

Table 1

CZECH PLANTS

Scientific name	Common name	Habitus	Flower color	Flower color group	Fruit color	Fruit color group
<i>Castanea sativa</i>	sweet chestnut	tree	yellow	yellow	green	NA
<i>Citrus sinensis</i>	sweet orange	tree	white	white	orange	NA
<i>Corylus avellana</i>	common hazel	tree	yellow	yellow	green	NA
<i>Cornus mas</i>	Cornelian cherry	tree	yellow	yellow	red	red
<i>Cucurbita pepo</i>	pumpkin	herbaceous	yellow	yellow	orange	NA
<i>Fragaria vesca</i>	wild strawberry	herbaceous	white	white	red	red
<i>Pisum sativum</i>	pea	herbaceous	white	white	green	NA
<i>Prunus domestica</i>	plum	tree	pink	NA	yellow	yellow
<i>Prunus spinosa</i>	blackthorn	shrub	white	white	blue	blue/black
<i>Ribes petraeum</i>	rock currant	shrub	pink	NA	red	red
<i>Rubus fruticosus</i>	blackberry	shrub	white	white	blue	blue/black
<i>Sambucus nigra</i>	elder	shrub	white	white	blue	blue/black
<i>Solanum lycopersicum</i>	tomato	herbaceous	yellow	yellow	red	red
<i>Vaccinium myrtillus</i>	blueberry	shrub	pink	NA	blue	blue/black

AFRICAN PLANTS

Scientific name	Common name	Habitus	Flower color	Flower color group	Fruit color	Fruit color group
<i>Abelmoschus esculentus</i>	okra	herbaceous	white, yellow	white/cream	red, brown	red/brown
<i>Adansonia digitata</i>	baobab	tree	white, yellow	white/cream	green	green
<i>Annona senegalensis</i>	African custard apple	shrub	white, yellow	white/cream	yellow, brown	brown/yellow
<i>Blighia sapida</i>	ackee apple	tree	yellow	yellow	red, brown	red/brown
<i>Calodendrum capense</i>	Cape chestnut	tree	white, pink	NA	green	green
<i>Carissa macrocarpa</i>	Natal plum	shrub	white	white/cream	red	red/pink
<i>Combretum erythrophyllum</i>	river bushwillow	tree	red	red/pink	red, brown	red/brown
<i>Diospyros lycioides</i>	bushveld bluebush	shrub	yellow	yellow	red, brown	red/brown
<i>Dovyalis caffra</i>	Kei apple	tree	yellow	yellow	yellow	yellow
<i>Euclea racemosa</i>	sea guarrie	tree	white, brown	brown/yellow	blue	NA
<i>Garcinia livingstonei</i>	African mangosteen	tree	yellow, green	NA	orange	NA
<i>Grewia flava</i>	grewia	shrub	yellow	yellow	red, brown	red/brown
<i>Kigelia africana</i>	sausage tree	tree	red, brown	red/brown	white, brown	white/cream
<i>Lagenaria siceraria</i>	calabash	herbaceous	white	white/cream	green	green
<i>Momordica balsamina</i>	balsam apple	herbaceous	yellow	yellow	orange	NA
<i>Parkia biglobosa</i>	African locust bean	tree	red	red/pink	green	green
<i>Passiflora edulis</i>	passion fruit	herbaceous	violet, white	NA	violet, brown	red/brown
<i>Syzygium cordatum</i>	water berry	tree	pink	red/pink	pink, violet	red/pink
<i>Tamarindus indica</i>	tamarind	tree	pink, yellow	NA	brown	brown/yellow
<i>Vachellia tortilis</i>	umbrella thorn	tree	yellow	yellow	brown, green	brown/yellow

A list of stimuli used in study A (Czech plants) and study B (African plants)

Note: Flower/Fruit color = the color(s) of flowers/fruits of a given species.

Flower/Fruit color group = the color group to which we assigned a given species for the purpose of ANOVA.

Fig. 1: Examples of stimuli

Note: Wild strawberry (*Fragaria vesca*) used in Study A. Left = close-up, center = 0.5- 1m, right = whole plant.
Top = flowering, bottom = fruiting.

The photographs are public domain ([CC0](#)) except for bottom center: "[Fragaria vesca 003.JPG](#)" by H. Zell, licensed under [CC BY-SA 3.0](#)

3.3. Statistical Analysis

The whole dataset is available on Figshare: <https://doi.org/10.6084/m9.figshare.11956632.v1>

We excluded data from color-blind participants as well as from all participants who showed no variance in their ratings or rated less than 24 out of 28 photographs (36 out of 40 in study B) or failed on both questions testing the attention of the responders, e.g., “Please check number 2 on the scale”.

We used R 3.5.1 (R Core Team, 2019) and RStudio 1.1.463 (RStudio team, 2019) for the statistical analyses and ggplot2 (Wickgham, 2016) and ggstatsplot (Patil, 2018) packages for the graphs.

We set the alpha level for all statistical tests to 0.05.

To test the hypothesis that fruiting plants score higher than flowering plants in the rating of preference, we compared each participant’s mean rating for fruiting plants with that for flowering plants. Because each participant rated the same species in two growth stages, and we held an assumption about the preferred growth stage (fruiting), we used a one-sided paired t-test for the comparison. We ran the test separately for each distance. We used a two-sided paired test in Study B (see section 4.2. of the Results for the explanation).

We used a pwr package (Champely, 2018) for power analysis. The sample size necessary for the determination of the effect size of 0.15 with the power of 0.9 equaled to 382 in Study A (one-sided test) and to 469 in Study B (two-sided). Since our research was a part of a broader online survey, we waited until the survey termination and analyzed all obtained data. That is why our sample size exceeded the requirements of the power analysis (see Results)

We used the Holm-Bonferroni method for the correction of multiple tests.

In the exploratory part of the study, we used two-way ANOVAs to find out whether there were any sex differences in the rating of fruits and flowers. We also used Welch’s ANOVA and a subsequent Games-Howell post hoc test to explore the possible influence of differently colored fruits and flowers on the preference ratings.

4. Results

4.1. Study A – Czech plants

Nine hundred and seventeen participants (mean age = 35.02 ± 12.80 ; F = 591, M = 326) rated the close-up photographs, 921 participants (mean age = 34.31 ± 12.52 ; F = 630, M = 291) rated the photographs taken from 0.5 to 1 meter and 954 participants (mean age = 34.27 ± 12.58 ; F = 625, M = 329) rated the photographs of the whole plant.

Because our hypothesis assumed a preference for fruits, we used one-sided paired t-tests. We compared each participant’s mean preference rating for fruiting plants with that for flowering plants. We tested the hypothesis separately for each distance.

In the close-ups, the participants liked the photographs of fruits more than the photographs of flowers (Fig. 2). However, the effect size was very small ($t = 2.07$, $df = 916$, $p\text{-value} = 0.019$, mean

difference = 0.042 points, 95% CI [0.086, ∞], Cohen's $d = 0.068$). We did not find higher ratings for fruits at the other two distances (one meter: mean difference = -0.033 points, 95% CI [-0.060, ∞], $t = -2.00$, $df = 920$, $p\text{-value} = 0.98$, Cohen's $d = 0.066$; several meters: mean difference = 0.019 points, 95% CI [-0.0022, ∞], $t = 1.47$, $df = 953$, $p\text{-value} = 0.071$, Cohen's $d = 0.047$). After correcting for multiple tests, no statistically significant differences remained.

The distribution of species by the preference for their flowering or fruiting stage (only in the close-up photographs) is shown in Fig. 3.

Fig. 2: Differences between the mean preference rating of fruiting and flowering Czech plants

Note: X-axis: distance; Y-axis: mean rating (in points) of all plants in fruiting (orange) and flowering (blue) growth stages. The whiskers represent 1.5 IQR.

Fig. 3: Scatterplot of the mean preference rating of the close-up photographs of Czech plants.

Note: X-axis: the mean rating of the flowering stage; Y-axis: the mean rating of the fruiting stage. The red line represents values where the preference rating for both growth stages is the same.

Study A – exploratory part

We used a two-way ANOVA to determine whether women and men differed in their ratings of flowers and fruits. Each rater's mean difference between the preference rating of flowering and fruiting plants represented the dependent variable. The rater's gender (man, woman) and the photographic distance displayed to the rater (close-up, 0.5- 1m, whole plant) represented the factors.

Overall, the ANOVA model revealed a significant interaction between distance and gender, but no effect of gender per se. The subsequent summary model ($F_{5, 2786} = 3.52$, $p\text{-value} < 0.0036$, $R^2 = 0.0062$) showed that the only difference between men and women occurred at the "whole-plant" distance, where men preferred fruits slightly more than women. However, the difference was negligible (mean difference women = 0.01 points, mean difference men = 0.05 points. The maximal possible difference was 5 points).

To study the possible influence of color on the preference ratings of flowers and fruits in our sample, we used one-way ANOVA, where the mean rating for both fruiting and flowering plant species (from all respondents) served as the dependent variable, and the fruit and flower colors were the factors. This means we analyzed both fruiting and flowering plants together (Analyzed colors: blue/black, red, white, and yellow. We excluded green, orange, and pink fruits and flowers from the analysis because of their low number. See Table 1). We performed the testing separately for each distance. Due to the low number of observations per group (4-6) and their unequal variances at all distances, we used Welch's ANOVAs. We did not find any statistically significant differences among colors at any of the distances. However, yellow color had the lowest mean rating at all distances.

4.2. Study B – plants of the African savannas

As we explained above, the participants rated only the close-up photographs of plants in this study. We obtained data from 743 participants (mean age = 34.3 ± 13.36 , $F = 457$, $M = 286$).

Because the difference in the rating between the flowering and fruiting plants was clearly in the opposite direction than we hypothesized, it would not make any sense to use a one-sided paired t-test. We decided to use a two-sided paired t-test instead. It confirmed that flowering plants were liked more than fruiting plants and that the effect size was very large ($t = -33.94$, $df = 743$, $p\text{-value} < 0.0001$, mean difference = -0.70 points, Cohen's $d = 1.24$). See Fig. 4.

The distribution of species by the preference for their flowering or fruiting stage is shown in Fig. 5

Fig. 4: Differences between the mean preference rating of fruiting and flowering African plants.

Note: X-axis: growth stage (fruiting, flowering); Y-axis: mean rating (in points) of all plants. The whiskers represent 1.5 IQR.

Fig. 5: Scatterplot of the mean preference rating of the close-up photographs of African plants.

Note: X-axis: the mean rating of the flowering stage; Y-axis: the mean rating of the fruiting stage. The red line represents values where the preference rating for both growth stages is the same.

Study B – exploratory part

To explore possible differences between the preference rating of women and men, we used an independent samples two-sided t-test, where each rater's mean difference between the rating of fruiting and flowering plants represented the dependent variable and the rater's gender was the factor. We found that both women and men preferred flowering plants, but this difference was more pronounced in women ($t = -4.58$, $df = 741$, $p < 0.0001$, Cohen's $d = 0.35$, mean difference women = -0.77 points, mean difference men = -0.58 points).

To test the effect of colors on preference, we used a one-way Welch's ANOVA. The reason for this decision was that the number of observations per group was not balanced, and the groups had substantially different variances. We used the Games-Howell post hoc test to compare the differences between groups. The analyzed flowers and fruits rarely had a basic color, so we identified several color groups: green, reddish-brown, brown/yellow, red/pink, white/cream, yellow (we excluded seven photographs from the analysis because of their unique color or color combination). The model showed that there were statistically significant differences between colors ($F_{5, 10.85} = 43.85$, $p\text{-value} < 0.0001$, $\omega^2 = 0.48$). When corrected for multiple comparisons by Holm's method, the Games-Howell test found a significant difference only between green and yellow colors, where yellow was preferred. However, there was a clear trend showing that green and brownish yellow were among the least preferred colors and pink and pure red among the most preferred (Fig. 6).

Fig. 6: Preference scores of African plants by color

Note: One-way Welch's ANOVA of mean preference ratings of African plants with different colors of flower/fruit. **X-axis:** color groups (G = green, Br/Y = brownish yellow, R/Br = brownish red, Y = bright yellow, W = white or cream, R/P = red or pink). **Y-axis:** Mean preference rating of all plants (in points). The colored dots represent each plant species (flowering and fruiting stages of the same species are represented as separate dots).

5. Discussion

Contrary to the assumptions we derived from the simple variant of the habitat selection theory proposed by Heerwagen and Orians, respondents rated fruits as almost equally (study A) or less attractive (study B) than flowers.

In study A in the close-up photographs, the preference for fruits was statistically significant. However, the effect size was negligible (Cohen's $d = 0.068$), and the mean difference in preference was only 0.042 points (the maximal possible difference was 5 points). Moreover, the difference turned non-significant after correcting for multiple tests.

The lack of any observed difference between flowers and fruits is not surprising for the photographs of the whole plants. In some cases, it might be problematic to distinguish flowers from fruits from such a distance. On the other hand, at the other two distances (close-ups and 0.5 – 1m), flowers and fruits were easily recognizable. Furthermore, the stimuli represented edible fruits commonly grown in the Czech Republic, and we can assume that the majority of participants knew that the displayed fruits were safe to eat and tasty. Also, many of the species grown for fruits have rather small and inconspicuous flowers that are not among the most attractive (for the results of preference ratings of diverse Czech flowers, see Hůla & Flegr, 2016). Nevertheless, we observed practically no preference for fruits.

In Study B (African plants), there was a strong preference for flowers. The mean difference was equal to 0.70 points, and the effect size was very large (Cohen's $d = 1.24$). Although all species had edible fruits, they were probably unknown to most of the Czech raters. Also, a study conducted on the geographically and culturally very close Slovak population found that children could not distinguish the toxicity of unknown fruits and that this inability did not improve with age (Prokop and Fančovičová, 2014). Such uncertainty about the edibility of African fruits could have accounted for their lower rating.

Another factor that could possibly influence the rating of the stimuli was the color of the flowers and fruits. Even though we tried to assure an equal distribution of the same colors between fruits and flowers, we were severely limited by the required edibility of the fruits. This resulted in a relatively higher distribution of blue and red among fruits and yellow and white among flowers in our set of stimuli. In African plants, the colors were more evenly distributed, but there were more brownish colors among African fruits (See table 1). Our previous research on flowers found that blue was the most and yellow the least preferred flower color (Hůla & Flegr, 2016). Research conducted on Slovak high school students revealed that red fruits were considered edible and attracted the most attention of the raters (Prokop & Fančovičová, 2012). Also, blue and red have been rated as the most and brown and yellow as the least appealing colors in general (Camgöz, Yener, & Güvenç, 2002; Palmer & Schloss, 2010; but see Taylor, Clifford, & Franklin, 2013). We can thus assume that if the color of a stimulus influenced its rating, it should have been in favor of fruits in the case of Czech plants because they had a higher proportion of generally preferred colors. However, when we performed ANOVA to distinguish whether there were any differences in the preferences for differently colored stimuli, we found no significant difference between color groups in the Czech sample.

In the case of African plants, there was a difference between green stimuli (all of which were fruits) and yellow stimuli (predominantly flowers); the green stimuli had the lowest mean rating (see fig. 6). The difference between green and yellow stimuli is also interesting because, as we already discussed in various parts of this paper, yellow is considered as one of the least favorite colors in general and also as one of the least preferred flower colors. This might mean that the observed difference is not due to the color of the stimuli, but due to their type (flower vs. fruit). Moreover, previous research found that in the case of flowers, color played only a minor role in the overall preference rating; shape properties were the most important (Hůla & Flegr, 2016).

In general, people prefer shapes with several axes of symmetry (Tinio & Leder, 2009), round contours (Bar & Neta 2006, 2007, Leder, Timio, & Bar, 2011; Silvia & Barona, 2009, Westerman et al., 2012), medium levels of complexity (Akalın et al., 2008; Enquist & Johnstone, 1997; Reber, Schwarz, & Winkielman, 2004) and high levels of prototypicality, which is a measure of how representative an object is of a category (Reber, Schwarz, & Winkielman, 2004, Whitfield & Slatter, 1979, Winkielman et al., 2006). It is difficult to objectively compare the levels of prototypicality and complexity of flowers and fruits. However, in both our samples, the fruits were usually rounder and had more axes of symmetry than the flowers.

We can summarize that if there was any influence of shape, color, or edibility on the preference for fruits or flowers, it was probably in favor of fruits in Study A (Czech plants). Still, the fruits and flowers were rated similarly.

In Study B (African plants), the unfamiliarity of the raters with the fruits, and also the higher number of fruits with a less liked green color, might have lowered their rating. However, the flowers were equally unknown to the raters, and they also featured some of the generally least attractive colors (yellow). Moreover, the preference for flowers was so overwhelming that it could not have been caused only by the differences in colors or knowledge about the edibility of the fruits. For example, when we removed the photographs with the least preferred and predominantly fruit colors – green and brownish yellow (7 fruits and 1 flower) – and then compared the mean preference ratings for all flowers and fruits again, the difference was still 0.51 points (0.70 points before the removal). Furthermore, the habitat selection theory assumes that flowers and fruits elicit aesthetic responses because they represent signals of resource availability. From this point of view, once flowers and fruits are distinguished from other types of objects, their color or shape should not be that important.

On the other hand, the results are not so unexpected when we look at the importance of flowers in art and culture. When people want to please others with something beautiful, they usually choose a flower, not a fruit. Decorations depict flowers rather than fruits, and ornamental gardens are also associated predominantly with flowers. Most people would probably describe attractive fruits as tasty or delicious and attractive flowers as beautiful. The aesthetic responses to flowers thus seem to be related to characteristics other than food availability, especially in a direct way. Flowers should serve as predictors of the availability of food in the future, but the same also applies to fruits. It is questionable whether a group of gatherers should explore and remain in an environment full of flowers that will turn into edible fruits or nuts in a month or even longer, or whether they should instead choose a place with ripening fruits that promise a source of nutrition at the given moment and also in subsequent weeks.

One may argue that flowers helped our ancestors to identify not only the presence of food, but also other useful resources such as medicine. However, the same also applies to fruits or at least to the conspicuous ones we used as stimuli. Nonetheless, an important source of energy for African hunters-gatherers and African primates are underground tubers. Flowers of these plants might be beneficial in identifying their exact location. The problem is that geophytes usually bloom only once a year and for a short period. Therefore, it would be useful to operate with flowers as location cues only over very long time scales simply because they are not present for most of the year. Another factor that might play a significant role in the aesthetic appreciation of flowers is seasonal change; flowers represent proof that the dry period (or winter) is over.

The fact that we found a strong preference for flowers in the sample from African savannas but not in the Czech sample is worthy of attention. It might indicate that the preference for flowers is more pronounced for plants that relate more to the supposed ancestral environment or for plants unknown to the raters. However, it remains an open question for further study.

Even though our results do not support the hypothesis we derived from the habitat selection theory, this certainly does not mean that a connection between flowers as signals of resources and the aesthetic responses towards them does not exist. Such a connection most likely plays an important role in the preference for both flowers and fruits. The preference for fruits is simple and straightforward because they are considered as food. On the other hand, the connection between flowers and resources is more intricate. What our data show is that there probably exist other factors that further enhanced the attractiveness of flowers over the course of human evolution.

6. Limitations and future directions

We used photographs in this study because it was impossible to display real plants simultaneously in the flowering and fruiting stage. On the other hand, the use of photographs is very common in this type of research, and our previous results showed no substantial differences between the rating of real flowers and that of their photographs. However, we might get more in-depth insight by designing an experiment with various real flowering and fruiting plant species in natural settings. We could also abandon the requirement of fruit edibility to be able to prepare a set of stimuli with fully balanced colors and shape properties of flowers and fruits.

It would undoubtedly be beneficial to repeat the study with different stimuli to make sure that the results were not mere artifacts of some unknown methodical error.

Future research should focus on other factors that might account for human attraction towards flowers. We should explore whether it is only a by-product of generally preferred shapes and colors or whether there are some characteristics (or their combinations) unique to flowers that make them beautiful to human eyes.

7. Conclusion

The habitat selection theory of Heerwagen and Orians offers an attractive explanation for the origin of human aesthetic responses to flowers. Our data imply that the relation of flowers with resource availability is not the only factor that explains our preference for them, although it probably plays an important role. The question of why flowers provoke strong aesthetic responses in humans remains

partly unexplored. The habitat selection theory proposes a solid basis for further investigations of other factors that could extend this theoretical framework. The issue is crucial for anyone who studies people-plant interactions and deserves renewed attention from researchers working in related fields.

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