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Evolutionary Aspects of the Human Aesthetic Responses to Flowers
Evoluční aspekty estetického vnímání květin člověkem

Doctoral thesis

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Prohlášení:

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V Praze, 26. 10. 2023 ……………………………………………

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Abstrakt

Estetické vnímání květů člověkem bylo dlouho opomíjeným tématem ve výzkumu interakcí člověka a rostlin. Teorie, které se zabývaly estetickým vnímáním rostlin a vlivem rostlin na well-being člověka, většinou používaly obecné pojmy jako vegetace, zeleň nebo pokojové rostliny, a ignorovaly tak obrovskou rozmanitost tvarů a barev jednotlivých rostlin. Jsme přesvědčeni, že specifické rysy různých rostlinných druhů hrají klíčovou roli při vzbuzování estetických reakcí člověka, a možná také ovlivňují sílu efektů na lidský well-being. Rozhodli jsme se, že se pokusíme identifikovat některé rysy květin, které by mohly ovlivňovat estetické reakce člověka, a empiricky otestujeme jejich relevanci. Výběr rysů květin vycházel z evolučních teoretických rámců, které se zabývají původem estetických reakcí člověka na květiny (Teorie výběru habitatu), různé tvary (Teorie zpracování informací) a barvy (Teorie ekologické valence).

V první studii jsme nechali více než 2000 účastníků hodnotit krásu fotografií 52 českých divokých květin. Naše výsledky ukázaly na silnou shodu mezi hodnotiteli. Typičnost květin měla pozitivní efekt na hodnocení jejich krásy. Také silně negativně korelovala s komplexitou květin. Důležitá byla i květní symetrie. Bilaterálně symetrické květiny byly považovány za velmi komplexní a velmi málo typické a měly nízké hodnocení krásy. U radiálně symetrických květů jsme pozorovali opak. Při hodnocení krásy květin měla barva menší roli než tvar. Modrá byla hodnocena nejlépe a žlutá nejhůře.

Ve druhé studii jsme se zaměřili na předpoklady vlivné, ale dosud empiricky netestované Teorie výběru habitatu. Ta tvrdí, že v průběhu lidské historie hrály květiny úlohu signálů odkazujících na úrodnost prostředí a příslib budoucí dostupnosti potravy (plodů). Vztah mezi potravou a květinami je prý základem lidských estetických reakcí na květiny. Zůstali jsme věrni logice této teorie, která předpokládá, že čím silnější je daný signál, tím silnější bude i reakce na něj. Proto jsme srovnali květiny se silnějším signálem dostupnosti potravy – s plody. Ve třech nezávislých studiích s více než 2500 účastníky jsme nechali lidi hodnotit kvetoucí a plodící stádia českých a afrických jedlých rostlin. Naše výsledky neodhalily žádné rozdíly v hodnocení květů a plodů u českých rostlin, ale ukázaly na výrazně silnější estetickou reakci na květy afrických rostlin. Na základě našich výsledků usuzujeme, že teorie výběru habitatu nemá oporu v datech.

Ve třetí studii jsme zkoumali mezikulturní podobnosti a rozdíly v estetických reakcích na květiny. Srovnali jsme 150 osob z Česka a Keni, které řadily vytištěné fotografie 40 květin podle toho, jak se jim líbily, od nejlepší po nejhorší. Následně jsme korelovali průměrné umístění každé květiny mezi českým a keňským souborem. Objevili jsme velmi silnou pozitivní korelaci mezi Čechy a Keňany a jen drobné rozdíly ve struktuře jejich řazení. Naše data podporují myšlenku, že estetické reakce na květiny mohou být vlastní člověku jakožto druhu. Naše studie byla však příliš omezená na to, abychom mohli její výsledky generalizovat.

Poslední studie měla za cíl replikovat výsledky naší první studie a prozkoumat, zda estetické reakce na květiny zůstávají neměnné v čase a napříč různými stimuly a hodnotiteli. Také jsme chtěli srovnat validitu fotografických stimulů, upravených obrázků z internetu a reálných květin. Během tří nezávislých měření s více než třemi stovkami účastníků jsme zjistili, že hodnocení krásy květin velmi silně pozitivně korelují napříč typy stimulů, a fotografie a upravené obrázky z internetu tedy mohou sloužit jako náhrada za reálné květiny. Ostatní výsledky byly velmi podobné těm z naší první studie. Taktéž jsme úspěšně uplatnili novou metodu pro hodnocení efektu barvy na celkové hodnocení při

současné kontrole na tvar – hodnocení pod monochromatickým (červeným) světlem a následně pod polychromatickým (žlutým) světlem.

Doufáme, že výsledky našich studií budou nápomocné pro pracovníky zapojené do globálního trhu s květinami, odborníky na ochranu životního prostředí a na vzdělání, a pro výzkumníky zabývající se lidským vnímáním.

Abstract

Human aesthetic responses to plants and flowers have long been an unexplored topic in people-plant interactions research. Theories focusing on aesthetic responses to plants and studies testing the effects of plants on human well-being have usually used general terms such as vegetation, greenery, or houseplants, thus ignoring the immense diversity of individual plant shapes and colors. We argue that specific features of different plant species play a key role in eliciting human aesthetic responses and possibly also influence the strength of their effects on human well-being. We decided to identify some flower features that might influence the aesthetic response and to test their relevance empirically. The choice of flower features was derived from evolutionary theoretical frameworks that discuss the origin of human aesthetic responses to flowers (Habitat selection theory), shapes (Information processing theory), and colors (Ecological valence theory).

In the first study, we asked more than 2,000 participants to rate the beauty of 52 Czech wildflowers in photographs. Our results showed a strong agreement between raters. The prototypicality of flowers had a positive effect on the rating of their beauty. At the same time, the ratings were strongly negatively correlated with flower complexity. Floral symmetry was also important. Bilaterally symmetrical flowers were considered very complex and not prototypical at all and received low ratings for beauty. We saw the opposite in radially symmetrical flowers. Colors played a less important role than shape in the rating of flower beauty, with blue being the best and yellow the worst rated.

In the second study, we focused on the premises of the influential, yet never empirically tested theory of Habitat selection. This theory postulates that in human history, flowers played a role as signals of an environment rich in resources and a promise of the future availability of food (fruits). Thus, the link between food and flowers is the source of human aesthetic responses to flowers. We followed the logic of the theory that claims that the stronger a signal is, the stronger the reaction to it. We thus compared flowers with a stronger signal of food – fruits. In three independent studies with more than 2,500 participants, we asked people to rate the flowering and fruiting stages of Czech and African edible plants. Our results showed that there were no differences in the aesthetic responses to flowers and fruits in the Czech sample but significantly stronger responses to flowers in the African sample. We conclude that the premises of the habitat selection theory were not supported by our data.

Our third study looked for intercultural similarities and differences in the aesthetic responses to flowers. We compared 150 Czech and Kenyan individuals who ranked printed photographs of 40 flowers from the most to the least liked. We subsequently correlated the mean ranks of each flower stimulus between the Czech and Kenyan samples. We found a very high positive correlation between Czech and Kenyans and only minor differences in the pattern of their rankings. Our data support the idea that aesthetic responses to flowers might be shared by humans as a species. However, our study was too limited to allow us to draw any generalizations.

The last study aimed to replicate the results of our first study and to explore whether aesthetic responses to flowers remain stable over time as well as across different stimuli and different raters. We also wanted to assess the validity of photographs as stimuli, by comparing the ratings of real flowers, their standardized photographs, and edited images from the internet. We showed in three consecutive experiments with 300 participants that the ratings of flower beauty highly correlate across different stimuli types, and therefore photographs and edited internet images can be used as substitutes for real flowers. Otherwise, the results were in line with our first study. We also successfully employed a novel method for the assessment of the effect of color on the overall ratings

when controlling for shape – a consecutive rating under monochromatic (red) and polychromatic (yellow) light.

The outcomes of our studies will hopefully be helpful for workers in the flower business, specialists involved in nature conservation and education, and researchers interested in human cognition.

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List of publications:

This work consists of a summary of the topic of evolutionary aspects of the human aesthetic responses to flowers and four related original research papers. Two of the papers have already been published, one is in press, and one is ready to be submitted to a journal. The listed publications are in the appendices, which are integral parts of this work.

Hůla, M., & Flegr, J. (2016). What flowers do we like? The influence of shape and color on the rating of flower beauty. *PeerJ*, 4, e2106. – appendix 1

Hůla, M., & Flegr, J. (2021). Habitat selection and human aesthetic responses to flowers. *Evolutionary Human Sciences, 3*, E5. doi:10.1017/ehs.2020.66 – appendix 2

Hůla, M., & Šámalová, P. (in press). Does flower preference differ across cultures? A study of Czech and Kenyan populations. *Psychology of Aesthetics, Creativity, and the Arts*. – appendix 3

Submitted, but not published:

Hůla, M., Šámalová, P., & Flegr, J. Symmetry, prototypicality, complexity, color, and human aesthetic response to real flowers and their photographs. – appendix 4

CONTENTS:

1. Introduction

I have dedicated my entire professional life to the study of people-plant interactions and, more specifically, to the human aesthetical attraction to flowers. The main body of my dissertation focuses on four research papers that explore some of the questions related to this topic. This summary aims to put the research papers into a broader context but also to describe another integral part of the scientific process – the train of thought leading from vague original ideas to the testing of specific research questions. I will discuss why I decided to study this topic and the reasons I find it important, what were my original intentions, how they developed in light of existing (and non-existing) research, and what new ideas and questions emerged over time and are still waiting to be answered.

1.1. The fly on the wall

The good manners of scientific etiquette require that researchers present themselves as unbiased observers of objective reality, i.e., tempered, serious, distant, and depersonalized entities not unlike machines. The truth, however, cannot be further from this description. Researchers are and must be extremely motivated to spend their entire lives studying mostly niche topics, often under harsh conditions, that only a handful of people in the world can entirely understand.

There exist external motivators for anything people are doing – namely money and social status. However, anyone working in science, especially in basic research, would not think of money as the reason for doing science – not many people have gotten rich by doing science.

Social status might apply in some cases, especially when researchers disguise themselves in descriptions too vague to question, such as being a scientist, or too specific to understand, like being an evolutionary aesthetician. Unfortunately, this strategy does not always work, and the more that researchers describe what they do, the more the initial admiration and interest of listeners fade away, being replaced by misunderstanding, ironic remarks, and questions about the usefulness of the research topic. Sometimes, similar questions can be heard from fellow researchers as well. These probably originate from some mechanisms to cope with long-lasting doubts about their own research – channeling it to someone else, or delusionally convincing themselves that only their research is superior and worthy of any credit. It is thus evident that there are less complicated ways to improve one's social status than doing science.

Since external motivators do not apply to researchers, internal ones must play a crucial role. Curiosity, fascination, and a passionate relationship with the topic are among the most powerful. Researchers often choose the focus of their professional careers based on their personal and even intimate inner tuning to their chosen topic. Therefore, they have an emotional bond with what they do. They might love it or hate it, but they are not indifferent. This bond drives them to explore the topic in depth, but also makes them sensitive to external critique and internal doubts.

Researchers are thus forced to become a sort of cosplayer – passionate, enthusiastic, and fragile people pretending to be coldhearted, purely rational, and self-confident professionals. When they are asked why they are doing their research, they cannot say it is because they find it fascinating, but instead have to come up with a socially acceptable explanation, such as how it will help humanity by saving lives, making people happier or at least earn them money. Conferences are important for researchers in a similar way as conventions for cosplayers. They are an opportunity for like-minded people to gather, play their roles during the official program, and then, in the evening in a pub, share with relief their true selves with others.

For me, wildflowers have always been a source of endless awe and fascination. I might spend some time in introspection and speculate about the reasons for my strong bond with flowers. Maybe they represented an escape to a calm and beautiful world of wonders for a little and introverted boy going through turbulent times, maybe it was something else. The important thing is that, even as an adult, spending the whole day crawling among the cliffs of the Czech Karst just to see a blooming Austrian dragonhead brings me pure and unconditional joy.

In the second year of my studies of biology, we went to southern Moravia for a zoological field trip. There were opportunities to sit informally with our professors in wine cellars and listen to their stories and bits of knowledge they were willing to share. I remember one renowned herpetologist and ethologist telling me that the only thing that matters in science is to choose a topic one is passionate about. When we do something we like, grants, publications, money, and even the interest of others will come eventually, not the other way around. I took this advice to heart. My research will probably not save many lives, but I feel a deep sense of satisfaction in what I am doing, and that is the reason I chose it.

2. Phytophilia

The cornerstone of this work is a phenomenon called phytophilia (Eibl-Eibesfeldt, 1989). This postulates that humans as a species spent almost their entire history in deep connection with the plant world, using it as food, for medicinal purposes, as material for building tools and shelters, and for understanding and predicting seasonal changes. Some authors claim that humans are so attuned to being surrounded by plants that their absence in modern man-made environments is distressing. People try to compensate for this absence by growing house plants and by applying plant motives to fabrics, furniture, jewelry, and other objects of everyday use (Appleton, 1996; Eibl-Eibesfeldt, 1989).

2.1. Plants and human well-being

Research on phytophilia and people-plant interactions mostly focuses on reporting the positive effects of plants on various aspects of human well-being, such as reducing stress (Cackowski & Nasar, 2003; Grahn & Stigsdotter, 2010) or improving concentration, cognitive functioning (Herzog et al., 1997; Lohr et al., 1996; Raanaas et al., 2011; Tennessen & Cimprich, 1995) and mood (Haviland-Jones et al., 2005; Larsen et al., 1998; Shibata & Suzuki, 2002). The beneficial aspects of plants have been recently recognized in so-called horticultural therapy (Cipriani et al., 2017; Kamioka et al., 2014) and forest bathing (Antonelli et al., 2022; Kondo et al., 2018), the latter even being accepted as an official form of clinical therapy for patients, recommended and paid for by Japanese public health insurance institutions (Schuh & Immich, 2022). Research on forest bathing is growing dynamically, especially with the incorporation of modern technologies such as virtual reality, for example by testing whether virtual forests affect people similarly as do real ones (Björling et al., 2022; Mattila et al., 2020; Reese et al., 2022) . The author of this work is also involved in this line of research (Hejtmánek et al., 2022).

There are three principal theories, all based on evolutionary grounds, that try to explain the positive effects of plants on human well-being. The Biophilia Hypothesis (Kellert, 1995; Wilson, 1984) has the same postulates as the works on phytophilia, but it is not limited to plants but to all living organisms surrounding us. The authors argue that the connection with other organisms is something that makes us human. If we destroy natural habitats and seclude ourselves in man-made environments where other organisms are replaced by technologies, it will negatively affect our well-being, making us similar to animals kept in captivity. The presence of other organisms in our surroundings should thus be considered a baseline. Therefore, being in touch with plants does not improve our well-being, but not having them around certainly worsens it.

Another theory that tries to explain the positive effect of plants on humans is called the Attention Restoration Theory (R. Kaplan & Kaplan, 1995; S. Kaplan, 1995). Its main premise is linked to the necessity of humans to rapidly and reliably sort the information coming from the environment to be able to correctly react to potential threats. When people engage in long, monotonous, or repetitive tasks (which are plentiful in the modern world) that require directed attention, they encounter mental fatigue, a state in which their attention capacity is depleted, resulting in a bad mood, inability to focus, and a risk of making mistakes. Such a state is unpleasant for modern people, but it might have been life-threatening for our ancestors. ART argues that plants can easily restore depleted sources of human attention by providing enough inputs to elicit soft fascination. This triggers our indirect attention, but in a subtle and non-threatening way, allowing our mind to safely wander and restore its capacities.

The last theory formulated by Roger Ulrich (R. Ulrich, 1983; R. S. Ulrich et al., 1991) is called the Stress Recovery Theory. Ulrich claims that stress, as a complex reaction to a potentially threatening situation, is very useful in the short-term, but when its duration is too long (such as chronic stress in modern societies), it prevents us from functioning normally and focusing on other important tasks. A way to deal with stress is to spend time in a safe and positively seen environment. Vegetation has such properties because it can provide both shelter and food.

2.2. Human well-being and aesthetic responses to plants

The abovementioned theories are not very specific about the properties that make plants ideal for recovery or stress reduction. The Kaplans indeed provided a complex set of properties for restorative landscapes, but they never went to the level of specific plants, instead they mostly used the term vegetation. Wilson also writes about plants in general, and the same applies to Eibl-Eibesfledt and the vast majority of empirical studies. Such an approach makes it seem as if there are no differences between human attitudes to different plants. I have always found this premise absurd.

For example, I could not imagine a study focusing on the impact of the presence of animals on human well-being without specifying which animals were used as stimuli. Similarly, stating that the presence of animals helps people reduce stress might work, for example, for hamsters, but I doubt it would also apply to rats or bats. It seems evident to me that a walk in a young spruce monoculture would be a different experience than a walk in an old-growth oak forest and that having a flower bouquet on one’s work desk would elicit a different feeling than a potted cactus.

It is true that in recent years, some studies have at least distinguished between different types of forests when studying their effect (Chiang et al., 2017; Guan et al., 2017), but otherwise, distinguishing individual plant species has been largely neglected. I think this is a clear example of the plant awareness disparity, formerly known as plant blindness (Achurra, 2022; Prokop & Fančovičová, 2023; Schussler & Olzak, 2008) - a general lack of knowledge and interest in plants and an inability to distinguish and remember individual species. It is mostly discussed as a potential threat to the conservation of natural biotopes, but it also affects other areas.

The empirical studies also completely overlook the possibility that aesthetic responses to different plants or biotopes might modulate the strength of their effect on the studied variables (well-being, stress reduction, mood, etc.). My student explored this issue in a study targeting different forest types and their effect on mood (Arnot, 2022). He asked participants to complete the Profile of Mood States questionnaire before and after a 5 minute-long exposure to photographs of different forest types and an urban setting. The exposure to forests, but not to the urban setting, had a positive effect on the mood of participants. There were also differences between the types of forests and some subscales of the POMS questionnaire, old-growth and broadleaf forests being more effective than a secondary coniferous forest. Moreover, there was a positive correlation (r = 0.37) between the strength of the aesthetic response to stimuli and the increase in mood.

These results confirm my initial concern that aesthetic responses to plants should be taken into account. When people buy houseplants, pick flowers, or wear a dress with a floral pattern, they do it primarily because they find it aesthetically pleasing. Of course, it can subsequently elevate their mood or reduce stress, but the aesthetical experience (Redies, 2015) was the main motivation. It is surprising how the aesthetic aspect of plants, and especially flowers, has been omitted in the research of people-plant interactions.

2.3. Flowers as model organisms for the research of aesthetic responses to plants

I decided to center my work around the aesthetic aspects of flowers, and I wanted to explore the topic in greater depth. I acknowledged that from the immense spectrum of plant forms, flowers traditionally have a high aesthetical value to humans and are therefore the best starting point for inquiries about the aesthetic responses to plants. Many questions rose before me. Are aesthetic responses to flowers in general universal to humans or are they limited only to some cultures and time periods? Do people agree on which flowers are considered beautiful and which are not? Are the aesthetic responses to particular flowers more influenced by individual taste, cultural background, or some universal rules? Why do humans like flowers in the first place? Why did aesthetic responses to flowers evolve? Are flowers in some way unique, or do they simply possess a combination of properties that would elicit aesthetic responses in any object? I was convinced that if we could find answers to these questions, the whole field of people-plant interactions research might benefit from them.

3. Origins of human aesthetic responses to flowers

To orient myself in the problem, I first wanted to look into the literature to find theories that would explain the origins of human aesthetic responses to flowers. I planned to subsequently find empirical studies focusing on preferred and non-preferred flowers to see if the theories have support in the data. After thoroughly searching through the published literature, I was perplexed to find that there were no evolutionarily-based theories concerning flowers, except for one – The Habitat Selection Theory by Judith Heerwagen and Gordon Orians (Heerwagen & Orians, 1995; Orians & Heerwagen, 1992). I therefore decided to expand the scope of my search and include theories focusing on the origins of general human aesthetic responses to various objects, shapes, and colors. Then, I tried to apply these theories to flowers.

3.1. Evolutionary Aesthetics

All of the theories I am going to present are to some extent rooted in the framework of evolutionary aesthetics (Voland & Grammer, 2003), which postulates that humans had to adapt in order to quickly and reliably react to potentially threatening or beneficial situations they encountered throughout their evolutionary history. Avoiding predators or dangerous organisms, pathogens, enemies, or unfavorable environmental conditions on one side, and approaching possible mates, shelter, or sources of food and water on the other side, would increase their biological fitness and, therefore, be adaptive. The proponents of evolutionary aesthetics claim that instead of evaluating each situation or encounter individually, more rapid emotional reactions to such situations turned out to be more efficient. These reactions were triggered by perceived beauty or ugliness. In other words, humans evolved to consider beneficial organisms or environments beautiful, resulting in positive emotional reactions and approach behavior. The same principle applies to threats. What is dangerous is also ugly, provoking negative emotional reactions and avoidance. These reactions, shaped over the course of hundreds of thousands of years of human history as hunter-gatherers, have persisted until the present.

3.2. Habitat Selection Theory

This theory explains mainly the origins of landscape preferences, but it also explicitly (yet briefly) mentions flowers. The authors consider flowers important signals of resource-rich environments and the presence of food. They stress the role of flowers as indicators of favorable seasonal change and a promise of future availability of edible fruits. As far as the flowers' properties are concerned, the authors describe their conspicuous colors as their main quality, because they allowed humans to evaluate a favorable landscape from a distance. In their latter work (Heerwagen & Orians, 1995), the authors also link flowers to the presence of honey, the only natural source of pure sugar, which was highly esteemed. They suggest that bilaterally symmetrical flowers should be preferred to radially symmetrical ones because they contain larger amounts of nectar, thus they would be a better source of honey. The authors also mention flowers as possible direct sources of food because in general, they tend to contain nutrients rich in nitrogen and less toxic compounds than other plant organs.

3.3. Information Processing Theory

Another branch of research points out the importance of the need for orientation in the environment as well as efficacy (maximizing information transmission) and efficiency (information processing at low metabolic costs) in information processing (Renoult, 2016; Renoult & Mendelson, 2019). Without this ability, humans would be overwhelmed by stimuli incoming from their surroundings. As a result, they would easily overlook a potential threat or miss potentially beneficial situations.

Some properties of objects and organisms seem to increase the fluency of information processing. There is also a considerable body of research that shows that people respond to such properties aesthetically (see for example (Reber et al., 2004) for review). Such properties include:

Symmetry – symmetrical objects tend to be preferred to asymmetrical ones (Enquist & Arak, 1994; Enquist & Johnstone, 1997; Jacobsen et al., 2006), and the number of axes of symmetry tends to increase the fluency of information processing (Tinio & Leder, 2009). On the other hand, humans show strong aesthetic responses to bilateral symmetry, possibly as a by-product of mate recognition (Evans et al., 2000).

Complexity – often described by the number of elements of a certain object, and their distribution also influences the aesthetic responses (Jacobsen et al., 2006; Reber et al., 2004). Studies typically show an inverse U shape of the response: Too simple objects are described as too boring and too complex objects as difficult to understand (Akalin et al., 2009; Hekkert & Wieringen, 1990)

Prototypicality –the closeness of a given object to the idea of a typical representative of its category. Prototypical objects are usually preferred to atypical ones (Hekkert et al., 2003; Hekkert & Wieringen, 1990; Winkielman et al., 2006).

Familiarity – can be defined by the number and frequency of encounters with a given object. Familiar objects tend to be preferred to unfamiliar (Pedersen, 1978; Song et al., 2021; Verhaeghen, 2018). This phenomenon is also known as the mere exposure effect (Harrison, 1977; Montoya et al., 2017; Zajonc, 1968).

3.4. Angularity

Another shape property that does not directly influence information processing, but is widely studied, is angularity. Objects with round contours are typically preferred to objects with sharp contours. This difference is explained by the link of sharp objects to danger (thorns, claws, horns, pointy rocks) and the tendency to protect oneself from wounds (Bar & Neta, 2006, 2007). However, there are also studies claiming sharp contours are often related to the feeling of mystery and might and are considered aesthetically pleasing (Coss, 2003).

3.5. Colors

Research on preferred flower colors has a long tradition. Studies usually report blue to be one of the most preferred colors, while brownish yellow is the least preferred (Camgöz et al., 2002; Schloss et al., 2012; Zemach et al., 2007). Red is often described as highly arousing (Humphrey, 1976), but it is unclear whether it is also preferred (it can be linked to ripe fruits or blushing, as well as to blood). However, there are important cultural differences (Saito, 1996; Taylor et al., 2013), and probably also sex differences (Hurlbert & Ling, 2007), that according to some authors are caused by different attuning of the visual systems of men and women. Men tend to better recognize colors on the blue-yellow spectrum, while women on the red-green. Authors further attribute these differences to the different dominant activities of men and women in a hunter-gatherer society. Men had to better recognize moving objects during hunting, while women had to distinguish static objects against the background during foraging (Hurlbert & Ling, 2007). It is also true that trichromatic vision evolved quite late in primates, possibly as an adaptation for the recognition of ripe red fruits in green vegetation (Osorio & Vorobyev, 1996).

A more elaborate theory describing the differences in color preferences is called Ecological Valence Theory (Palmer & Schloss, 2010; Schloss et al., 2012). This theory combines both evolutionary and ontogenetic approaches by postulating that people prefer colors that are typically attributed to objects with positive valence. They might thus include evolutionarily relevant cues such as clean water and sky (blue), or feces and dead vegetation (brownish yellow). Moreover, culturally or individually important cues would also be important.

4. Study I: What flowers do we like?

After I examined the possible flower traits that can play a role in the aesthetic response to them, I wanted to see how the premises of all the mentioned theories correspond with the data. The cultivation and breeding of ornamental plants both have a long tradition, and the volume of the global market of cut flowers reaches tens of billions of dollars per year (Mamias, 2018). Therefore, I expected to find many studies that would evaluate the aesthetic responses to various flowers. Certainly, the flower sellers and breeders would study what products would suit their customers the most. I could not have been more wrong. Few studies compared the preferred colors of single species of cut (Yue & Behe, 2010), outdoor-grown (Todorova et al., 2004), or potted flowers (Behe et al., 1999). One study also took into account the number of flowers on the plant (Behe et al., 1999). However, the studies related to trade mixed the features of the flowers with marketing variables, such as the price, packaging, and sales environment. There was no comprehensive study comparing different flower shapes and colors across a wider variety of flowers.

The only logical solution to this situation for me and my colleagues was to conduct such a study on our own (see (Hůla & Flegr, 2016) - appendix 1 - for the outcome). We had to reduce the immense diversity of flowers to a reasonable number while retaining as much ecological variation as possible. Since we were interested in general aesthetic responses to flowers that possibly stemmed from the human past, we decided to use wildflowers as stimuli. Because we were testing the responses of Czech raters, we limited the diversity of wildflowers to those growing in Czechia. To recruit as many raters as possible, we decided to use photographs of flowers and conduct the study online. We were interested in the features of flowers, so we decided to show only the photographs of flowers, not the whole plants. Every wildflower has different leaves and overall appearance, which would bring an excessive amount of noise to the data. Our final sample consisted of 52 wildflowers with a diverse range of shapes and colors. We then asked more than two thousand people to rate the flowers on a six-point scale by expressing the level of their agreement with the statement that the flower in the picture is very beautiful. The same participants also rated the flowers in a sepia tone (devoid of color), which allowed us to explore the effect of color when the shape features were controlled for. We also asked an independent set of participants to rate the same set of flowers, but this time according to their perceived prototypicality and complexity.

We found a striking agreement in the raters' aesthetic responses. Individual differences (such as the sex of the raters) had only a minor role in the ratings. We found a strong link between the perceived prototypicality, complexity, and type of floral symmetry. Radially symmetrical flowers were rated as prototypical and not very complex. Bilaterally symmetrical flowers, on the other hand, scored high in complexity and low in prototypicality. Prototypicality also had the most important positive effect on the overall rating of flower beauty. Bilaterally symmetrical flowers were rated significantly worse than radially symmetrical flowers. Flowers with sharp contours also scored better than round flowers. The effect of color was less prominent than the effect of shape. Blue/violet color increased the overall rating of beauty. When we analyzed only the effect of color after controlling for flower shape (using the difference in the ratings of the colored and sepia photographs), we found a positive effect of blue/violet and purple and a negative effect of yellow.

Our results created a foundation for basic orientation in the aesthetic responses to various flower features. They confirmed expectations based on the research on colors. The role of prototypicality was also unsurprising. The predictions of the habitat selection theory were supported only partly (high ratings of blue and low ratings of yellow). Contrary to the claims of the authors, color did not play the most important role. However, the flowers were rated from a close distance and the authors were discussing colors in the context of a greater distance. Bilaterally symmetrical flowers were also rated worse than radially symmetrical ones, which is in contrast to the suggestions of Heerwagen and Orians. The link of bilateral symmetry with face recognition, however, could apply to flowers, but in a different manner than expected. Some participants reported that bilaterally symmetrical flowers reminded them of animals or open mouths, and that is why they did not like them. The tendency to relate bilateral symmetry to faces led to a misattribution of flowers to the wrong category and subsequent confusion and frustration.

5. Study II: Testing a theory

Thanks to our research on preferred floral traits, we were able to evaluate the expectations derived from the habitat selection theory and information processing theories in light of our newly acquired empirical data. Our results corresponded well with the information processing theory, but only partly with the habitat selection theory.

In our second study (Hůla & Flegr, 2021) – appendix 2) we decided to focus solely on the habitat selection theory. Some of the premises of the theory seemed rather bold to us from the very beginning (for example, the preference for bilaterally symmetrical flowers because of a greater chance to find honey). We also found the link between flowers and the presence of food and resources in the environment to be somehow insufficient to trigger the strong aesthetic responses to flowers we can observe in our society. However, the theory has been widely cited and is the only theory that explicitly mentions flowers. Instead of speculating about its validity, we decided to test whether it has empirical support.

We followed the logic of the theory and accepted that flowers are found beautiful because they signal a resource-rich environment and the presence of food in the future. We also took into account that the stronger and more relevant a signal is, the higher will be the aesthetic response to it. We then identified comparable, but stronger, signals than flowers – edible fruits. Fruits also signal food and an environment rich in resources but in a very straightforward way. Whereas flowers represent a promise of food in the future, fruits are the food in the present. Also, flowers typically last for only a few days, whereas fruits remain on plants much longer. Both fruits and flowers can also have conspicuous colors. According to the theory, fruits should thus elicit stronger aesthetic responses than flowers.

We conducted three separate studies. In the first one, we identified 14 species of Czech plants with edible fruits and let people rate their photographs. Each species was depicted in the flowering stage and the fruiting stage. Moreover, we also used photographs taken from three different distances (the whole plant is visible, approximately 1 meter from the fruit/flower, a close-up of the fruit/flower). More than 700 participants rated the flowering and fruiting plants at each distance. They expressed their agreement with the statement that the presented plant is very beautiful on a six-point scale. When we compared the ratings of flowering plants with the ratings of fruiting plants, we found no statistically significant difference in the ratings. It was not very surprising for the „whole-plant “ distance, because it was difficult to distinguish flowers from fruits. However, we expected to find differences in the two closer distances, especially when the fruits were well-known in Czechia. The raters certainly knew that they were edible and tasty. Moreover, the flowers of some of the plants were quite small and inconspicuous.

In a subsequent study (744 raters), we used the same procedure but replaced Czech plants with plants from the African savanna (a place claimed to be home biome of humans for the majority of their history). We also used only the close-up photographs, since the three distances did not show any differences in the first study. This time, we found a significantly higher rating for flowers. After a closer examination of the data we noticed that the ratings of flowers were comparable across the two studies, but the rating of fruits dropped in the savanna study. This was probably because the plants were unknown to Czech raters, therefore they had no information about their edibility. A third study (more than 800 raters) repeated the design of the second one but used a forced-choice rating method. Again, flowers were preferred to fruits in most cases.

We also compared the effect of the color of flowers and fruits and found the highest ratings for red/purple and the lowest for green and brown.

We concluded that the premises defined by the logic of the habitat selection theory were not supported by our data. This theory is therefore probably not capable of fully explaining the aesthetic responses to flowers.

6. Study III: Intercultural study

When we did not find support for the universal theory of habitat selection, we directed our attention to the generalization of the aesthetic responses to flowers in all humans. Although it seemed omnipresent at first sight, some authors attributed the tendency to give flowers any aesthetic value only to some cultures (Goody, 1993). Such cultures were thought to be agricultural, socially stratified, and located in areas rich in flowers. Moreover, aesthetic responses to flowers were limited only to the highest social classes as a form of a culture of luxury. We conducted a thorough search of the literature (Hůla & Flegr, 2021 – appendix 2) and showed that the usage of flowers for ornamental and decorative purposes is present in non-agricultural societies, in agricultural societies without social stratification, and also in areas where flowers are very scarce (deserts, arctic regions). Thus, we argue that a tendency to respond to flowers aesthetically is probably universal, but environmental and cultural factors influence the strength of its manifestation.

We were curious about the importance of cultural factors. For this reason, we conducted a small-scale study in which we compared the responses of Czech and Kenyan individuals (Hůla & Šámalová, 2023) – appendix 3). The study was conceived as a first step in intercultural research. We plan to learn from the acquired experience while designing a future large-scale study on several cultures.

Czech and Kenyans represent socially, culturally, and ecologically different populations. Therefore, we expected to find larger differences than when comparing Czechs with other European populations. We also employed a different method of data acquisition – the ranking of printed photographs. This method is easy to use and understand by people from different cultural backgrounds and was successfully used in the intercultural research of aesthetic responses to animals (Frynta et al., 2011; Landová et al., 2018).

We used 40 photographs of Czech wildflowers from our previous study (Hůla & Flegr, 2016 – appendix 1) and let people rank them from the most to the least liked. We collected data from 54 Kenyans and two independent sets of Czech raters (n = 54 and 48), and explored how their mean rankings correlated. We found very high positive correlations (r= 0.79 and r= 0.77) between the Kenyan and the two Czech samples. The correlation between the Czech samples was even higher (r= 0.92). We also found that bilaterally symmetrical flowers received worse rankings than radially symmetrical flowers in all samples. The difference was less pronounced in the Kenyan sample and in the second Czech sample, which was partly composed of Czech botany experts. We speculate that the observed greater tolerance for bilaterally symmetrical flowers might be caused by familiarity with this type of flower (bilaterally symmetrical flowers seem to be more abundant in Kenya than in Czechia) and by the raters‘ overall level of knowledge of flowers. We want to stress that the samples were small and heterogeneous, and the stimuli were known to Czechs and unknown to Kenyans. Still, we found very high correlations in the rankings. Our data suggest that intercultural differences in the aesthetic responses to flowers might be less important than one would expect. Our results support the idea that humans as a species share a substantial amount of aesthetical preferences towards flowers. A similar intercultural agreement was also reported in the case of animals (Frynta et al., 2011; Landová et al., 2018).

7. Study IV: Are aesthetic responses stable over time and across different types of stimuli?

Although we found the results of our first study (Hůla & Flegr, 2016 – appendix 1) convincing, we wanted to make sure that they could be replicated. Since no similar studies by other researchers have been published to date, we decided to conduct a second study four years after the original data collection (Hůla, Šámalová & Flegr, not published – appendix 4). We sought to determine whether the aesthetic responses to flowers are stable over time and across independent raters and different sets of stimuli. Also, we compared how the raters agreed when rating real flowers, their standardized photographs, and edited images from the internet.

We prepared three consecutive studies. Two studies contained Czech wildflowers, and one study contained cut ornamental plants. Each species of ornamental plant was present in at least four color variants, including red (which is almost absent in Czech native flora). We were therefore able to better assess the effects of different colors. The design of all the studies was the same. Participants rated the flowers on the same scales as in our first study (Hůla & Flegr, 2016 – appendix 1). First, they rated standardized photographs of the flowers online. Several weeks later, they came into our lab and rated the real flowers of the same species as in the photographs. The rating of real flowers had two parts. In the first part, the flowers were presented under red light which prevented the raters from distinguishing flower colors. The second part of the rating took place under yellow light, which resembled normal daylight conditions. This design allowed us to compare the effect of color while controlling for the shape properties (in the same way as the sepia-tone photographs in the first study). Two weeks after their visit to our lab, the participants rated edited internet images of the same flowers online. There were 72 participants in the first wildflower study, 127 in the second wildflower study, and 80 in the ornamental flower study. Independent sets of participants rated the flowers online according to their perceived complexity and prototypicality.

Our results found strong positive correlations between the ratings of all types of stimuli (real flowers, standardized photographs, internet images), suggesting that real flowers can be replaced by 2D photographs in the study of aesthetic responses. This result is important for the design of our future research. Although photographs are commonly used in psychological research, there are not many studies that compare how reliably they represent real-world objects. A study comparing the scenic beauty of different types of landscapes was rather skeptical of the usage of photographs (Hull et al., 1992). To our knowledge, there is only one study on the aesthetic responses to snakes that found similar results as our study (Landová et al., 2012). A recent study by Grygorczyk and colleagues (Grygorczyk et al., 2019) also stresses that we have to compare the comparable. They found that the in-person ratings of rose bushes do not correlate with the ratings of close-up photographs of single flowers of the same cultivars, commonly used in flower catalogs.

The ratings of real flowers brought similar results as our first study. There was a strong link between the type of floral symmetry and the rating of prototypicality and complexity. The new results also showed that prototypicality had a positive effect on the ratings. In one study, there was an interaction of prototypicality with bilateral symmetry. Prototypicality canceled the negative effect of bilateral symmetry on the ratings. In other words, bilateral flowers lowered ratings of beauty, but when they had high levels of prototypicality, this effect disappeared.

Color had a somewhat stronger effect on the ratings than in the first study. When the shape properties were not filtered out, blue (wildflowers 2) and red (ornamental flowers) had positive effects, while white and yellow had negative effects (wildflowers 1). When controlling for shape, red and purple were rated significantly better than white and yellow.

Contrary to the results of our previous research, we observed a far less important effect of symmetry. The effect was present only in the ornamental flowers study, which had only a small selection of flower shapes (8 in total). The observed effect might have been caused by a specific flower species that happened to be bilateral, rather than by the symmetry per se. While inspecting the data from the two wildflower studies, became apparent that bilateral symmetry itself does not account for the low ratings. Bilateral symmetry is often a by-product of fused corollas, drooping flowers, and other morphological peculiarities. These are rated as very complex and not prototypical at all. This fact plays a role in the low rating of their beauty.

We confirmed, at least among the Czech raters, that the aesthetic responses to different flower shapes and colors remain stable across time and stimuli. The observed effects were similar to those observed in our previous study (Hůla & Flegr, 2016 – appendix 1). We also found a positive effect of red color on the ratings of flower beauty. We confirmed that standardized photographs or edited internet images can substitute for real flowers in this type of research. Finally, we successfully applied a new method for studying the effect of color on objects differing in shape – rating under red and yellow light.

8. Recent research on aesthetic responses to flowers and plants

When we conducted our studies, the literature on aesthetic responses to flowers was very scarce. However, the situation is gradually changing.

Some studies compared the effect of different colors of roses on their perceived beauty, revealing red to be the most preferred (H. Wang et al., 2017). A rating of computer-generated flower beds (Zhang et al., 2023) showed that participants preferred blue, orange, and white flowers the most, and yellow and brown the least. Red and purple had average ratings. It is important to note, however, that the flowers named red were, in fact, reddish-brown. The images depicted flower beds from a distance of several meters, so the shape of the flowers was not well visible. Both studies seem to be in line with our results – blue and red being preferred while yellow and brown were not.

One study also took into account the effect of symmetry on the rating of ornamental flowers, reporting the beauty scores of radially symmetrical flowers to be the highest, asymmetrical flowers medium, and bilaterally symmetrical flowers the lowest (Wu et al., 2021). Another study pointed out that flowers are not perfectly symmetrical, because there is a naturally occurring variation in shapes. However, when they compared the photographs of flowers with edited photographs with perfect symmetry, they found no differences in the ratings of beauty. Interestingly, there were differences in abstract shapes, landscapes, and faces (Bertamini et al., 2019). Again, the results are in line with our research.

Many studies have reported that humans prefer objects with round contours to objects with sharp contours (see (Gómez-Puerto et al., 2016) for review); this phenomenon is known as the curvature effect (Clemente et al., 2023; Corradi & Munar, 2022). Some studies report that it also applies to plants, specifically to the canopy of indoor plants (Berger et al., 2022) and the avoidance of spiky plants by infants (Włodarczyk et al., 2018). Our results found an opposite effect: Angular flowers received higher ratings of beauty than curvilinear flowers. We should investigate whether this was only an artifact of our flower stimuli choice or the method of stimuli presentation. For example, a recent meta-analysis (Chuquichambi et al., 2022) found that the preference for rounded contours is most prominent in forced-choice tasks, with anchoring words on scales using semantic differentials, and with non-expert participants. However, it is also possible that the curvature effect is not present in the ratings of flower beauty. We need a proper study focusing on this issue to be able to draw more convincing conclusions.

It is also commendable that recent research studying the effects of plants on human well-being has started to take their colors and shapes into account. A study with indoor plants found a positive effect of a round canopy (Berger et al., 2022), blue color (Elsadek & Liu, 2021; Zhang et al., 2023) and a relatively stronger effect of shape than color (Y. Wang et al., 2021). Employing knowledge about the aesthetic value of different flowers was also recently recommended in guidelines for creating well-being gardens (Harries et al., 2023).

Finally, the importance of flower beauty was recognized in the assessment of the biodiversity of different landscapes and the implications for their conservation (Breitschopf & Bråthen, 2023; Tribot et al., 2018)

It is evident from the recent literature that the focus of the scientific community is slowly turning towards more refined thinking about plants and flowers. They are no longer described by umbrella terms such as vegetation or greenery, but the characteristic features of individual species are taken into account. Our research might serve as a basis for further inquiries in this direction.

9. Future directions

Many questions are still awaiting answers, and there are still many unexplored topics related to aesthetic responses to plants and flowers. I am going to list those that I find the most important. Please note that the list is certainly not exhaustive.

Universality of aesthetic responses – we searched the literature and found that the existence of aesthetic responses to flowers is to some extent omnipresent and probably also stable over time (Hůla & Flegr, 2021 - appendix 2). Another question is if the patterns of aesthetic responses are also shared by all humans. Our small-scale study on Czechs and Kenyans (Hůla & Šámalová, 2023 - appendix 3) suggests that this might be the case. However, we certainly need a large-scale intercultural study on people from the most diverse cultural and ecological backgrounds possible.

Another way to assess the possible universally shared patterns of aesthetic responses is to **work with infants**. This approach was successfully employed in studies of plant avoidance (McNamara & Wertz, 2021; Rioux & Wertz, 2021; Wertz & Wynn, 2014b; Włodarczyk et al., 2018) and related social learning about their edibility (Oña et al., 2019; Wertz & Wynn, 2014a, 2019). Studying plant preferences among infants might result in valuable insights.

We repeatedly encountered the issue of **familiarity** in our research. Some of the observed differences between Czechs and Kenyans (appendix 3), as well as between the ratings of flowers and fruits (appendix 2), might be attributed to familiarity. Future research should certainly focus on its role in the aesthetic responses to flowers.

Closely related to familiarity is the **level of expertise**. This was nicely illustrated in our intercultural study (Hůla & Šámalová, 2023 - appendix 3) in which botany experts ranked two flowers in a very different manner than other raters. One of them was *Santina*, a flower that is not native to the Czech flora but is commonly sold as an ornamental plant. It received a good ranking among laypeople and a bad ranking among botany experts, who would probably think of it as an invasive species or a too-basic flower. We saw an opposite situation in the case of *Erythronium dens-canis*. This flower has an unusual shape and is drooping. Laypeople gave it bad rankings, whereas botany experts gave it good rankings. This flower grows only in one locality in Czechia, and the origin of its distribution is a botanical mystery. Czech botanists often organize field trips to the locality to see this mysterious flower in bloom. We think that this knowledge played a crucial role in the rankings of botanists. It would also be interesting to compare the aesthetic responses to toxic and edible or medicinal plants between people with and without knowledge of the plant properties.

Another interesting line of research might be a deeper focus on **individual differences** between raters. Sex, age, attitudes toward plants, individual memories related to specific flowers, and maybe even some psychological factors might influence the aesthetic responses to flowers. For example, the majority of our participants across all our studies were women. Men did not find the topic attractive. However, the pattern of their responses was the same.

The angularity of flowers calls for further research because our results (Hůla & Flegr, 2016 - appendix 1) are clearly in opposition to the majority of the literature. A carefully conducted study could help us decide whether the observed higher ratings of the beauty of angular flowers are a real phenomenon or a mere artifact.

Increasing the ecological validity of the studies seems extremely important. Our approach applied only visual assessment of flowers. The presentation of the stimuli was very different from the occasions in which people encounter flowers in their normal lives. This reductionist approach was necessary for our initial orientation on the topic. However, we can imagine studies that would explore this topic in greater complexity. For example, **rating the whole plants or their groups,** and **using more senses**, such as touch and smell, during the ratings seems to be more relevant to everyday situations than a simple visual observation. The texture of plants and the odor of flowers might have an important effect on aesthetic responses. We could also move beyond online surveys and laboratory experiments and perform **observations in the field**, for example by analyzing the composition of private ornamental gardens or flower exhibits.

Our studies (Hůla & Flegr, 2016 - appendix 1, and Hůla, Šámalová & Flegr (not published) - appendix 4) might give the impression that what makes flowers aesthetically valuable is the combination of their shapes, colors, or other features such as complexity and prototypicality. From this point of view, any object or organism should follow these rules, and people might have similar aesthetic responses to them, as far as they have similar combinations of features. I think flowers are more than that. Their liveness, autonomy, fragility, and transience might be the reason why people seem to find flowers more aesthetically attractive than other objects. Unfortunately, we do not have any data to test this premise. We might, for example, observe the reactions of people to real flowers, artificial flowers, and objects that are clearly not flowers but have the same shape and color properties (such as origami).

10. Conclusion

This work has presented four studies by which I and my colleagues contributed to the research of people-plant interactions. We tried to raise awareness of the importance of aesthetic responses to plants and flowers for studies focusing on plants and human well-being. We also tried to establish a basic body of flower features that elicit aesthetic responses and have support in the data. Furthermore, we explored some theoretical aspects of human aesthetic responses to flowers and made a first step towards generalizing our results across cultures. The outcomes of our studies would hopefully be helpful for workers in the flower business, specialists involved in nature conservation and education, and researchers interested in anthropology and evolutionary psychology. Finally, I showed that there are still many questions in the field of the aesthetic responses to plants and flowers. I am looking forward to searching for the answers in the years to come.

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APPENDICES

APPENDIX 1

What flowers do we like? The influence of shape and color on the rating of flower beauty

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ABSTRACT

There is no doubt that people find flowers beautiful. Surprisingly, we know very little about the actual properties which make flowers so appealing to humans. Although the evolutionary aesthetics provides some theories concerning generally preferred flower traits, empirical evidence is largely missing. In this study, we used an online survey in which residents of the Czech Republic ($n = 2006$) rated the perceived beauty of 52 flower stimuli of diverse shapes and colors. Colored flowers were preferred over their uncolored versions. When controlling for flower shape, we found an unequal preference for different flower colors, blue being the most and yellow the least preferred. In the overall assessment of beauty, shape was more important than color. Prototypical flowers, i.e., radially symmetrical flowers with low complexity, were rated as the most beautiful. We also found a positive effect of sharp flower contours and blue color on the overall rating of flower beauty. The results may serve as a basis for further studies in some areas of the people-plant interaction research.

Subjects Psychiatry and Psychology
Keywords People-plant interactions, Beauty, Aesthetic preference, Floral morphology, Evolutionary aesthetics, Phytophilia

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INTRODUCTION

People across cultures find flowers beautiful. The aesthetic appreciation of flowers is manifested in many ways. We grow flowering plants in our apartments and gardens, horticulturists put much effort into breeding new types of ornamental flowers, and floral motifs are often present on paintings, fabrics, china or jewelry (*Appleton, 1996*; *Eibl-Eibesfeldt, 1989*). Flowers also serve as traditional and highly esteemed gifts (*Haviland-Jones et al., 2005*). This human attitude towards plants and flowers is known as phytophilia (*Eibl-Eibesfeldt, 1989*).

Many aspects of people-plant relationships have been explored in past years, especially the effects of plants and flowers on the human psyche. Some researchers have suggested that the presence of plants positively affects mood (*Larsen et al., 1998*; *Shibata & Suzuki, 2002*; *Haviland-Jones et al., 2005*) and attention (*Herzog et al., 1997*; *Kaplan & Kaplan, 1995*; *Kaplan, 1995*; *Lohr, Pearson-Mims & Goodwin, 1996*; *Raanaas et al., 2011*; *Tennessen & Cimprich, 1995*), reduces stress (*Cackowski & Nasar, 2003*; *Grahn & Stigsdotter, 2010*) and even decreases recovery time after surgery (*Ulrich, 1984*).

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The perceived beauty of flowers might influence the psychological benefits they provide to humans. It is thus reasonable to ask if there exist any common human flower preferences or whether the perceived beauty of flowers depends solely on individual taste. Although several studies targeted on best-selling flower products provide us with some data (*Behe et al., 1999*; *Yue & Behe, 2010*), they have two major limitations. First, they typically focus on only one segment of products (such as geraniums or single stem cut flowers), so it is not possible to generalize their results. Moreover, these studies do not attempt to explain the causes of the observed preferences. Second, the studies combine the effect of morphological traits (color, number or size of the flowers on the plant etc.) with the effect of price, product packaging etc.

In our study, we address the issue from a more general perspective. We postulate that if there are any common preferences for different flower traits, they would have been shaped in the course of human evolution. We thus use theories and hypotheses from evolutionary aesthetics to predict which flower colors and shapes should generally be more preferred than others. Probably only one theory that explicitly mentions flowers has been published—the habitat selection theory of *Heerwagen & Orians* (*1993*), *Orians & Heerwagen* (*1995*) which we describe below. We also present other evolutionary hypotheses focused on general color and shape preferences and try to apply their outcomes to flowers. We then present the design and results of our study, which aimed to empirically test the validity of these hypotheses for flower preference. To increase the readability of the text, we discuss the preferred flower colors and shapes in two separate sections.

Preferred flower colors

The habitat selection theory of Orians and Heerwagen regards flowers as important signs that could have helped our ancestors find a suitable habitat for living. The ability to choose a rich and safe habitat was essential for the survival of our ancestors, thus an innate preference for signs of such a habitat (and the avoidance of opposite signs) was highly adaptive. It is for this reason that we perceive these signs as beautiful. Flowers signal a rich environment and promise the presence of edible bulbs or fruits (*Heerwagen & Orians, 1993*; *Orians & Heerwagen, 1995*; *Pinker, 1999*). Flower signs have to be visible from a distance, so we should mainly prefer their vivid and contrasting colors.

General color preference may also influence the beauty of many objects with the same color, including flowers. Green and blue colors could be preferred because they signal a rich and safe habitat (lush vegetation, water, clear sky). Brown or yellow are connected with barren land, drought, dead vegetation or feces and could be avoided (*Orians & Heerwagen, 1995*, pp. 567–569; *Palmer & Schloss, 2010*). On the other hand, edible fruits and nuts are often yellow or brown, so the predicted avoidance of these colors is somewhat dubious. Red color may signal edible fruits, sexual arousal or blood (*Humphrey, 1980*). Red objects should be regarded as stimulating, but whether as beautiful is uncertain.

Some studies targeting the behavior of florist shop customers reported red and pink flowers as the most preferred and blue and yellow flowers as the least preferred (*Behe et al., 1999*; *Yue & Behe, 2010*). A study examining the beauty of street flowers found equal preference for diverse flower colors (*Todorova, Asakawa & Aikoh, 2004*). When people rated their favorite color of a tree canopy, they most preferred red (*Kaufman & Lohr, 2004*; *Heerwagen & Orians, 1993*). However, in another study, a red canopy was the least preferred and blue had the highest rating (*Müderrisoğlu et al., 2009*).

People who rated the beauty of diverse birds appreciated the presence of blue and yellow coloration and overall lightness (*Lišková & Frynta, 2013*). Similar results were found in the case of parrots (*Frynta et al., 2010*), while blue and green were the most preferred colors of pita birds (*Lišková, Landová & Frynta, 2014*).

Studies examining overall color ranking have usually described blue and red as the top colors (blue was usually preferred slightly more by men and red by women) and yellow near the bottom (*Camgöz, Yener & Güvenç, 2002*; *Ellis & Ficek, 2001*; *Hurlbert & Ling, 2007*; *Schloss, Strauss & Palmer, 2013*; *Zemach, Chang & Teller, 2007*). Color preferences also seem to be culturally dependent. For example, East Asian cultures have a preference for white color (*Saito, 1996*), while members of the African Himba tribe highly esteem yellow and do not like blue (*Taylor, Clifford & Franklin, 2013*).

Palmer & Schloss (*2010*) proposed the ecological valence theory, which integrates evolutionary and ontogenetic approaches in the research of human color preferences. The authors write that people should be attracted to colors they associate with salient objects they like and repulsed by colors associated with salient objects they dislike. They found a preference for blue color and a dislike for brown and dark shades of yellow. This pattern was consistent across several cultures (with slight variations). The authors thus concluded that some portion of color preference is probably universal while another portion is influenced by culture and individual experiences.

Preferred flower shapes

The influence of flower shape on the perception of flower beauty was largely neglected by the theoretical and empirical works mentioned above. This is quite surprising, especially when we take into account the astonishing diversity of flower forms and the large number of studies documenting the importance of shape in the perception of beauty of many objects and organisms (see below).

Many authors have suggested that humans tend to aesthetically appreciate objects that are quickly recognizable and fluently processed by their brains. The presence of such objects assures easy orientation in the environment and rapid evaluation of its potential threats and benefits. Human attraction to these environments should be highly adaptive (*Humphrey, 1980*; *Kaplan, 1987*, *Kaplan 1988*; *Reber, Schwarz & Winkielman, 2004*). Objects that are fluently processed tend to be symmetrical (*Enquist & Arak, 1994*; *Enquist & Johnstone, 1997*; *Jacobsen et al., 2006*; *Van der Helm & Leeuwenberg, 1996*), prototypical (*Winkielman et al., 2006*), and moderately complex (*Reber, Schwarz, & Winkielman, 2004*). Empirical research has confirmed that people prefer prototypical objects and animals (*Hekkert, Snelders & Wieringen, 2003*; *Hekkert & Wieringen, 1990*; *Reber, Schwarz & Winkielman, 2004*).

Complexity influences the preference for objects (*Jacobsen et al., 2006*; *Reber, Schwarz & Winkielman, 2004*), but not linearly. Studies have reported that objects with very low or very high complexity are preferred less than moderately complex ones (*Akalin et al., 2009*; *Hekkert & Wieringen, 1990*). People dislike highly complex objects because they cannot be easily and rapidly recognized and categorized, while objects with very low complexity are just boring. It is questionable whether we would observe an effect of boredom in the case of flowers, because even the simplest ones reach a certain base level of complexity.

Symmetrical objects are also considered beautiful (*Jacobsen & Höfel*, *2002*; *Jacobsen et al.*, *2006*; *Leder et al.*, *2004*). The processing fluency and the preference for objects increase with the number of their axes of symmetry (*Evans, Wenderoth & Cheng*, *2000*; *Tinio & Leder*, *2009*). This implies that radially symmetrical flowers should be preferred more than bilaterally symmetrical flowers. On the other hand, some researchers claim humans have a very strong preference for bilaterally symmetrical objects, which may be a by-product of the selection of partners (*Little & Jones*, *2003*) and the recognition of partners or enemies (*Johnstone*, *1994*; see also *Mithen*, *2003*). According to the habitat selection approach of *Heerwagen & Orians* (*1993*), the type of symmetry could provide information about the nutritive value of flowers. Bilaterally symmetrical flowers usually have more nectar than radially symmetrical ones and indicate richer habitats. For this reason, they should be regarded as more beautiful.

Recent studies have shown that people prefer round objects over objects with sharp contours (*Bar & Neta*, *2006*; *Leder, Tinio & Bar*, *2011*; *Silvia & Barona*, *2009*; *Westerman et al.*, *2012*). According to *Bar & Neta* (*2007*), this difference is due to the fact that objects with sharp contours evoke a subconscious feeling of danger and fear, which we inherited from our ancestors. However, another study suggested that the preference for round objects may be just a temporary fashion trend (*Carbon*, *2010*). Richard Coss argued that piercing forms (such as thorns, spikes, canines or horns) were certainly dangerous for our ancestors and even today arouse strong emotions, but not necessarily negative ones. Pointed forms may be strongly symbolic of power and mystery and could be aesthetically pleasing. One of his experiments showed that pedestrians and joggers actually approached plants with pointed leaves at a shorter distance than plants with round leaves. In another study, people rated silhouettes and patterns with sharp contours as more attractive than their rounded counterparts (*Coss*, *2003*).

Relationship between shape and color

Research focusing on object recognition and representation has shown that shape plays the main role, but color is important too. When objects with typical colors (color diagnostic objects), such as a lime or carrot, are presented, a congruent color (orange carrot) facilitates performance while an incongruent color (blue carrot) causes performance to deteriorate (*Therriault, Yaxley, & Zwaan*, *2009*). A recent meta-analysis showed that color has some positive effect even on the recognition of objects without typical colors (non-color diagnostic objects). Color also had a stronger effect on natural objects than on artificial objects (*Bramão et al.*, *2011*). On the other hand, the relative weight of shape and color is context-dependent and can be influenced by both the nature of the object (for example fruit vs. animal) and also the task (categorization vs. motion evaluation) (*Scorolli & Borghi*, *2015*). If we assume that the beauty of an object is closely linked to the ease with which we can recognize and categorize it (see the section above), we should observe a stronger effect of shape than color on the rating of flower beauty, although the presence of color should also serve to increase the perceived beauty of flowers.

Aim of the study

The primary aim of this study was to determine which (if any) flower colors and shapes are more preferred than others. According to some of the mentioned theories from evolutionary aesthetics, flowers should be preferred because of their conspicuous colors. On the other hand, many studies have revealed that some shape properties influence the aesthetic appreciation of an object or a person. It is very likely that flower shape also plays a role in the assessment of the flower beauty. The literature is equivocal concerning the effect of some shape properties on preference (type of symmetry, sharp contours). Also, some of the well documented effects of shape on general object preference may be different when applied to flowers (complexity).

A second main objective of the study was to compare these theories with the empirical evidence and to evaluate the relative importance of color and shape. We wanted to answer the following questions: (1) Are there any general flower preferences? (2) Is the flower color more important than the flower shape? (3) Are some flower colors or shapes more preferred than others?

Hypotheses

We proposed several hypotheses based on the research discussed above:

(1) We expected to find clear common flower preferences in our data set.
(2) We assumed that the presence of color would increase the rating of flower beauty.
(3) We expected to find differences in the beauty rating based on the specific flower color.
(4) We hypothesized that flower beauty would increase with perceived prototypicality,
(5) that moderately complex flowers would be considered more beautiful than those with very low or very high complexity, and
(6) that round flowers would be rated as more beautiful than those with sharp contours.
(7) Finally, we expected symmetry would play an important role in the evaluation of flower beauty, but it was not clear whether bilateral or radial symmetry should be more preferred.

MATERIALS AND METHODS

To test our hypotheses, we conducted two independent online surveys targeted to the Czech population. Both surveys were based on the rating of photographs of flowers. First, we describe how we obtained the flower stimuli, then we present the design of both surveys. The dataset and flower stimuli are available at Figshare: https://figshare.com/s/7306f12659f68f7f3d9d.

Flower Stimuli

We wanted to create a set of flower stimuli that would reflect the diversity of flower shapes and colors. However, it had to remain sufficiently small and easy to work with. For these reasons, we created a primary set of flowers that met the following conditions:

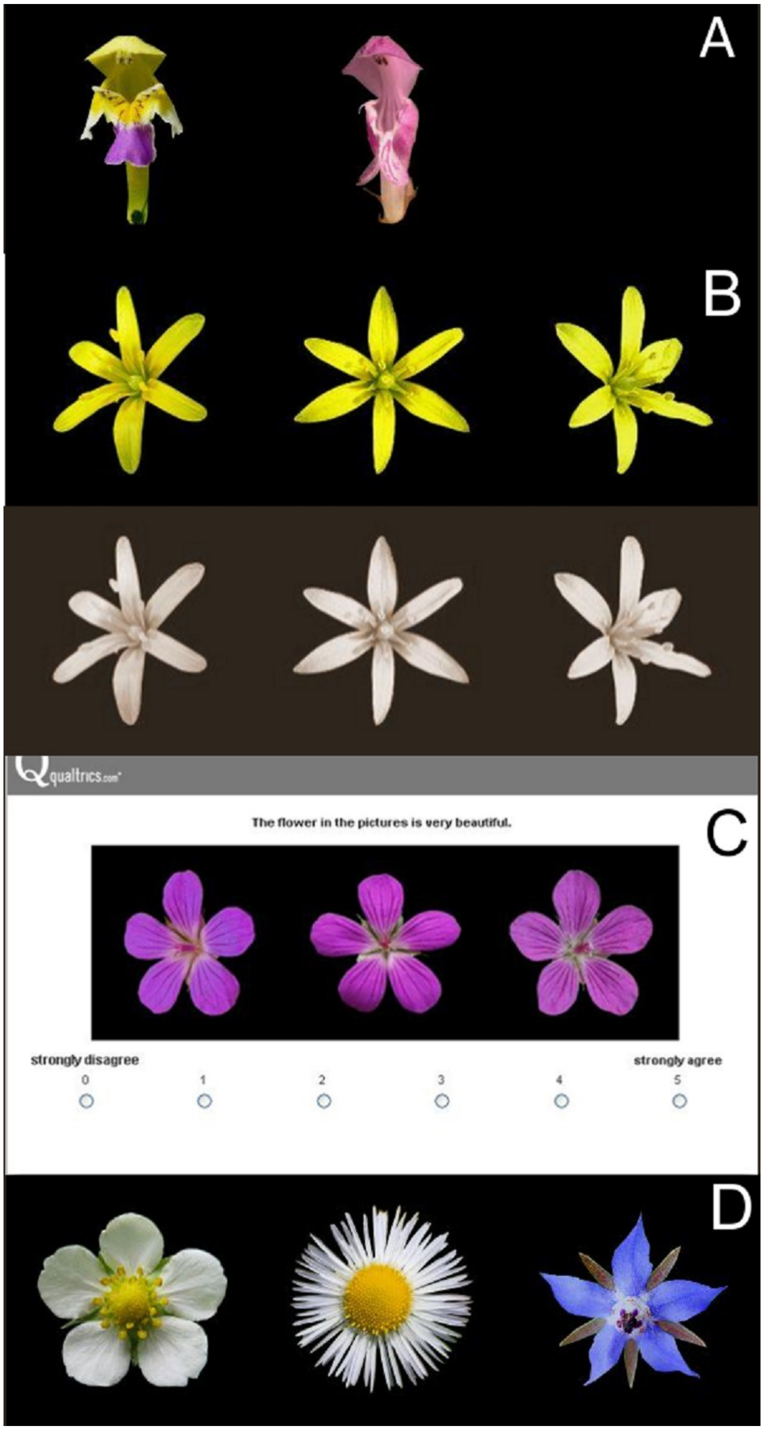
1. The plant is native to the Czech Republic.
2. The plant has no strong cultural connotations in the Czech environment (e.g., a rose is symbolic of love, etc.)
3. The size of the flower is between 1 and 4 cm in diameter.
4. Each flower can be clearly distinguished.

These conditions allowed us to reduce the immense number of flowering plants while maintaining a high morphological diversity. The flowers were not absolutely unknown or notoriously familiar to the respondents, as both of these situations could possibly lead to biased results. The flower size limit guaranteed that the shape of the real flowers could be normally seen with the naked eye. The preparation of the flower stimuli set also included the conversion of photographs to a single size, and it was desirable to keep the converted flower size close to the real one. The last condition eliminated possible problems with compact inflorescences, because it is arguable whether we should distinguish the appearance of single flowers in the inflorescence or treat the whole inflorescence as a single flower. The only exceptions to the last condition were the inflorescences of the aster family (*Asteraceae*). We included aster family members in the stimuli set because they are very common and the vast majority of people (laypersons) perceive their inflorescences as single flowers.

We found all the Czech flowering plant species in the Key to the Flora of the Czech Republic (*Kubát et al.*, *2002*). When the flowers met the inclusion criteria, we included them in the working flower set. In the case of genera with very similar species (e.g., *Rubus, Taraxacum*), we included the flower of just one species in the working set. The working set comprised flowers of 199 species, which we divided into 26 groups according to their shape. From each group we selected two flowers with different color (e.g., Fig. 1A) and added them to the final flower set (see Table 2).

We found freely available high quality photographs of each flower on the internet. To properly illustrate the true shape of the flowers, we used three photographs for each flower. These photographs were displayed together. The photograph in the center showed the flower from above (or *en face* in the case of bilaterally symmetrical flowers), while the photographs on the left and right sides depicted flowers that were turned slightly to the left and to the right, respectively (Figs. 1B and 1C).

We used Corel Photo Paint X7 to replace the original flower background by a neutral black color. The black background did not favor any flower (flowers are usually seen on a green, brown, grey or blue background) and provided enough contrast for the clear distinction of the flowers. We then centered the flowers and placed them in the same position, the top petal or tepal pointing directly upwards. Finally, we converted all of the flowers to the same size, optimal for displaying on most computer screens (flower = 150 pixels, flower + background = 200 pixels, the three photographs next to each other = 600 pixels). We also copied the final flower set and converted the photographs in it to a sepia tone (Fig. 1B). This new set was thus devoid of colors and helped us to test the influence of color on the rating of flower beauty. We did not use a conversion to a greyscale because grey photographs on a black background seemed somehow gloomy, which could negatively influence their rating.



The flower in the pictures is very beautiful.

strongly disagree 0 ○ 1 ○ 2 ○ 3 ○ 4 ○ 5 ○ strongly agree

Figure 1 **Flower stimuli.** (A) examples of bilaterally symmetrical flowers with similar shape (left: *Galeopsis speciosa*, right: *Lamium maculatum*)—only the en face photographs; (B) colored flower stimulus and its sepia tone version (*Gagea lutea*); (C) example of a rating question setting (*Geranium palustre*); (D) Flowers with different angularity levels. Left: round (*Fragaria viridis*), center: mixed (*Erigeron annuus*), right: sharp (*Borago officinalis*).

The final set of flower stimuli consisted of 26 pairs of photographs, the flowers in each pair having a similar shape but a different color. There was also a sepia tone set of flower stimuli

Determination of flower traits

Symmetry

All flower stimuli in the set were symmetrical, but they differed in the type of symmetry. We distinguished radially symmetrical flowers (40 in total; e.g., Figs. 1B–1D) and bilaterally symmetrical flowers (12 in total; e.g., Fig. 1A), respecting the usual convention (for more details see, e.g., *Judd et al., 2002*, pp.: 66–67). We considered the inflorescences of the aster family (*Asteraceae*) as single radially symmetrical flowers.

Angularity

We followed the approach of *Bar & Neta* (*2006*) when determining flower angularity. We divided flowers into three groups according to the curvature of their contours. There were flowers with round contours (21 in total), sharp contours (15 in total) and both round and sharp contours (16 in total). See Fig. 1D.

Color

First we determined whether the flower had only a single color (22) or more colors (30). We also identified a dominant flower color (occupying at least 2/3 of the flower surface). To determine the dominant flower color, we cut a 30 x 30 pixels square (or its equivalent) from the area with the dominant color in each flower photograph. We then computed its average value in the hue-lightness-saturation (HLS) color space. The hue values correspond to the angles of a color wheel, where certain angles are associated with certain colors. We adopted the hue ranges published by *Newsam* (*2005*). To properly distinguish flower color, we had to avoid overlaps between the hue ranges of pink and purple. We set the range for purple to 270°–315° and the range for pink to 316°–350°. White, grey, and black colors can be defined by setting empirical thresholds of lightness (L) and saturation (S) values (*Lišková, Landová & Frynta, 2014*; *Newsam, 2005*). L and S can vary from 0 to 100. In our case, we defined white color as having $L > 70$ and $S < 35$. This combination of L and S values best matched the flowers perceived as white. With the described procedure, we defined the following color groups, which were later used in color preference analysis (the numbers in brackets represent the number of flowers within each group): white (14), yellow (8), blue (9), purple (8) and pink (7). Six flowers had a unique dominant color (*Hieracium aurantiacum*—orange, *Atropa bella-donna*—brown, *Arctium tomentosum* —green) or no dominant color (*Epipactis palustris*, *Galeopsis speciosa, Kickxia elatine*), and we excluded them from further color preference analysis.

Survey design

Each survey consisted of a single questionnaire created in a Qualtrics environment.

In the first questionnaire the respondents rated a set of photographs of flowers by their beauty. The questionnaire also contained several sets of questions concerning basic information about the respondents, their attitude towards plants, color preferences and psychological characteristics.

Because the number of the flower stimuli was quite high (52 flowers in color and sepia tone), we decided to show each respondent only half of them (the first flower of each pair in color and in sepia tone, i.e., subset 1, or the second flower of each pair in color and sepia tone, i.e., subset 2). Although the flower stimuli in each subset remained the same, we randomized their display order. To prevent the respondents from rating the colored flower stimuli under the influence of the sepia tone stimuli and vice versa, we randomized the display order of the colored and sepia tone stimuli and also separated their rating by a set of questions.

For each flower stimulus, respondents expressed their agreement with the statement "The flower in the pictures is very beautiful." The respondents were choosing one point on a six point scale, where 1 meant "strongly disagree" and 6 meant "strongly agree" (Fig. 1C). The respondents moved to the next flower stimulus by clicking on the "next" button. Once the new flower stimulus appeared, it was no longer possible to change the rating of the previous ones (this fact was clearly explained before the start of the rating procedure).

In the second questionnaire the respondents rated the same set of photographs as in the previous questionnaire, but this time by their prototypicality and complexity. There was also a set of questions concerning basic information about the respondents and their attitude towards plants.

The second questionnaire contained fewer questions than the previous one, and it was also not necessary to rate the sepia tone flower stimuli. This allowed us to present each respondent with the whole set of flower stimuli (subset 1 and subset 2 together). We separated the rating of flower complexity and prototypicality by a set of questions and randomized the display order of each rating. The order of flower stimuli in each rating was also randomized. The rating instructions explained what flower complexity and prototypicality meant. For illustration, we also added two examples of the complexity and prototypicality rating of birds and butterflies. The rating procedure was the same as for the determination of flower beauty, but this time, the respondents expressed their agreement with the statements "This is how I imagine a complex flower." and "This is how I imagine a typical flower."

There was a break of several months between the start of the first and second surveys. We distributed the link to both surveys mainly via the Facebook group *Pokusní králíci* (Guinea Pigs; www.facebook.com/pokusnikralici, which is administered by the members of our laboratory (see *Flegr & Hodný, 2016*; for details). The link was also displayed on other web pages; anyone could share the link.

Respondents gave their informed consent to the data collection by proceeding with the questionnaire (this fact was clearly explained on the first page of the questionnaire). Both surveys were completely anonymous. The research was approved by the IRB of the Charles University, Faculty of Science (Approval number: 2015/31).

Characteristics of the respondents

The first questionnaire, in which flower beauty was determined, was completed by 2,006 people (1,484 women, 521 men and one person of unknown sex). Fifty percent of the respondents were between 23 and 33 years old; the youngest respondent was 12 and the oldest 74. Forty-five percent of the respondents lived in towns with more than 50 thousand inhabitants. Fifty percent of the respondents had a college education, while twenty-eight percent of the respondents studied or worked in the field of biology.

The second questionnaire, in which flower complexity and prototypicality were determined, was completed by 582 people (427 women, 153 men and two people of unknown sex). Fifty percent of the respondents were between 25 and 38 years old. The youngest respondent was 10 and the oldest 88. Forty-three percent of the respondents lived in towns with more than 50 thousand inhabitants. Fifty-three percent of the respondents had a college education, while twenty-five percent of respondents studied or worked in the field of biology.

Color blind respondents were excluded from the data set.

The characteristics of the respondents were very similar in both questionnaires, and it is likely that many people completed both questionnaires. We can thus assume that the ratings from both questionnaires are mutually relevant and comparable.

Statistical analyses

We analyzed the data using R software, version 3.1.3. The significance level α was set to 0.05 in all tests.

We computed the scores of the mean beauty, complexity and prototypicality rating of each flower from all respondents. The scores could theoretically vary from 1 to 6 points. The score of flower beauty represented the dependent variable. In the color preference analysis, we computed the difference between the beauty scores of each colored flower and its sepia tone version. The difference could theoretically vary from -5 to $+5$ points. This difference then served as the dependent variable.

To determine the relationship between beauty, complexity and prototypicality, we used Pearson's correlation test (for normal distributions) or Spearman's rank correlation. We used the partial Kendall's correlation (R package 'ppcor') when it was necessary to filter the effect of a confounding variable. When comparing the means of two groups, we used Student's t-test (for normal distributions) or Wilcoxon's rank sum test. We also created general linear models to determine the relative importance of flower traits in the rating of flower beauty. We simplified the initial full model by stepwise backward elimination in order to ensure that the final reduced model could not differ significantly from the initial full model.

Comparison of stimuli subsets

Each stimuli subset was rated by one-half of the respondents. We divided the stimuli into 26 pairs with similar (not identical) shapes and different colors. We allocated one member of each pair to subset 1 and one member to subset 2. We wanted to ensure that the flower stimuli in each pair had similar beauty scores when we controlled for the effect of color. We used a paired t-test to compare the beauty scores between the members of each pair (sepia tone version); no significant differences were found (mean difference $= 0.017$ point, 95% CI [–0.18–0.21], $t = 0.18$, $df = 25$, $p = 0.86$, Cohen's d $= 0.035$). We found a strong positive correlation between the beauty scores of subset 1 and subset 2 ($r = 0.63$,

Table 1 **The influence of display order on the beauty scores.**

	color		**sepia**	
	mean	var	mean	var
color first	4.08	0.22	3.89	0.36
sepia first	4.14	0.27	3.99	0.3

Notes.

Color, colored stimuli set; sepia, sepia tone stimuli set; color first, the colored stimuli set was displayed first; sepia first, the sepia tone stimuli set was displayed first; mean, mean beauty score; var, variance of the beauty score.

95% CI [0.32–0.82], $t = 4.00$, $df = 24$, $p < 0.001$). For this reason, we pooled the data from both subsets and analyzed them together.

Exposure to the colored images could have influenced the ratings of the sepia tone images or vice versa. Therefore, one part of the participants first rated the sepia and then the colored images, while the second part of the participants first rated the colored and then the sepia images. We calculated the mean beauty scores and variances of the flower stimuli for each display option (Table 1).

The mean beauty scores of the sepia tone flowers were lower when they were displayed after the colored flowers than when they were displayed before the colored flowers ($t = -4.50$, $df = 51$, $p < 0.001$, mean difference $= -0.096$, 95% CI [-0.14–-0.05]). The variance followed the opposite trend.

Similarly, the mean beauty scores of the colored flowers were lower when they were displayed after the sepia tone flowers than when they were displayed before the sepia tone flowers ($t = -2.98$, $df = 51$, $p = 0.0044$, mean difference $= -0.052$, 95% CI [-0.087–-0.017]). Again, the variance followed the opposite trend.

We took these findings into account in the subsequent analyses.

RESULTS

Flower color

We used a paired t-test to compare the mean beauty rating of colored and sepia tone flowers. Colored flowers had a significantly higher rating than the sepia tone ones (mean color = 4.13, sd = 0.50; mean sepia = 3.98, sd = 0.56; mean difference = 0.15, 95% CI [0.07–0.22], $t = 4.02$, $df = 51$, $p < 0.001$, Cohen's d = 0.56). There was a strong positive correlation between the beauty rating of colored flowers and their sepia tone versions ($\rho = 0.85$, 95% CI [0.75–0.91], $S = 3609.1$, $p < 0.001$).

To determine whether the dominant flower color (hue) influenced its beauty rating, we created a general linear model in which the difference between the beauty score of each colored flower and its sepia tone version was the dependent variable. As explanatory variables we used the flower traits that could theoretically influence this difference. These were: dominant flower color (hue), lightness of the dominant flower color, saturation of the dominant flower color, number of colors in each flower, and flower prototypicality, symmetry and angularity. The initial full model (adjusted $R^2 = 0.56$) showed a significant effect of dominant flower color and symmetry. However, the final model (see Table 3) consisted of only one explanatory variable—the dominant flower color (hue)—and was

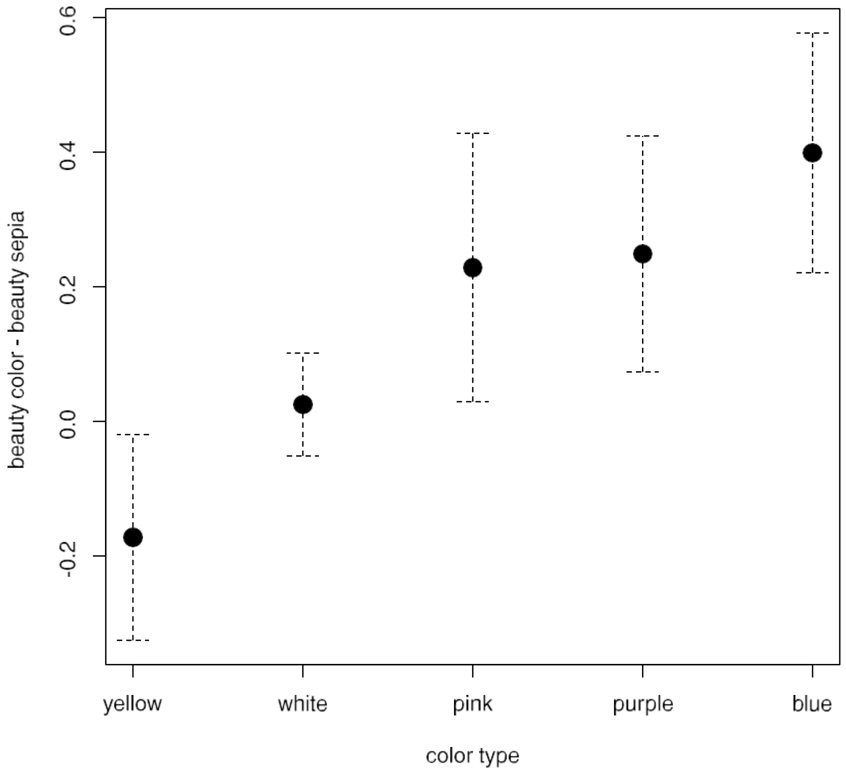


Figure 2 **Effect of flower color on the estimation of beauty.** X axis: different flower colors (hues), Y axis: difference between the mean beauty rating of the colored flowers and their sepia tone versions. Error bars represent the 95% CI.

highly significant (adjusted $R^2 = 0.49$, $F_{4,41} = 11.91$, $p < 0.001$). Tukey–Krammer's post hoc test revealed that blue color was the most preferred. The mean difference between the rating of blue flowers and their sepia tone versions was 0.40. Blue was followed by purple (0.25 point) and pink (0.23 point). White color had no significant effect, and yellow flowers were rated even worse than their sepia tone versions (-0.17 point). See Fig. 2 and Table 4 for details.

To test the influence of the display order of the stimuli (colored set first vs. sepia tone set first), we applied the same model to the group in which the sepia tone stimuli were shown first and to the group in which the colored stimuli were shown first. In the "sepia-first" group, the final model only slightly differed in the values of the estimates (see Table 5 and Table 6). In the "color-first" group, however, the final model also revealed a significant positive effect of bilateral symmetry (apart from the effect of the dominant color). See Table 7 and Table 8.

Beauty scores and flower traits

We determined the relationship between the scores of flower beauty, complexity and prototypicality. There was a significant positive correlation between the beauty and prototypicality scores ($\rho = 0.75$, $S = 36660.39$, $p < 0.001$; Fig. 3B). We found a significant negative correlation between the flower beauty and complexity scores ($\rho = -0.56$,

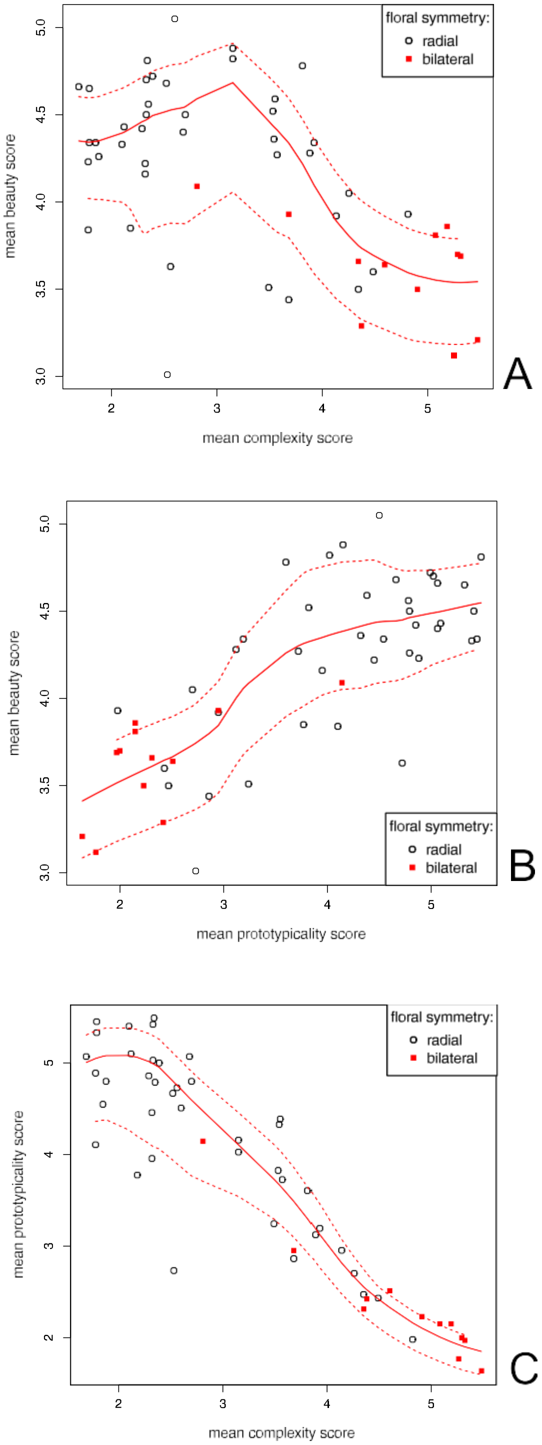


Figure 3 Correlation between the mean beauty, complexity and prototypicality ratings. Each variable could vary from 1 (least beautiful/complex/prototypical) to 6 (most beautiful/complex/prototypical). A LOESS fitted line is shown (full line). Dashed lines represent the function spread (±SD) (A) Correlation between the beauty and complexity scores. $S = 36660.39$, $p < 0.001$, $\rho = -0.56$, 95% CI [−0.72–0.34]; (B) Correlation between the beauty and prototypicality scores. S = 5750.47, $p < 0.001$, $\rho = 0.75$, 95% [0.60–0.85]; (C) Correlation between the prototypicality and complexity scores. $t = -15.61$, $df = 50$, $p < 0.001$, $r = -0.91$, 95% CI [–0.95–−0.85].

$S = 5750.47, p < 0.001$; Fig. 3A). There was, however, a very strong negative correlation between the complexity and prototypicality scores ($r = -0.91$, $t = -15.61$, $df = 50$, $p < 0.001$, 95% CI [−0.95–0.85]; Fig. 3C). For this reason, we also computed the Kendall's partial correlation between the beauty and complexity scores, when controlling for prototypicality (and vice versa). There was still a significant positive correlation between the beauty and prototypicality scores when we excluded the effect of complexity ($z = 4.13$, $df = 50$, $p < 0.001$, $\tau = 0.40$), but there was no correlation between the beauty and complexity scores when we excluded the effect of prototypicality ($z = 0.41$, $df = 50$, $p = 0.68$, $\tau = 0.040$).

We used a Wilcoxon rank sum to determine the differences in the complexity and prototypicality scores of bilaterally and radially symmetrical flowers. To reveal the difference in beauty scores between bilaterally and radially symmetrical flowers, we used a two sample t-test. Radially symmetrical flowers scored higher in beauty (mean difference = 0.65 points, 95% CI [0.37–0.93], $t = 4.65$, $p < 0.001$, Cohen's d = 2.00) and prototypicality (median bilateral = 2.19 points, median radial = 4.42 points, $W = 447.5$, $p < 0.001$, Hodges-Lehmann estimator = 2.02, 95% CI [1.25–2.56]). Bilaterally symmetrical flowers had higher scores in complexity (median bilateral = 4.99 points, median radial = 2.55 points, $W = 30$, $p < 0.001$, Hodges-Lehmann estimator = −1.93, 95% CI [−2.61–1.26]). All significant results remained significant also after performing the Bonferroni correction for multiple tests.

To determine the relative importance of different flower traits for rating their beauty, we created a general linear model in which the flower beauty scores served as the dependent variable. We wanted to include the dominant flower color (hue) in the model. At the same time, we also wanted to use the information contained in those flowers with a unique or uncertain dominant color (hue), which were deleted from the dataset in the previous color analysis. For this reason, we converted the factor variable dominant color (hue), which had five levels, into five binary variables (with levels of *no* and *yes*): white, yellow, purple, pink and blue. We also used the same procedure with the variable angularity. This step allowed us to gain information from the whole dataset and avoid reducing the degrees of freedom. As further explanatory variables we used the following flower traits: prototypicality, the number of colors in each flower, symmetry, lightness of the dominant flower color and saturation of the dominant flower color (or the most common color in the case of flowers with an uncertain dominant color). We did not include complexity in the model because of its very strong correlation ($r = -0.91$) with flower prototypicality.

The initial full model ($R^2 = 0.75$, adjusted $R^2 = 0.68$) revealed a significant effect of prototypicality, blue color, angularity and saturation. The final reduced model (Table 9) confirmed only the effect of prototypicality, blue color and sharp contours (adjusted $R^2 = 0.70$, $F_{3,48} = 39.81$, $p < 0.001$). All three of these variables had a significant positive effect on the mean flower beauty rating. The most important was prototypicality, followed by blue dominant color and sharp flower contours (Table 10).

As a control, we also created another linear model in which the flower hues were represented as levels of a single factor variable and the flowers with a unique or uncertain dominant color were deleted from the dataset. The final reduced model was very similar to the model in which no flowers were excluded from the data set (adjusted $R^2 = 0.64$, $F_{7,38} = 12.50$, $p < 0.001$), and it contained the same variables with similar significant effects (prototypicality: estimate = 0.32, 95% CI [0.23–0.42], $t = 7.02$, $p < 0.001$; dominant blue color: estimate = 0.35, 95% CI [0.09–0.62], $t = 2.72$, $p = 0.010$; sharp contours: estimate = 0.30, 95% CI [0.076–0.53], $t = 2.70$, $p = 0.010$).

To test the influence of the display order of the stimuli (colored set first vs. sepia tone set first), we applied the same models to the group where the sepia tone stimuli were shown first and to the group where the colored stimuli were shown first. In both groups, the models only slightly differed in the estimate values (see Tables 11–14).

DISCUSSION

We found that the presence of color generally slightly increased the beauty rating of flowers. When we compared colored and sepia tone versions of the same flowers, we found significant differences in the effects of specific colors. Blue was the most preferred, followed by pink and purple. As expected, white flowers did not differ from their sepia tone versions in their ratings, because both versions looked very similar. Yellow flowers were rated as less beautiful than their sepia tone versions. We were not able to measure the effect of red because only one genus (*Papaver*) native to the Czech Republic typically has red flowers.

Our results partly correspond with the habitat selection theory (*Heerwagen & Orians, 1993*) and also with the ecological valence theory (*Palmer & Schloss, 2010*). Both theories suggest people like blue color, which is typically related to clear sky or water, and tend to dislike brown and some shades of yellow because they are related to feces, death, vegetation or drought. The habitat selection theory links color preferences to the signs of the environment that were crucial for the survival of our ancestors. It assumes that our color preferences are a heritage of the past, hardwired in our brains. The ecological valence theory also recognizes inborn preferences but argues that these preferences can change during the course of an individual's life. It states that our color preferences are influenced by the valence of typically colored objects in our surroundings.

According to empirical research on the perceived beauty of simple colors (*Camgöz, Yener, & Güvenç, 2002*; *Ellis & Ficek, 2001*; *Hurlbert & Ling, 2007*; *Schloss, Strauss & Palmer, 2013*; *Zemach, Chang & Teller, 2007*); and tree canopies (*Müderrisoğlu et al., 2009*), blue is the most and yellow the least attractive color. A preference for blue was also reported for pita birds, which are very similar in shape but differ in coloration (*Lišková, Landová & Frynta, 2014*). We can assume that the general human color preference (as determined in American and European populations) also applies to flowers.

We must point out, however, that the yellow color (least preferred) in our set of stimuli was saturated. It is evident that clear yellow is more related to the sun or ripe fruits than to dead vegetation or drought. In our opinion, the habitat selection theory cannot fully explain the dislike of saturated yellow. Studies based on the ecological valence theory reported a low preference only for dark shades of yellow, whereas saturated yellow had an average preference. If we follow the assumptions of the ecological valence theory, we could argue that the Czech population tends to particularly dislike salient objects that typically have a saturated yellow color. This in turn could lead to a low general preference for saturated yellow and explain the observed dislike of yellow flowers.

There is no agreement on the effect of lightness on the beauty rating of objects and organisms. *Lišková & Frynta*, (2013) stated that the beauty rating of birds increased with the overall lightness of their coloration. Schloss and colleagues (2013) found that lightness had no effect on the rating of color squares, a negative effect on the rating of small objects (e.g., t-shirt, pillow) and a positive effect on the rating of large objects (walls). We found no effect of lightness on the beauty rating of flowers. These differences in results may be caused by the use of different procedures to determine the degree of lightness and also by differences in stimuli presentation. It is also probable that the relative importance of lightness is context dependent.

It is important to note that although there were differences in flower color preference, they had only a minor effect when compared to the importance of flower shape. Only the presence of blue color significantly affected the beauty rating of flowers with diverse shapes. This relative unimportance of color was also found in the beauty rating of birds, whereas their shape (such as the length of the tail) had the major effect. However, blue and yellow colors also affected the perceived beauty of birds (*Frynta et al.*, 2010; *Lišková & Frynta*, 2013). Our results argue against the habitat selection theory, which suggests people like flowers mainly because of their vivid colors. According to our findings, flower market surveys might consider paying more attention to the shape of their products when trying to explore the preferences of their customers.

We report a very close relationship between the perceived flower prototypicality, complexity and type of symmetry. We expected to find a negative correlation between the prototypicality and complexity scores, but not as strong as our results actually indicate ($r = -0.91$). It would be helpful to compare the perceived complexity scores with some objective measurements. Unfortunately, it is very difficult to find an objective measurement method that could be applied to flowers with such a diversity of shapes.

The observed relationship between the flower beauty and complexity scores was close to an inverse U shape (Fig. 3A). This finding is in accord with previous research (*Akalin et al.*, 2009; *Hekkert & Wieringen*, 1990). Overly simple objects are usually described as boring, while very complex objects are difficult to process, which could explain their low preference (*Reber, Schwarz & Winkielman*, 2004). We can see, however, that people still rated very simple flowers as quite beautiful, especially when compared with their rating of very complex flowers. This finding supports our assumption that flowers always have some base level of complexity, which assures they are never too boring to appreciate.

Bilaterally symmetrical flowers scored very low in prototypicality and very high in complexity. It is true that bilaterally symmetrical flowers are less common in the Czech Republic (and also worldwide). They often have fused floral parts and are highly three dimensional, so it might be difficult to describe their shape. These facts may account for their low prototypicality and high complexity scores.

We observed large differences in beauty scores between bilaterally and radially symmetrical flowers (radially symmetrical flowers scored higher). This supports the hypothesis that more axes of symmetry should lead to more fluent processing of the object and its higher preference (*Evans, Wenderoth & Cheng*, 2000). The results of our study go against the assumptions of *Heerwagen & Orians* (1993), who expected to find higher preference for bilaterally symmetrical flowers because they signaled richer habitats than radially symmetrical flowers. Our findings may quite paradoxically support the hypothesis that people tend to associate bilateral symmetry with human faces and bodies or with animals (*Little & Jones*, 2003; *Mithen*, 2003), but they are in opposition to its predicted outcome—a preference for bilateral symmetry. Bilaterally symmetrical flowers might be difficult to categorize. Their confounding animal- or even humanlike appearance might lead to their low preference. Anecdotal evidence supports this hypothesis. When we asked some of the raters about the flower stimuli, they often described the bilaterally symmetrical flowers as menacing and bizarre. The flowers reminded them of open mouths, snake heads and even aliens.

Partial correlations and the linear models also revealed that prototypicality encompasses both complexity and symmetry and is the main predictor of flower beauty. When we included prototypicality in our model, complexity and symmetry had no effect on flower beauty. Prototypical flowers had high beauty and low complexity ratings and were radially symmetrical.

Angularity also had a significant effect on the beauty scores. It turned out that sharp contours positively affected the flower beauty scores, while mixed contours had no effect. Our results disagree with those of some recent studies (*Bar & Neta*, 2006; *Silvia & Barona*, 2009), perhaps due to the different rating methods used. Previous research used forced choice methods in which the participants had to choose between two similar objects with different contours (e.g., sofa, watch, flower, rectangle etc.). In our study, each flower was rated separately, and we created no matching pairs with different levels of angularity. We have already mentioned that in some cases, sharp contours could be aesthetically pleasing (*Coss*, 2003), thus we cannot dismiss the possibility that a preference for roundness and an avoidance of sharpness are context-specific and do not apply to flowers.

The display order of the stimuli (colored set shown first vs. sepia tone set shown first) affected the results of the linear model that examined the influence of color on flower preference. In the "sepia-first" group, only the effect of flower color was revealed. In the "color-first" group, we observed the effect of flower color and a positive effect of bilateral symmetry. In other words, the difference between the beauty scores of the colored and sepia tone versions of the same flower was greater for bilaterally symmetrical flowers than for radially symmetrical flowers.

In contrast to the radially symmetrical flowers, the bilaterally symmetrical flowers were generally rated as very complex and atypical. We can thus assume that they were difficult to recognize and categorize. Inês Bramão and her colleagues (2011) found that the recognition of non-color diagnostic objects (flowers are such objects) was facilitated when color was present. According to a number of works mentioned previously, an increase in processing fluency (the ease with which our brain can recognize objects) also increases the preference of the perceived object. This may explain the observed relative importance of color for rating the beauty of bilaterally symmetrical flowers when compared to radially symmetrical ones. It is unclear, however, why we observed this effect only in the "color-first" group and not in the "sepia-first" group.

Limitations and prospects

We have already mentioned some limitations of our study. First, we cannot overly generalize the results because the survey was conducted only on a non-representative (although quite large) sample of the Czech population. Cultural and individual differences in the evaluation of flower beauty (such as the effect of age, education or level of expertise) should certainly be explored in the future.

The display order of the stimuli (colored set first vs. sepia tone set first) influenced the beauty rating. It did not markedly affect the outcomes of most of the analyses, but the potential importance of the display order should be kept in mind when designing future studies.

Another limitation of our study was the fact that the respondents rated only photographs of single flowers. We should design an experiment in which real flowers would be rated and compare the results to those of the present study. A growing body of research shows that the human recognition and categorization of objects and entities is closely linked to, and often facilitated by, interaction with the environment through a sensory-motor activity (*Morlino et al., 2015*; *Scorolli & Borghi, 2015*; *Smith, 2005a*; *Smith, 2015b*). It would certainly be beneficial to take this into account in the research of flower beauty. We could, for example, ask people to touch the flowers or to imagine that they pick/smell/give/receive the displayed flowers and then have them rate their beauty.

The relationship between prototypicality, complexity and symmetry is worthy of greater interest, not only in the case of flowers, but also in general. Attention should also be paid to the effect of red color on the rating of flower beauty, possibly by repeating the study with a more heterogeneous set of flowers not native to the Czech Republic.

The existence of unequal preferences for diverse flower traits opens an interesting question concerning the effects of flowers and plants on human health and performance. We should explore whether the effects of flowers and plants on human well-being change with their perceived beauty.

CONCLUSION

Our research provides some empirical evidence for the evolutionary theories concerning the aesthetic evaluation of flowers. The results suggest that people share common preferences for certain flower traits. It seems that perceived flower beauty is influenced by flower color. Blue color increased and yellow decreased the perception of flower beauty, which is partially in accordance with the habitat selection theory of Heerwagen and Orians and also with the ecological valence theory. However, our results also showed that flower shape is the dominant feature in the beauty rating, substantially more important than color, and that prototypicality has a major positive effect on the perceived beauty of flowers.

APPENDIX 1. LIST OF FLOWER STIMULI

List of Flower Stimuli is available in Table 2.

Table 2 List of flower stimuli.

Scientific name	English name	Family	Pair	Symmetry	Beauty-color	Beauty-sepia	Complexity	Prototypicality	Angularity	Color
Alisma plantago-aquatica	common water-plantain	*Alismataceae*	1	radial	3.51	3.64	3.49	3.24	mixed	pink
Sagittaria sagittifolia	arrowhead	*Alismataceae*	1	radial	4.16	3.88	2.32	3.95	round	white
Anthericum liliago	st Bernard's lily	*Asparagaceae*	2	radial	4.34	4.32	1.85	4.54	sharp	white
Gagea lutea	yellow star of Bethelem	*Liliaceae*	2	radial	4.26	4.5	1.88	4.79	round	yellow
Anoda cristata	spurred anoda	*Malvaceae*	3	radial	4.23	4.33	1.78	4.88	round	purple
Linum austriacum	asian flax	*Linaceae*	3	radial	4.66	4.29	1.69	5.06	round	blue
Dianthus superbus	fringed pink	*Caryophyllaceae*	4	radial	3.93	4.06	4.81	1.98	sharp	white
Lychnis flos-cuculi	ragged-robin	*Caryophyllaceae*	4	radial	3.5	3.21	4.34	2.47	sharp	purple
Dianthus carthusianorum	carthusian pink	*Caryophyllaceae*	5	radial	4.68	4.45	2.52	4.66	sharp	pink
Mycelis muralis	wall lettuce	*Asteraceae*	5	radial	4.22	4.3	2.32	4.45	sharp	yellow
Aster alpinus	alpine aster	*Asteraceae*	6	radial	4.81	4.66	2.34	5.48	round	blue
Erigeron annuus	annual fleabane	*Asteraceae*	6	radial	4.5	4.32	2.33	5.41	mixed	white
Eruca sativa	salad rocket	*Brassicaceae*	7	radial	3.01	3.05	2.53	2.73	round	white
Lunaria annua	annual honesty	*Brassicaceae*	7	radial	3.84	3.2	1.78	4.1	round	purple
Erythronium dens-canis	dogtooth violet	*Liliaceae*	8	radial	4.05	3.76	4.25	2.7	sharp	purple
Lilium martagon alba	white Turk's cap lily	*Liliaceaea*	8	radial	4.28	4.31	3.88	3.12	mixed	white
Euphrasia rostkoviana	eyebright	*Orobanchaceae*	9	bilateral	3.81	3.78	5.07	2.15	mixed	white
Melittis melissophyllum	bastard balm	*Lamiaceae*	9	bilateral	3.29	3.12	4.37	2.42	round	pink
Anemone ranunculoides	yellow anemone	*Ranunculaceae*	10	radial	4.34	4.52	1.79	5.44	round	yellow
Fragaria viridis	wild strawberry	*Rosaceae*	10	radial	4.33	4.34	2.1	5.39	round	white
Galeopsis speciosa	large-flowered hemp nettle	*Lamiaceae*	11	bilateral	3.69	3.24	5.31	1.97	mixed	NA

(*continued on next page*)

Table 2 (*continued*)

Scientific name	English name	Family	Pair	Symmetry	Beauty-color	Beauty-sepia	Complexity	Prototypicality	Angularity	Color
Lamium maculatum	spotted dead-nettle	*Lamiaceae*	11	bilateral	3.12	2.68	5.25	1.77	round	pink
Convolvulus arvensis	field bindweed	*Convolvulaceae*	12	radial	3.85	3.91	2.18	3.77	round	white
Gentiana acaulis	stemless gentian	*Gentianaceae*	12	radial	4.88	4.21	3.15	4.15	sharp	blue
Althaea officinalis	marsh-mallow	*Malvaceae*	13	radial	4.42	4.13	2.29	4.85	round	white
Geranium palustre	marsh cranesbill	*Geraniaceae*	13	radial	4.65	4.37	1.79	5.32	round	purple
Geum urbanum	wood avens	*Rosaceae*	14	radial	4.36	4.83	3.54	4.32	mixed	yellow
Potentilla sterilis	barren strawberry	*Rosaceae*	14	radial	4.52	4.63	3.53	3.82	mixed	white
Crepis biennis	rough hawksbeard	*Asteraceae*	15	radial	4.4	4.37	2.68	5.06	sharp	yellow
Hieracium aurantiacum	orange hawkweed	*Asteraceae*	15	radial	4.59	4.15	3.55	4.38	sharp	NA
Hypericum perforatum	St John's wort	*Hypericaceae*	16	radial	4.5	4.84	2.7	4.79	mixed	yellow
Rubus fruticosus agg.	blackberry	*Rosaceae*	16	radial	3.63	3.7	2.56	4.72	mixed	white
Atropa bella-donna	deadly nightshade	*Solanaceae*	17	radial	3.44	3.59	3.68	2.86	mixed	NA
Campanula rotundifolia	harebell	*Campanulaceae*	17	radial	5.05	4.87	2.6	4.5	sharp	blue
Lathyrus tuberosus	tuberous pea	*Fabaceae*	18	bilateral	3.66	3.14	4.34	2.31	round	pink
Pisum sativum	garden pea	*Fabaceae*	18	bilateral	3.64	3.66	4.59	2.51	mixed	white
Gentiana verna	spring gentian	*Gentianaceae*	19	radial	4.82	4.12	3.15	4.02	round	blue
Silene dioica	red campion	*Caryophyllaceae*	19	radial	4.27	4.12	3.57	3.72	round	pink
Viola biflora	alpine yellow-violet	*Violaceae*	20	bilateral	3.93	3.85	3.68	2.95	mixed	yellow
Viola reichenbachiana	early dog-violet	*Violaceae*	20	bilateral	4.09	3.57	2.81	4.14	round	blue
Borago officinalis	borage	*Boraginaceae*	21	radial	4.78	4.31	3.81	3.6	sharp	blue
Swertia perennis	felwort	*Gentianaceae*	21	radial	4.34	4.27	3.92	3.19	sharp	blue
Ficaria verna	lesser celandine	*Ranunculaceae*	22	radial	4.43	4.63	2.12	5.09	mixed	yellow
Xeranthemum annuum	immortelle	*Asteraceae*	22	radial	4.7	4.44	2.33	5.02	sharp	purple

(*continued on next page*)

Table 2 (*continued*)

Scientific name	English name	Family	Pair	Symmetry	Beauty-color	Beauty-sepia	Complexity	Prototypicality	Angularity	Color
Cymbalaria muralis	ivy-leaved toadflox	*Orobanchaceae*	23	bilateral	3.5	3.04	4.9	2.23	mixed	blue
Kickxia elatine	cancerwort	*Orobanchaceae*	23	bilateral	3.21	3.04	5.47	1.64	mixed	NA
Epipactis palustris	marsh helleborine	*Orchidaceae*	24	bilateral	3.86	3.74	5.18	2.15	mixed	NA
Ophrys apifera	bee orchid	*Orchidaceae*	24	bilateral	3.7	3.5	5.28	2	round	pink
Geranium pyrenaicum	hedgerow geranium	*Geraniaceae*	25	radial	4.72	4.64	2.39	4.99	round	purple
Stellaria holostea	greater stitchwort	*Caryophyllaceae*	25	radial	4.56	4.51	2.35	4.78	round	white
Arctium tomentosum	downy burdock	*Asteraceae*	26	radial	3.6	3.12	4.48	2.43	sharp	NA
Cirsium arvense	creeping thistle	*Asteraceae*	26	radial	3.92	3.67	4.13	2.95	mixed	purple

Notes.

1, least beautiful/complex/prototypical; 6, most beautiful/complex/prototypical.

APPENDIX 2. COLOR ANALYSIS—ANOVA TABLES OF THE GENERAL LINEAR MODELS

ANOVA tables and coefficient estimates of the final reduced models are shown. The difference between the mean beauty scores of the colored and sepia tone flowers was used as the dependent variable. All effect remained significant after backward sequential correction for multiple tests. See sections 'Determination of flower traits,' 'Survey design' and 'Flower color.' for details of the explanatory variables.

Table 3 Color analysis – ANOVA table of the general linear model (all respondents).

	df	Sum of squares	*F*	*p*-value
Hue	4	1.72	11.91	<0.001
Residuals	41	1.48		

Table 4 Color analysis – coefficient estimates of the general linear model (all respondents).

	Coefficients estimate	95% CI	*t*-value	*p*-value
Intercept (hue = white)	0.025	[−0.077–0.13]	0.49	0.62
Hue = yellow	−0.20	[−0.37–0.02]	−2.35	0.024
Hue = pink	0.20	[0.026–0.38]	2.32	0.026
Hue = purple	0.22	[0.054–0.39]	2.66	0.011
Hue = blue	0.37	[0.21–0.54]	4.61	<0.001

Notes.

Residual standard error, 0.19; df, 41; adjusted R^2, 0.49; *p*-value, 1.64e–06.

Table 5 Color analysis – ANOVA table of the general linear model (respondents who first rated the sepia tone flowers).

	df	Sum of squares	*F*	*p*-value
Hue	4	1.43	10.48	<0.001
Residuals	41	1.40		

Table 6 Color analysis – coefficient estimates of the general linear model (respondents who first rated the sepia tone flowers).

	Coefficients estimate	95% CI	*t*-value	*p*-value
Intercept (hue = white)	0.046	[−0.05–0.15]	0.92	0.36
Hue = yellow	−0.19	[−0.35–0.022]	−2.29	0.028
Hue = pink	0.15	[−0.021–0.32]	1.77	0.084
Hue = purple	0.21	[0.047–0.38]	2.59	0.013
Hue = blue	0.34	[0.18–0.50]	4.30	<0.001

Notes.

Residual standard error, 0.18; *df*, 41; adjusted R^2, 0.46; *p*-value, 6.086e-06.

Table 7 Color analysis—ANOVA table of the general linear model (respondents who first rated the colored flowers).

	df	Sum of squares	*F*	*p*-value
Hue	4	2.83	17.33	<0.001
Symmetry	1	0.86	21.14	<0.001
Residuals	40	1.63		

Table 8 Color analysis—coefficient estimates of the general linear model (respondents who first rated the colored flowers).

	Coefficients estimate	95% CI	*t*-value	*p*-value
Intercept	−0.039	[−0.15–0.073]	−0.71	0.48
Hue = yellow	−0.23	[−0.41–0.047]	−2.54	0.015
Hue = pink	0.17	[−0.034–0.37]	1.68	0.10
Hue = purple	0.29	[0.11, 0.47]	3.19	0.0028
Hue = blue	0.46	[0.29–0.64]	5.32	<0.001
Symmetry = bilateral	0.38	[0.22–0.55]	4.60	<0.001

Notes.

Residual standard error, 0.20; *df*, 40; adjusted R^2, 0.66; *p*-value, 2.37e-09.

APPENDIX 3. SHAPE AND COLOR ANALYSIS—ANOVA TABLES OF THE GENERAL LINEAR MODELS

ANOVA tables and coefficient estimates of the final reduced models are shown. The mean beauty score of the colored flowers was used as the dependent variable. All effect remained significant after backward sequential correction for multiple tests. See 'Determination of flower traits,' 'Survey design' and 'Beauty scores and flower traits. for details of the explanatory variables.

Table 9 Shape and color analysis—ANOVA table of the general linear model (all respondents).

	df	Sum of squares	*F*	*p*-value
Prototypicality	1	7.48	96.37	<0.001
Hue = blue	1	1.18	15.20	0.00030
Angularity = sharp	1	0.61	7.88	0.0072
Residuals	48	3.72		

Table 10 Shape and color analysis—coefficient estimates of the general linear model (all respondents).

	Coefficients estimate	95% CI	*t*-value	*p*-value
Intercept	2.84	[2.58, 3.11]	21.74	<0.001
Prototypicality	0.31	[0.24, 037]	9.30	<0.001
Hue = blue	0.35	[0.14, 0.56]	3.33	0.0017
Angularity = sharp	0.25	[0.07, 0.43]	2.81	0.0072

Notes.

Residual standard error, 0.28; *df*, 48; adjusted R^2, 0.70; *p*-value, 4.53e-13.

Table 11 Shape and color analysis—ANOVA table of the general linear model (respondents who first rated the sepia tone flowers).

	df	Sum of squares	*F*	*p*-value
Prototypicality	1	8.15	100.96	<0.001
Hue = blue	1	1.085	13.44	<0.001
Angularity = sharp	1	0.62	7.68	0.0079
Residuals	48	3.87		

Table 12 Shape and color analysis—coefficient estimates of the general linear model (respondents who first rated the sepia tone flowers).

	Coefficients estimate	95% CI	*t*-value	*p*-value
Intercept	2.80	[2.53–.069]	20.99	<0.001
Prototypicality	0.32	[0.25–0.39]	9.56	<0.001
Hue = blue	0.33	[0.12–0.55]	3.11	0.0032
Angularity = sharp	0.25	[0.069–0.43]	2.77	0.0079

Notes.

Residual standard error, 0.28; df, 48; adjusted R^2, 0.70; p-value, 3.13e-13.

Table 13 Shape and color analysis—ANOVA table of the general linear model (respondents who first rated the colored flowers).

	df	Sum of squares	*F*	*p*-value
Prototypicality	1	5.66	78.85	<0.001
Hue = blue	1	1.54	21.52	<0.001
Angularity = sharp	1	0.47	6.60	0.013
Residuals	48	3.44		

Table 14 Shape and color analysis—coefficient estimates of the general linear model (respondents who first rated the colored flowers).

	Coefficients estimate	95% CI	*t*-value	*p*-value
Intercept	2.96	[2.71–3.22]	23.56	<0.001
Prototypicality	0.26	[0.20–0.33]	8.29	<0.001
Hue = blue	0.41	[0.21–0.61]	4.10	<0.001
Angularity = sharp	0.22	[0.047–0.39]	2.57	0.013

Notes.

Residual standard error, 0.27; df, 48; adjusted R^2, 0.67; p-value, 2.86e-12.

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APPENDIX 2

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RESEARCH ARTICLE

Habitat selection and human aesthetic responses to flowers

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Abstract

Although the aesthetic appreciation of flowers is a well-known aspect of human behaviour, theories explaining its origin are missing. The only exception is the evolutionary theory of Heerwagen and Orians. Surprisingly, it has not yet been empirically tested. The authors suggest that humans aesthetically respond to flowers because they signal food availability. The logic of the theory implies that fruits are more reliable and direct food availability signals than flowers. Therefore, fruits should elicit stronger aesthetic responses than flowers. To test this assumption, we performed two online studies in the Czech Republic. The participants ($n = 2792$ and 744, respectively) indicated on a six-point scale their aesthetic response to photographs of 14 edible Czech plant species (study A) and 20 edible plant species from the African savannas (study B), varying in growth stage (flowering, fruiting). We found no difference between the Czech fruiting and flowering plants and a stronger aesthetic response to African flowering plants. A third study ($n = 817$) confirmed that flowers were preferred to fruits, using a forced-choice paradigm. Our results suggest that the theory cannot fully explain human aesthetic responses to flowers. We discuss alternative explanations. This topic deserves renewed attention from researchers working in related fields.

Keywords: evolutionary aesthetics; habitat selection; flower preference; perception of flowers

Media summary: Contrary to the assumptions of the habitat selection theory, flowers elicit stronger aesthetic responses than fruits.

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 appreciation of flowers in many different cultures and historical periods. Some authors consider the tendency to aesthetically appreciate plants and flowers as probably common to humans as a species and related to biotope choice (Appleton, 1996; Eibl-Eibesfeldt, 1989; Kellert, 1995; Wilson, 1984). One might ask why this behaviour evolved.

Terminological note: In this paper, following Renoult (2016), we call the mental process by which a rater decides where to place a stimulus on a rating scale from ugly to beautiful an *aesthetic evaluation*. We use the term *aesthetic preference* or just *preference* when a rater compares the attractiveness of two stimuli in terms of their beauty. By *aesthetic response*, we mean the result of an aesthetic evaluation (for example, the score a rater gave to a stimulus on a rating scale). Berlyne (1971) and Ulrich (1983, 1986) described the term *aesthetic response* as a preference or a like–dislike effect in association with pleasurable feelings caused by visual exposure to a stimulus, i.e. a focus predominantly on emotions and affects. Our definition is broader because the aesthetic evaluation that precedes the aesthetic response also includes perception and cognition (Redies, 2015; Renoult & Mendelson, 2019). This definition also corresponds well with the habitat selection theory (described in detail later in the paper). This theory states that environmental stimuli trigger perceptual, cognitive and emotional processes that lead to adaptive responses (Orians & Heerwagen, 1992). Although measurements of the aesthetic response might be performed using different scales (such as like–dislike or beautiful–ugly), such choices do not lead to significantly different results; the scales are highly correlated (Ulrich, 1986; Zube et al., 1975).

Some of the proponents of evolutionary aesthetics link the aesthetic response to function and adaptive value (Voland & 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 (Ruso et al., 2003; Thornhill, 2003; Ulrich, 1986). Therefore, emotional responses to beauty and ugliness should represent an adaptive reaction to potentially beneficial or harmful situations because they are very rapid and strong motivators of human behaviour (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 et al., 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 adaptive approach to evolutionary aesthetics in their theory of habitat selection (Heerwagen & Orians, 1995; Orians & Heerwagen, 1992). The theory incorporates environmental cues crucial for our ancestors' survival – 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 behaviour (e.g. the presence of a lake). The authors also argue that because a suitable habitat has to fulfil 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 localise different types of resources. Thus, paying attention to flowers had adaptive value because it improved human functioning in natural environments (Orians & Heerwagen, 1992).

In their latter work, the authors emphasise a more direct link between flowers and food. They describe flowers as a potential food source, rich in nitrogen compounds and relatively free from toxins (compared with other plant parts). Furthermore, bees use pollen from flowers to produce honey, which has long been a highly appreciated natural sugar source (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, a more recent empirical study 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).

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, in recent years there has been renewed interest in the study of the aesthetics of flowers and related human–plant interactions centred on plant morphology (Elsner & Wertz, 2019; Hůla & Flegr, 2016; Oberzaucher, 2017; Wertz & Wynn, 2014a, 2014b; Włodarczyk et al., 2018). There has also been a recent call for theory- and hypothesis-driven research in ethnobotany (Gaoue et al., 2017) with an emphasis on the integration of an evolutionary approach (de Albuquerque & Hanazaki, 2009). This leads us to believe that it is necessary to further explore the proposed theoretical framework of Heerwagen and Orains as it might be hugely beneficial for the whole field if supported by empirical data.

As we described above, Heerwagen and Orians suggest that food and resource availability cues trigger aesthetic responses in humans. They argue that flowers represent such a cue, and that is why humans like them. We decided to follow the habitat selection theory's logic and compared two types of stimuli related to seasonal change and resource availability – flowers and fruits. Both cues 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 large African primates. In contrast, fruits are among the most important food sources (Heymann, 2011; Marlowe & Berbesque, 2009; Newton-Fisher, 1999; Peters et al., 1981, 1984). Fruits also usually contain large amounts of sugar and are generally nutritionally richer than flowers. On the other hand, flowers represent a fallback food for some primates (Heymann, 2011; Hogan et al., 2016), including some populations of chimpanzees (Newton-Fisher, 1999). However, research on Hadza hunter–gatherers showed that even an essential fallback food (tubers) was the least preferred of all food types (Marlowe & Berbesque, 2009).

Flowers are ephemeral when compared with fruits. A flower blooming for a week is 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 and uncertain future resource availability. In contrast, fruits are an instant, direct and strong signal of the presence of resources at a given moment and, thanks to their relatively greater longevity, in the near future (weeks). This leads us to the conclusion that, if the habitat selection theory is correct, fruits should elicit stronger responses and should be preferred more than flowers.

Surprisingly, Heerwagen and Orians do not pay much attention to fruits. They only mention ripening fruits as a positive cue related to seasonal change (Orians & Heerwagen, 1992). This might be due to the fact that the relationship between fruits and food is simple and straightforward and does not require a particular explanation in their eyes.

2. Hypothesis

Our main objective was to determine if there is empirical evidence for the theory of human aesthetic responses to flowers proposed by Gordon Orians and Judith Heerwagen (Heerwagen & Orians, 1995; Orians & Heerwagen, 1992).

We formulated a testable hypothesis:

> Plant species with edible fruits will receive a higher score on the rating scale (from very ugly to very beautiful) 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 owing to the hypothetically predominant role of women as gatherers and men as hunters in human evolutionary history (Ruso et al., 2003). This differentiation of roles between men and women already serves to explain sex differences in other aspects of human behaviour and abilities, such as orientation in space – the so-called hunter–gatherer theory of spatial sex differences (Silverman et al., 2007; Silverman & Eals, 1992).

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

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 emphasises the importance of fruits and flowers in relation to food resources, so we wanted the raters to know that the fruits were 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 with a part of the plant (photographs were taken from a distance of 0.5–1 m); and 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 minimise 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 colours.

We used non-standardised freely available photographs from the internet. In a 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 × 450 px), see Figure 1. Data from an independent study show that images from the internet can be used as a substitute for real flowers or standardised images in preference ratings. These results were already presented to an international audience (Hůla et al., 2018), but have not yet been published. We also asked 12 independent raters to indicate the correct distance for each photograph. We then replaced a few problematic photographs in cases where one of the raters judged the distance incorrectly.

All stimuli are available from 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 colour 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, two growth stages) in random order.

Table 1. A list of stimuli used in study A (Czech plants) and studies B and C (African plants)

Scientific name	Common name	Habitus	Flower colour	Flower colour group	Fruit colour	Fruit colour group
Czech plants						
Castanea sativa	Sweet chestnut	Tree	Yellow	Yellow	Green	NA
Citrus sinensis	Sweet orange	Tree	White	White	Orange	NA
Corylus avellana	Common hazel	Tree	Yellow	Yellow	Green	NA
Cornus mas	Cornelian cherry	Tree	Yellow	Yellow	Red	Red
Cucurbita pepo	Pumpkin	Herbaceous	Yellow	Yellow	Orange	NA
Fragaria vesca	Wild strawberry	Herbaceous	White	White	Red	Red
Pisum sativum	Pea	Herbaceous	White	White	Green	NA
Prunus domestica	Plum	Tree	Pink	NA	Yellow	Yellow
Prunus spinosa	Blackthorn	Shrub	White	White	Blue	Blue/black
Ribes petraeum	Rock currant	Shrub	Pink	NA	Red	Red
Rubus fruticosus	Blackberry	Shrub	White	White	Black	Blue/black
Sambucus nigra	Elder	Shrub	White	White	Black	Blue/black
Solanum lycopersicum	Tomato	Herbaceous	Yellow	Yellow	Red	Red
Vaccinium myrtillus	Blueberry	Shrub	Pink	NA	Blue	Blue/black
African plants						
Abelmoschus esculentus	Okra	Herbaceous	White, Yellow	White/Cream	Red, Brown	Red/Brown
Adansonia digitata	Baobab	Tree	White, Yellow	White/Cream	Green	Green
Annona senegalensis	African custard apple	Shrub	White, Yellow	White/Cream	Yellow, Brown	Brown/Yellow
Blighia sapida	Ackee apple	Tree	Yellow	Yellow	Red, Brown	Red/Brown
Calodendrum capense	Cape chestnut	Tree	White, Pink	NA	Green	Green
Carissa macrocarpa	Natal plum	Shrub	White	White/Cream	Red	Red/Pink
Combretum erythrophyllum	River bushwillow	Tree	Red	Red/pink	Red, Brown	Red/brown
Diospyros lycioides	Bushveld bluebush	Shrub	Yellow	Yellow	Red, Brown	Red/brown

(Continued)

Table 1. (*Continued.*)

Scientific name	Common name	Habitus	Flower colour	Flower colour group	Fruit colour	Fruit colour group
Dovyalis caffra	Kei apple	Tree	Yellow	Yellow	Yellow	Yellow
Euclea racemosa	Sea guarrie	Tree	White, Brown	Brown/yellow	Blue	NA
Garcinia livingstonei	African mangosteen	Tree	Yellow, Green	NA	Orange	NA
Grewia flava	Grewia	Shrub	Yellow	Yellow	Red, Brown	Red/brown
Kigelia africana	Sausage tree	Tree	Red, Brown	Red/brown	White, Brown	White/cream
Lagenaria siceraria	Calabash	Herbaceous	White	White/cream	Green	Green
Momordica balsamina	Balsam apple	Herbaceous	Yellow	Yellow	Orange	NA
Parkia biglobosa	African locust bean	Tree	Red	Red/pink	Green	Green
Passiflora edulis	Passion fruit	Herbaceous	Violet, white	NA	Violet, Brown	Red/brown
Syzygium cordatum	Water berry	Tree	Pink	Red/pink	Pink, Violet	Red/pink
Tamarindus indica	Tamarind	Tree	Pink, yellow	NA	Brown	Brown/yellow
Vachellia tortilis	Umbrella thorn	Tree	Yellow	yellow	Brown, Green	Brown/yellow

Note: flower/fruit colour = the colour(s) of a given species' flowers/fruits; flower/fruit colour group = the colour group to which we assigned a given species for the purpose of ANOVA.

Figure 1. Examples of stimuli. Note: (a) wild strawberry (*Fragaria vesca*) used in Study A. Left = close-up, centre = 0.5–1 m, right = whole plant, top = flowering, bottom = fruiting. (b) Examples of stimuli used in Study B. Left = Bushveld bluebrush (*Diospyros lycioides*), centre = water berry (*Syzygium cordatum*), right = balsam apple (*Momordica balsamina*), top = flowering, bottom = fruiting. (a) The photographs are public domain (CC0) except for bottom centre: 'Fragaria vesca 003.JPG' by H. Zell, licensed under CC BY-SA 3.0, and bottom right: 'Jahodník obecný', photo courtesy of Planta Naturalis. (b) From top left: 'Diospyros lycioides Desf.' by S. Rügheimer et al., licensed under CC BY-NC; 'Syzygium cordatum Hochst. Ex O. Krauss' by P. Horn, licensed under CC BY-NC; 'Momordica balsamina 002.JPG' by H. Zell, licensed under CC BY-SA 3.0; 'Diospyros lycioides', and 'Syzygium cordatum', photos courtesy of Random Harvest Nursery; 'Momordica charantia, fruit' by Katja Schulz, licensed under CC BY 2.0.

3.2. Participants

The questionnaire was in Czech and aimed at the Czech (and partly Slovak) population. However, participation was open to anybody who understood Czech. The majority of participants came from the

Lab bunnies [Pokusní králíci] community grouped around the Facebook and web pages administered by our team. Lab bunnies consist of more than 20,000 Czech and Slovak volunteers willing to participate in evolutionary psychology experiments. 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.

We excluded data from colour-blind participants as well as from all participants who showed no variance in ratings, rated fewer than 24 out of 28 photographs, or failed on both questions testing their attention, e.g. 'Please check number 2 on the scale'. Nine-hundred and seventeen participants (mean age = 35.02 ± 12.80; female = 591, male = 326) rated the close-up photographs, 921 participants (mean age = 34.31 ± 12.52; female = 630, male = 291) rated the photographs taken from 0.5 to 1 m and 954 participants (mean age = 34.27 ± 12.58; female = 625, male = 329) rated the photographs of the whole plant.

3.3. Study B – plants of the African savannas

Study B's objective was to repeat study A with an independent set of stimuli and raters. Ten months after starting the online questionnaire data collection, we replaced the photographs used in study A with 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, two growth stages). Otherwise, the setting was identical to that of Study A.

We used only close-up photographs because we found no distance-related differences in the rating of the flowering and fruiting stages in study A (see Section 4.1 of Results). 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 native to this biome.

The stimuli are available from https://figshare.com/s/3c7cb1fa138b8fab6973

We obtained data from 743 participants (mean age = 34.3 ± 13.36, female = 457, male = 286). As in Study A, we excluded data from colour-blind participants as well as from all participants who showed no variance in ratings, rated fewer than 36 out of 40 photographs or failed on both questions testing their attention.

3.4. Study C – African plants: two-alternative forced-choice method

Since the rating paradigm might dramatically impact the results, as shown, for example, in Jones and Jaeger (2019), we decided to conduct a third additional study. We used the stimuli from study B (close-ups of the plants of African savannas). However, this time, the participants did not perform aesthetic evaluations using rating scales but expressed their preference in a two-alternative forced-choice paradigm.

The photographs were displayed in pairs placed horizontally next to each other. Each pair consisted of the same plant species in the flowering and fruiting growth stage. There were 20 pairs in total. The participants answered a question: 'Which plant do you like more?' by clicking on a preferred photograph. Again, we instructed the participants to express only how they liked the plant itself, not the photograph's composition or quality.

For each participant, we randomised the display order of the pairs of photographs and the position of the photographs within each pair.

817 participants (mean age = 36.6 ± 11.6, female = 570, male = 247) completed the questionnaire. We excluded participants who rated fewer than 18 out of 20 pairs. However, there were only seven cases with any missing values in our final dataset.

3.5. Statistical analysis

We used R 3.5.1 (R Core Team, 2019) and RStudio 1.1.463 (RStudio Team, 2019) for the statistical analyses and ggplot2 (Wickham, 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 aesthetic evaluation, we compared each participant's mean rating for fruiting plants with that for flowering plants (Studies A and B). Because each participant rated the same species in two growth stages, we used a two-sided paired t-test for the comparison. We ran the test separately for each distance.

In Study C, we calculated the proportion of preferred fruiting plants for each participant. A value of 0 meant the absolute preference for flowering plants and 1 the absolute preference for fruiting plants. We used a single sample t-test to compare this proportion with the assumption that there was no difference between the preference for fruiting and flowering plants (the proportion equals 0.5). We used a pwr package (Champely, 2018) for power analysis. The sample size necessary for the determination of an effect size of 0.15 with a power of 0.9 equalled 469 in all studies (A + B, two-sided paired t-tests; C, two-sided single sample t-test). Since our research was part of a broader online survey, we waited until the survey termination and analysed all obtained data, which is why our sample size exceeded the requirements of power analysis in Studies A and B. We conducted Study C later, as an independent survey. We terminated it when we obtained a similar sample size to that in the previous two studies. 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 determine 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 coloured fruits and flowers on the preference ratings.

4. Results

4.1. Study A – Czech plants

In the close-ups, the participants liked the photographs of fruits more than the photographs of flowers (Figure 2; $t = 2.20$, d.f. = 916, p-value = 0.028, mean difference = 0.042 points, 95% CI [0.048, 0.084], Cohen's $d = 0.073$). We found higher ratings for flowers at the distance of 1 m (mean difference = −0.033 points, 95% CI [−0.066, −0.0015], $t = -2.05$, d.f. = 920, p-value = 0.040, Cohen's $d = 0.068$). There was no difference between the ratings of fruits and flowers at the 'whole plant' distance (mean difference = 0.019 points, 95% CI [−0.0059, 0.044], $t = 1.49$, d.f. = 953, p-value = 0.14, Cohen's $d = 0.048$). However, the effect sizes were very small. After correcting for multiple tests, no statistically significant differences remained. The distribution of species by the rating of their flowering or fruiting stage (only in the close-up photographs) is shown in Figure 3.

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 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, 0.5–1 m, 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-value < 0.0036, $R^2 = 0.0062$) showed that the only difference between men and women occurred at the 'whole-plant' distance, where men liked fruits slightly more than women. However, the difference was negligible (mean difference women = 0.01 points, mean difference men = 0.05 points; the maximum possible difference was 5 points).

To study the possible influence of colour on the aesthetic evaluation of flowers and fruits in our sample, we used one-way ANOVA. The mean rating for both fruiting and flowering plant species

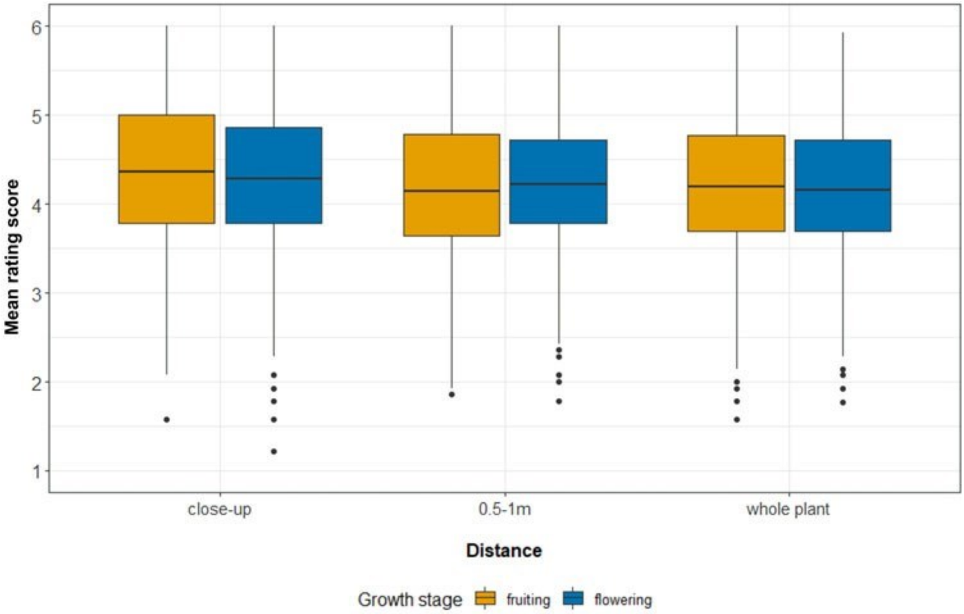

Figure 2. Differences between the aesthetic response to fruiting and flowering Czech plants. Note: *x*-axis, distance; *y*-axis, mean rating score (in points) of all plants in fruiting (orange) and flowering (blue) growth stages. The whiskers represent 1.5 interquartile range (IQR).

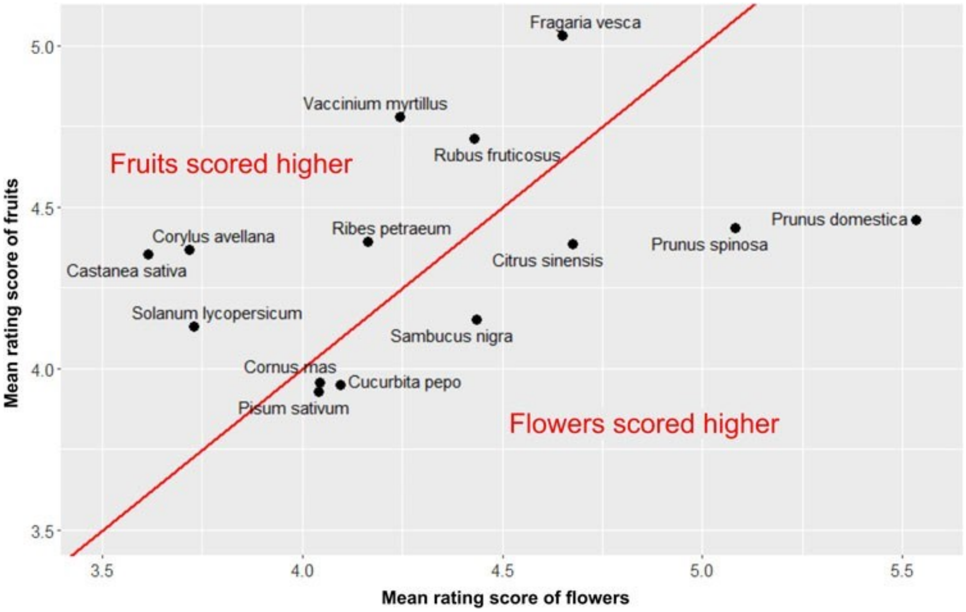

Figure 3. Scatterplot of the aesthetic response to the close-up photographs of Czech plants. Note: *x*-axis, the mean rating score of the flowering stage; *y*-axis, the mean rating score of the fruiting stage. The red line represents values where the rating scores for both growth stages are the same.

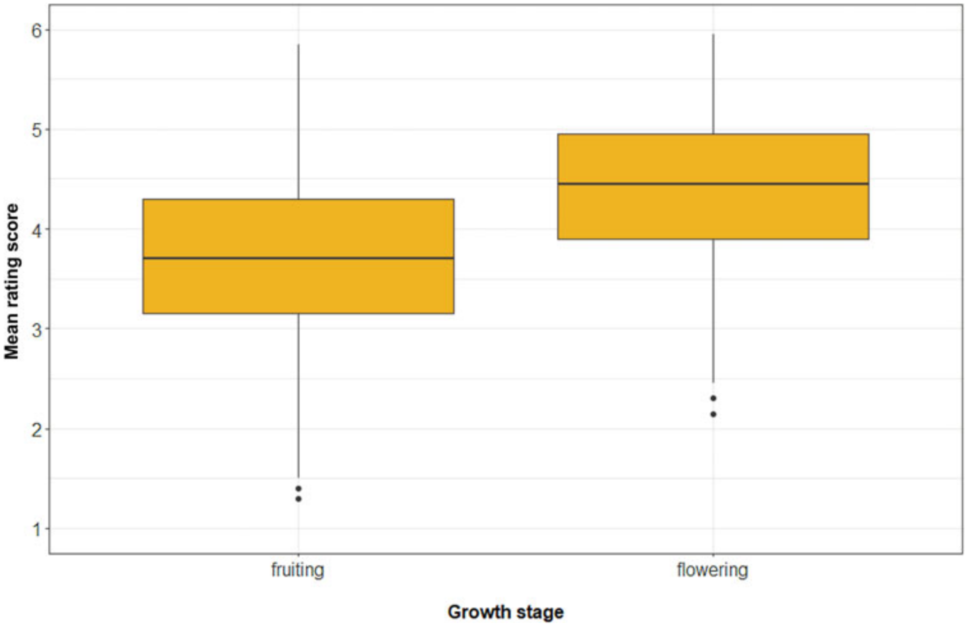

Figure 4. Differences between the aesthetic response to fruiting and flowering African plants. Note: *x*-axis, growth stage (fruiting, flowering); *y*-axis, mean rating score (in points) of all plants. The whiskers represent 1.5 IQR.

(from all respondents) served as the dependent variable, and the fruit and flower colours were the factors. This means that we analysed both fruiting and flowering plants together (analysed colours, 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. Owing to the low number of observations per group (four to six) and their unequal variances at all distances, we used Welch's ANOVAs. We did not find any statistically significant differences among colours at any of the distances. However, yellow colour 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. The difference in the ratings between the flowering and fruiting plants was clearly in the opposite direction than what we hypothesised. The two-sided paired t-test confirmed that flowering plants were liked more than fruiting plants and that the effect size was very large ($t = -33.94$, d.f. = 743, p-value < 0.0001, mean difference = −0.70 points, Cohen's $d = 1.24$; see Figure 4). The distribution of species by the rating of their flowering or fruiting stage is shown in Figure 5.

Study B – exploratory part

To explore possible differences between the ratings of women and men, we used an independent samples two-sided t-test. 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 gave flowering plants higher ratings, but this difference was more pronounced in women (mean difference women = −0.77 points, mean difference men = −0.58 points, $t = -4.58$, d.f. = 741, $p < 0.0001$, Cohen's $d = 0.35$).

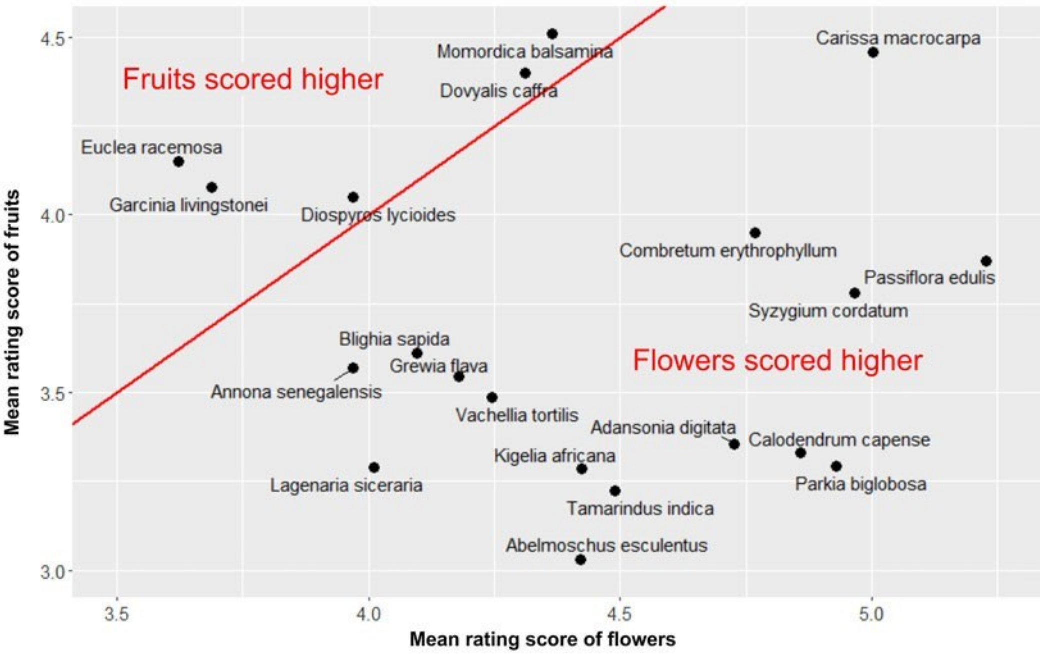

Figure 5. Scatterplot of the aesthetic response to the close-up photographs of African plants. Note: *x*-axis, the mean rating score of the flowering stage; *y*-axis, the mean rating score of the fruiting stage. The red line represents values where the aesthetic response to both growth stages is the same.

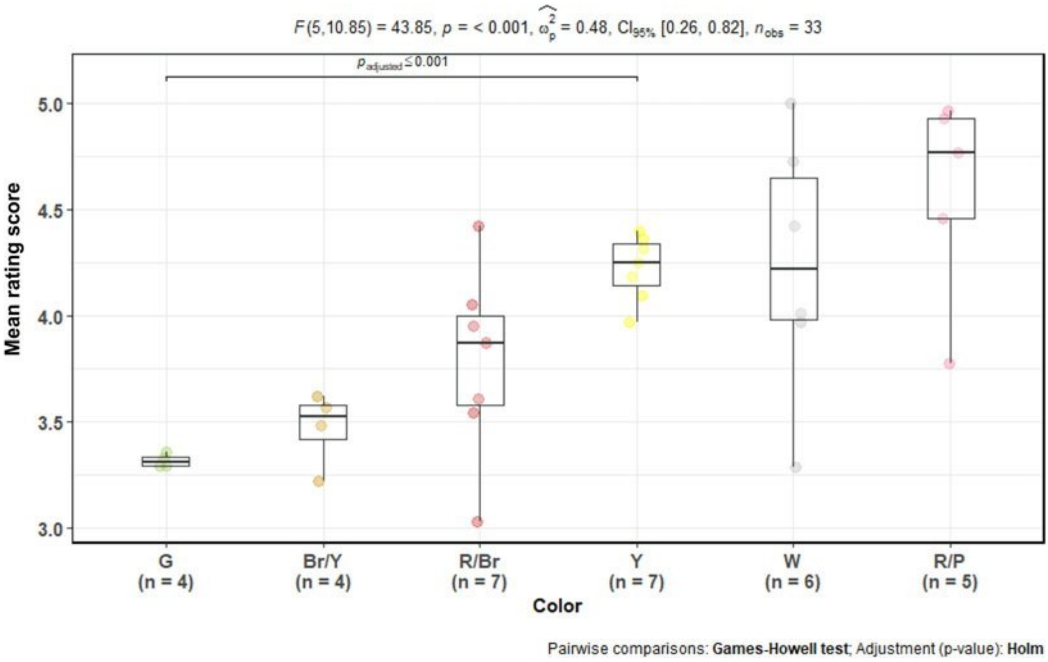

Figure 6. Aesthetic response to African plants by colour. Note: one-way Welch's ANOVA of mean rating scores of African plants with different flower/fruit colours. *x*-axis, colour groups (G = green, Br/Y = brownish yellow, R/Br = brownish red, Y = bright yellow, W = white or cream, R/P = red or pink). *y*-axis, mean rating score of all plants (in points). The coloured dots represent each plant species (flowering and fruiting stages of the same species are represented as separate dots).

To test the effect of colours on aesthetic evaluations, 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 analysed flowers and fruits rarely had a basic colour, so we identified several colour groups: green, reddish-brown, brown/yellow, red/pink, white/cream, yellow. We excluded seven photographs from the analysis because of their unique colour or colour combination. The model showed that there were statistically significant differences between colours ($F_{5,\ 10.85} = 43.85$, p-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 colours, where yellow had a higher rating. However, a clear trend showed that green and brownish yellow were among the least liked colours and pink and pure red among the most liked (Figure 6).

4.3. *African plants: two-alternative forced-choice method*

The single sample t-test showed that the proportion of preferred fruiting plants was significantly lower than the theoretical assumption of 0.5. The effect size was very large (mean proportion of preferred fruiting plants = 0.36, 95% CI [0.35, 0.37], $t = -23.885$, d.f. = 816, $p < 0.0001$, Cohen's $d = 0.84$). Participants in our dataset thus strongly preferred flowering plants over fruiting plants of the same species.

5. Discussion

We have divided the discussion into several sections. First, we briefly summarise the most important results, then we discuss the possible effect of the raters' familiarity and knowledge of the presented plants, a possible effect of the different colours and shapes of the stimuli, and cultural influences. In the general discussion, we place our findings into a broader theoretical context.

5.1. *Summary of results*

Contrary to the assumptions we derived from the simple variant of the habitat selection theory proposed by Heerwagen and Orians, respondents rated Czech fruits and flowers as almost equally attractive. The lack of any observed difference between flowers and fruits is not surprising for the whole plant photographs. In some cases, it might be problematic to distinguish flowers from fruits from such a distance. In contrast, at the other two distances (close-ups and 0.5–1 m), flowers and fruits were easily recognisable.

In Study B (African plants), participants rated fruits as much less attractive than flowers. The mean difference was equal to 0.70 points, and the effect size was very large (Cohen's $d = 1.24$).

In Study C (African plants – forced-choice), we confirmed the results from Study B on an independent set of raters and using a different display paradigm that tested explicitly for preference (choosing what one likes more). We observed a strong preference for the flowering stage (Cohen's $d = 0.84$).

The absolute rating scores of flowering and fruiting plants across Studies A and B are worth a look. We can see that the mean ratings of flowering plants were very similar for both Czech and African plants (4.30 and 4.41, respectively) but differed for fruiting plants (4.34 and 3.71, respectively; see also Figures 2 and 4). The mean rating of fruiting plants was much lower in the case of African species. Of course, one has to be cautious in drawing any conclusions from such a comparison. Although the display paradigm and rating scales were identical in both studies, they differed in stimuli, raters and the ratings' variance. On the other hand, the difference in variances was still acceptable (Study A – close-ups: var flowers = 0.91, var fruits = 0.89; Study B: var flowers = 0.64, var fruits = 0.67).

5.2. A possible effect of familiarity and knowledge of plants

Edibility

The stimuli in Study A represented edible fruits commonly grown or known in the Czech Republic. Although we did not explicitly ask the raters about their familiarity with each of the displayed plants, we can assume that the vast majority of participants knew that the displayed fruits were safe to eat and tasty. However, although all African species displayed in Study B (and C) had edible fruits, they were almost certainly unknown to most of the Czech raters. A study conducted on the geographically and culturally very close Slovak population found that children could not distinguish unknown fruits' toxicity and that this inability did not improve with age (Prokop & Fančovičová, 2014). Such uncertainty about the edibility of African fruits could have accounted for their lower rating.

Familiarity

The respondents' general familiarity with the stimuli might influence their ratings. Many studies have reported a positive correlation between familiarity and the aesthetic responses to various objects (for review, see, for example, Bornstein, 1989). Some studies also found this effect on environmental preference (Balling & Falk, 1982; Pedersen, 1978). However, more recent research suggests that the preference for familiarity differs across object categories. For example, Park et al. (2010) performed a series of experiments and found a preference for familiarity in faces, a preference for novelty in natural objects and scenes (including flowers), and no preference related to familiarity or novelty in geometric figures. It is thus uncertain whether familiar or unknown flowers and fruits should be preferred. Nevertheless, both flowers and fruits in Study B (African plants) were most probably unknown to the raters. Hence, familiarity could not account for the different ratings of African flowers and fruits. However, it might influence the ratings of the Czech sample. We can assume that Czech people easily identified the displayed fruits because they commonly buy and eat them. The raters' familiarity with the plants' flowering stages was probably lower since not everyone is interested in gardening or walks in nature.

Odour

Odours associated with the stimuli might also play some role in the ratings. Scents and pictures seem to exhibit interactive effects on sensory imagery (Lwin et al., 2010). For example, Koubaa and Eleuch (2020) showed that visually induced olfactory imageries influence taste perception and food consumption.

Flowers are usually associated with pleasant odours, which could influence the raters. On the other hand, the results of the studies mentioned above were obtained by working with specific scents that could be easily attributed to their source (such as rose and lavender in the case of flowers, vanilla, and chocolate of other stimuli). It would be challenging to associate most of the flowering plants in our research with their specific scents. We remind that the African species were almost certainly unknown to the raters. In the Czech plant sample, only two species had fragrant flowers (*Citrus sinensis* and *Sambucus nigra*). However, many of the fruits in the Czech sample (if not all) had a distinct and pleasant scent, known to the raters (such as blueberries, strawberries, plums and oranges). Thus, we can assume that if there was any effect of olfactory imagery on the ratings, it was probably in favour of fruits in Study A. It is questionable whether a general assumption that 'flowers smell nice' might affect the unknown plants' ratings in Studies B and C.

Prototypicality

In general, people prefer high levels of prototypicality, which is a measure of how representative an object is of a category (Reber et al., 2004; Whitfield & Slatter, 1979; Winkielman et al., 2006). It is difficult to objectively compare the levels of prototypicality of flowers and fruits. Both flowering and fruiting plants in our samples probably contained species with various levels of prototypicality.

5.3. A possible effect of colour

Another factor that could possibly influence the stimuli's rating was the colour of the flowers and fruits. Even though we tried to assure an equal distribution of the same colours between fruits and flowers, we were severely limited by the fruits' required edibility. This resulted in a relatively higher distribution of blue and red among fruits and yellow and white among flowers in our Czech stimuli set. The colours were more evenly distributed in African plants, but there were more brownish colours among African fruits (see Table 1). Previous research on flowers found that blue was the most and yellow the least liked flower colour (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 colours in general (Camgöz et al., 2002; Palmer & Schloss, 2010). Therefore, we can assume that if the colour of a stimulus influenced its rating, it should have been in favour of fruits in the case of Czech plants because they had a higher proportion of generally appealing colours. However, when we performed ANOVA to distinguish whether there were any differences in the ratings of differently coloured stimuli, we found no significant difference between colour 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 Figure 6). This difference between green and yellow stimuli is also interesting. As we already discussed in various parts of this paper, yellow is considered one of the least favourite colours in general and one of the least liked flower colours. This might mean that the observed difference is not due to the stimuli's colour but rather due to their type (flower vs fruit). Moreover, previous research found that in the case of flowers, colour played only a minor role in their overall attractiveness; shape properties were the most important (Hůla & Flegr, 2016).

5.4. A possible effect of shape properties

Some literature suggests that in general, people prefer shapes with several axes of symmetry (Tinio & Leder, 2009), round contours (Bar & Neta, 2006, 2007; Leder et al., 2011; Silvia & Barona, 2009; Westerman et al., 2012) and medium levels of complexity (Akalin et al., 2009; Enquist & Johnstone, 1997; Reber et al., 2004). As with prototypicality mentioned above, it is difficult to compare the levels of complexity across flowers and fruits objectively. However, in both our samples, the fruits were usually rounder and had more axes of symmetry than the flowers.

5.5. Cultural influences

Habitat selection theory considers the human aesthetic appreciation of flowers to be adaptive. However, some authors, such as Jack Goody (1993), try to explain human aesthetic responses to flowers by a combination of cultural and environmental factors.

According to Goody, extensive aesthetic interest in flowers appeared with the dawn of advanced agriculture, which brought the possibility to accumulate and store food surpluses and led to the formation of highly stratified societies. The people at the top of the societal hierarchy had enough food and wealth to pursue new, non-utilitarian activities and to develop a 'culture of luxury'. Flowers started to be domesticated, cultivated in ornamental gardens and used as luxury items for the rich, as motifs in visual arts, and during various ritual ceremonies (pp. 18, 415). However, Goody distinguishes the complex aesthetic appreciation of cultivated flowers from a simple aesthetic interest in wildflowers, the former being a product of advanced agriculture, while the latter not (p. 20).

Goody is especially intrigued by the striking lack of interest in both wild and cultivated flowers among Sub-Saharan African cultures. He points out that these societies are very socially homogenous and often practise simple hoe agriculture. However, this would only explain their lack of interest in cultivated flowers. For this reason, Goody further hypothesises that environmental factors play a role, namely the somewhat surprising absence of wildflowers in Africa's forests and savannas (pp. 13–14, 19). An environmental explanation for different cultural attitudes towards flowers was also proposed, for example, by Komárek (2009).

Nevertheless, Goody soon adds that even environmental factors are not a sufficient explanation. For example, the Barasana people from the flower-rich Amazon region in South America do not like wildflowers. He proposes that, in some cases, people deliberately rejected flowers, such as for religious reasons, but he is not sure whether this also occurred in Sub-Saharan Africa (pp. 20, 24).

What Goody describes as a *total* lack of interest in flowers is rather a *relative* lack of interest. In other words, Goody describes quantitative differences in the aesthetic interest in flowers, not qualitative differences. This is nicely illustrated in his description of the Barasana people. Goody quotes the observation of Stephen Hugh-Jones that the Barasana people are 'totally uninterested in wildflowers'. However, in the very next sentence, he writes that they use wildflowers as body decoration, usually wearing them as earrings or over the ear (p. 20).

As for environmental factors, there are non-agricultural societies living in areas where flowers are scarce, yet they still find aesthetic value in them. For example, the traditional Inuit societies of the arctic part of the Nunavut region of Canada use flowers as decorations (Norton, 2019). Nomadic Bedouin tribes in the deserts of southern Israel use intricate decorative floral motifs in their traditional embroidery (Fouze & Amit, 2019). The same applies to the traditional clothes of the Sámi people of northern Scandinavia (KulturIT, 2020 refers to the online depository of historical photographs and items from Scandinavian museums).

There have been observations of extremely flower-loving hunter–gatherer societies, such as the Lanoh people living in the mountains of Malaysia's upper Perak region. Flowers appeared as their most common decoration and in their origin myths (Evans, 1913, pp. 71, 159, 169). Flowers also play a role in the most important traditional head-hunting rituals of the Puyuma people in Taiwan (Cauquelin, 1991, p. 144). Some Micronesian societies were socially homogenous and without advanced agriculture, yet flowers were a vital part of their culture (Linton, 1926, pp. 64–67). Furthermore, flowers were used during burials in pre-agricultural societies (Nadel et al., 2013) and possibly even among the members of *Homo neanderthalensis* (Solecki, 1975), but see Sommer (1999).

These examples are not exhaustive. They only illustrate that an aesthetic appreciation of flowers appears even in extreme environments and that non-agricultural societies can also develop a complex and rich 'culture of flowers'. Flower-loving agricultural societies appeared independently in the Middle East, Eastern Asia and Central America. It seems improbable that all three cultures would independently choose flowers as their prominent aesthetic luxury items without any previous tendency towards their appreciation.

To conclude, we think it would be premature to say that the aesthetic appreciation of flowers is a purely cultural phenomenon. It is conceivable that there is an evolved universal tendency to appreciate flowers aesthetically, but that this tendency differs in the extent of its manifestation across cultures. The theory of Orians and Heerwagen tries to shed some light on the origin of this underlying tendency.

5.6. General discussion

We can summarise that if there was any influence of shape, colour or edibility on the aesthetic responses to fruits or flowers in our sample, it was probably in favour of fruits in Study A (Czech plants). Still, the fruits and flowers in this study were rated similarly.

In Study B and C (African plants), the raters' unfamiliarity with the fruits and the higher number of fruits with a less liked green colour might have lowered their rating. However, the flowers were equally unknown to the raters, and they also featured some of the generally least attractive colours (yellow). Moreover, the preference for flowers was so overwhelming that it could not have been caused only by the differences in colours. For example, when we removed the photographs with the least preferred and predominantly fruit colours – green and brownish yellow (seven fruits and one flower) – and then compared the mean ratings for all flowers and fruits again, the difference was still substantial: 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 cues of resource availability. From this point of view, once flowers and fruits are distinguished from other types of objects, their colour or shape should not be that important.

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 food availability 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. It might be more beneficial to 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 is 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 timescales 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. However, positive seasonal changes are not related solely to flowering plants, but also with the change of weather and temperature, the migration and awakening of animals, and especially with the growth of fresh leaves and other green parts of plants. This complex of environmental changes undoubtedly triggers human aesthetic feelings. Nevertheless, we think that a single cue (flowers) is a weaker stimulus than fruits. Fruits represent some of the most important human food sources, and they too serve as indicators of other resources and seasonal changes (although possibly not as strongly as flowers).

Flowers that try to attract pollinators are generally considered conspicuous. A general assumption is that they are probably more conspicuous than fruits. This might be correct, but to our knowledge, there is no work that would compare the conspicuousness of flowering and fruiting plants. Flowers are more numerous than fruits (because not all flowers survive until the formation of fruits), and they sometimes appear before leaves. However, fruits are usually larger than flowers and sometimes remain on plants even after the leaves fall. Many plant species use animals for seed dispersal, so they also need to attract them. Many primates (including humans), as frugivorous organisms, should be adapted to localise fruits effectively. Some authors suggest that primates' trichromatic vision evolved as an adaptation to distinguish ripening fruits from their background (Osorio & Vorobyev, 1996; Párraga et al., 2002; Regan et al., 2001; Sumner & Mollon, 2000). Moreover, in Study A, raters also evaluated photographs of the whole plants. The difference in the overall conspicuousness of flowering and fruiting plants should be very important in this case, especially when it was quite difficult to distinguish flowers from fruits at such a distance. Still, we observed no differences in the aesthetic response. Therefore, it is not certain that flowers are favoured over fruits because of their conspicuousness.

The fact that we found a stronger aesthetic response (Study B) and preference (Study C) 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 related to the supposed ancestral environment (although its localisation to African savannas has been widely criticised). Another explanation is that fruits are more context-dependent than flowers during aesthetic evaluation. Redies (2015) nicely illustrated the importance of context. In his model of visual aesthetic experience, he distinguishes stimulus processing in perceptual and cognitive channels. The perceptual channel focuses on the object's physical properties (such as shape or colour), while the cognitive channel operates with contextual information (such as familiarity or prototypicality). Aesthetic experience usually occurs when there is an appropriate response in both channels. Emotional processing can further modulate the extent of aesthetic experience. It seems that flowers have a strong *aesthetics of perception*, whereas fruits rely more on the *aesthetics of cognition*. In other words, flowers might be attractive for their appearance and fruits for what they mean. However, it remains an open question why flowers should be preferred on the perceptual level. It is possible that the information processing of flower stimuli has greater efficacy (maximising information transmission) and efficiency (information processing at low metabolic costs) than that of fruit stimuli. In such a case, the aesthetic response to flowers might be a by-product of processing bias (see Renoult and Mendelson, 2019 for details about this concept of information processing). Therefore, it would be highly beneficial to study possible differences between flowers and fruits from the perspective of information processing.

It is also possible that aesthetic responses towards flowers are not a human adaptation or even a purely cultural phenomenon. On the contrary, it could be an ancestral trait that humans share with other primates. As mentioned above, flowers are nutritionally important for some primate species.

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 cues of resources and the aesthetic responses towards them does not exist. Such a connection most likely plays some role in the aesthetic response to both flowers and fruits. The link to fruits is simple and straightforward because they are considered as food. Our results support this notion because the familiarity with fruits and knowledge about their edibility probably played an important role in their rating. On the other hand, the connection between flowers and resources is more intricate. Our data show that other factors probably exist that further enhanced the attractiveness of flowers throughout human evolution; as we discussed, cultural differences and information processing might be among them.

6. Limitations and future directions

We used photographs in this study because it was impossible to display real plants in the flowering and fruiting stage simultaneously. However, the use of photographs is widespread in this type of research, and our previous results showed no substantial differences between the rating of real flowers and that of their photographs. Nevertheless, 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 colours and shape properties of flowers and fruits.

It would undoubtedly be beneficial to repeat the study with different stimuli to ensure that the results were not mere artefacts owing to some unknown methodical error.

Cultural aspects certainly modify human attitudes towards flowers. The study should be repeated in other cultures, especially non-agricultural ones, to reveal to what extent our results are culture-dependent. Even among agricultural societies, there might be differences that influence their aesthetic responses to flowers and fruits, such as religion, educational system, traditions, landscape, etc. We cannot generalise our conclusions based on studies performed on a single society. We would like the readers to consider this paper as a mere first step that should draw their attention to this issue and encourage further research.

Future research should also focus on other factors that might account for human attraction towards flowers, especially efficacy and efficiency in information processing. We should explore whether such attraction is only a by-product of generally preferred shapes and colours or whether there are some characteristics (or their combinations) unique to flowers that make them beautiful to human eyes. We should also explore the role of cognitive processing (context) in the aesthetic evaluation of flowers and fruits, for example, by using a mixture of known and unknown or edible and poisonous stimuli.

7. Conclusion

The habitat selection theory of Heerwagen and Orians offers an attractive yet never empirically tested explanation for the origin of human aesthetic appreciation of flowers: the relation of flowers to food and resource availability. Our data imply that human aesthetic responses to flowers cannot be explained solely by this factor, although it might play some role. However, we urgently need data from a broader cultural sample to confirm our limited findings. The question of why humans tend to aesthetically appreciate flowers seems to remain partly unexplored. The habitat selection theory proposes a basis for further investigations of other factors, such as information processing, 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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Data availability. The data associated with this research are available at https://doi.org/10.6084/m9.figshare.11956632.v1

Author contributions. MH and JF conceived and designed the study. MH and JF conducted data gathering. MH performed statistical analyses. MH wrote the article.

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Conflict of interest. Martin Hůla and Jaroslav Flegr declare none.

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APPENDIX 3

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Does Flower Preference Differ Across Cultures? A Study of Czech and Kenyan Populations

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Despite the ubiquity of floral themes and motifs in art and culture, human esthetic responses to flowers remain a largely unexplored area of research. Our previous studies revealed that Czechs, irrespective of gender, age, education, or level of expertise, display very similar esthetic responses to flowers of diverse shapes and colors, that is, they like and dislike the same flowers. We wanted to explore further whether these findings are culturally or ecologically dependent. This study compares the flower preferences of the inhabitants of two culturally, geographically, and ecologically highly distinct countries—Czechia ($n = 54$ and $n = 48$) and Kenya ($n = 54$). We asked each subject to rank photographs of 40 species of Czech flowers from the most liked one to the least liked one. We then computed the mean ranking of each flower species in the Kenyan and Czech samples and compared them. We found a very strong positive correlation ($r = .79$ and $r = .77$) between the samples, suggesting that Czechs and Kenyans prefer the same flowers. This concordance was unexpected, especially given the small sample sizes and the large differences between them. Moreover, the Czech flower species used as stimuli were probably familiar to Czechs but unknown to Kenyans. Thus, our results suggest that cultural and individual factors might play only a minor role in flower preference, whereas more general inborn preferences may be more important.

Keywords: aesthetic responses to flowers, flower preference, phytophilia, cross-cultural study

For many years, the human esthetic response to flowers has been a largely neglected topic. Floral motifs are common in art and design. Flowers are appreciated for their ornamental and decorative function and play an important role in many social situations. Nevertheless, we still have limited knowledge about which flowers are generally preferred, which flower traits elicit stronger esthetic responses than others, and how time- or culture-dependent the preferences are.

To date, most studies concerning flower preference have been focused on customer experience and have mainly been used for marketing purposes (Boumaza et al., 2010; Grygorczyk et al., 2019; Santagostini et al., 2014; Wang et al., 2017; Yue & Behe, 2010). This is not surprising given the fact that global floral sales reach more than €15 billion per year (Mamias, 2018). However, these studies typically combine broadly defined flower traits, such as size or color, with purely commercial traits, such as price or packaging. Moreover, they often target at a single flower species. Therefore, these studies are not very informative when we seek to examine general esthetic responses.

In our previous research, we tried to fill in this knowledge gap. We performed a large-scale online study in which more than two thousand Czech respondents expressed their esthetic responses to various Czech wildflowers. We found a striking similarity in their responses, irrespective of age, sex, or the level of expertise of the participants. Czech respondents had stronger esthetic responses to flowers they perceived as prototypical and moderately complex. Such flowers were usually radially symmetrical. Perceived prototypicality and complexity were strongly correlated with the type of floral symmetry. Shape properties played a crucial role, whereas flower color only a minor one, with blue being the most and yellow the least preferred flower color (Hůla & Flegr, 2016). In the following years, we continued to collect data with different flowers, types of display (real flowers vs. photographs), and raters. Regardless of the experimental setting, we still found the same overall pattern of esthetic responses (data not yet published). We can thus conclude that at least in the Czech context, the esthetic responses to flowers are shared across people, and individual taste or experience do not play an important role.

The next logical step is to find out whether esthetic responses to flowers are similar across cultures. Some authors, particularly Goody (1993), claim that the esthetic perception of flowers is an entirely culturally dependent trait of human behavior. He presents examples of strongly flower-loving cultures while also mentioning some cultures that are not interested in flowers. Goody suggests that the tendency to treat flowers as esthetic objects emerged after the advent of agriculture, especially in highly stratified societies, among the highest (nonworking) classes. He also adds that there is a strong ecological factor—only those societies with an abundance of flowers in their environment are prone to place some esthetic value on them. However, there is evidence of the usage of flowers for ceremonial purposes even in prehistoric times (Nadel et al., 2013; Solecki, 1975; but see Sommer, 1999). Moreover, nonagricultural, and only weakly stratified societies across the world have traditionally used flowers and floral motifs for ornamental and decorative purposes (Cauquelin, 1991; Evans, 1913; Linton, 1926). The same

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also applies to ethnic groups living in areas very scarce in flowers, such as deserts (Fouze & Amit, 2019) or arctic regions (Norton, 2019). Therefore, contrary to Goody's assumptions, it seems that humans probably share some innate tendency to respond to flowers esthetically, whereas cultural and environmental factors only modulate the extent to which this tendency is developed.

There have been attempts to explain this tendency by describing flowers as food and resource indicators for our ancestors. Being attracted to biotopes rich in flowers would thus have increased the chance of survival for our ancestors and consequently their biological fitness, resulting in an adaptive fixation of flowers as attractive objects (Heerwagen & Orians, 1995; Orians & Heerwagen, 1992). However, a study that tried to test this theory did not provide any empirical evidence in its support (Hůla & Flegr, 2021). Flowers may also elicit esthetic responses thanks to their shape or color properties that are generally considered esthetically attractive. These properties, such as symmetry or high contrast, are easily detectable, thus helping with our orientation in space and object categorization. The increase in processing fluency, that is, the ease with which a perceiver can process objects, leads to a positive appreciation (Reber et al., 2004; Renoult & Mendelson, 2019). Familiarity is another factor that might come into play by increasing processing fluency (Song et al., 2021). It has been shown that previous exposure to stimuli leads to their greater preference (Bornstein, 1989; Zajonc, 1968). However, a more recent research finds rather inconclusive results (Leder, 2001; Montoya et al., 2017; Park et al., 2010).

As mentioned above, the most esthetically preferred flowers usually follow the assumptions one could derive from general shape preferences, such as more axes of symmetry (Tinio & Leder, 2009) or a medium level of complexity (Akalin et al., 2009; Enquist & Johnstone, 1997; Reber et al., 2004). However, to date, we have observed this pattern only in a single population (Hůla & Flegr, 2016).

Intercultural comparisons might shed some light on the factors that shape specific human esthetic responses to flowers. Are cultural background, ecological factors, or familiarity the main predictors of the most and least preferred flowers? Or are the preferences for particular shapes and colors rather innate? There exist several studies exploring intercultural comparisons of animal preferences, focusing on snakes (Frynta et al., 2011; Landová et al., 2018) and birds (Lišková & Frynta, 2013). All of these studies found a strong correlation across raters from different cultures. However, to our knowledge, no research on flowers has been conducted so far.

In this study, we take the first step by comparing two culturally, ecologically, and geographically different populations—Czechs and Kenyans. Both groups expressed their esthetic responses to a set of Czech wildflowers by ranking photographs from the most to the least beautiful. We investigated the extent of agreement and the pattern of preference between and within both groups.

Hypotheses

Based on our previous research and studies on the esthetic responses to animals, we expect to find a strong correlation between the mean ranking of flowers by Czech and Kenyan raters. However, we still expect to find some differences between the two cultures. Therefore, the correlation among Czech raters should be higher than that between Czech and Kenyan raters. The intercultural studies on animals had comparable sample sizes as our current study, and the correlations between various populations usually exceeded 0.6. On the other hand, it is difficult to extrapolate the results of esthetic rankings of snakes or birds to flowers. We are thus cautious to hypothesize about the exact correlation coefficients.

The results of our previous research on flowers allow us to formulate specific hypotheses about the shape and color preferences:

> *Hypothesis 1:* Bilaterally symmetrical flowers will be ranked worse than radially symmetrical flowers among both Czech and Kenyan raters.
>
> *Hypothesis 2:* There will only be minor differences in the ranking of differently colored flowers, with blue/violet flowers being ranked better than yellow flowers.

Material and Method

This study was approved by the institutional review board of the Charles University, Faculty of Science.

We used an in-person data collection method in this study. We asked the participants to order a set of 40 photographs of flowers from the one they liked (esthetically) the most to the one they liked the least. This approach is easily understandable to people across different cultural backgrounds and literacy levels and was successfully employed in the abovementioned similar studies on the esthetic responses to animals.

Stimuli and Display

In this study, we used some of the photographic stimuli from our previous research (Hůla & Flegr, 2016). They consisted of flower species that are native or commonly grown in Czechia (see Table 1). We tried to include the broadest diversity of colors and shapes while maintaining a reasonable number of stimuli. There were 20 pairs of flower species; each pair consisted of flowers similar in shape but differing in color. This composition of stimuli allowed us to create a more balanced sample, where flower colors were distributed across a broad spectrum of flower shapes. Since we aimed to analyze the effect of both shape and color properties on the preference, we did not want to associate particular shapes with specific colors.

We chose plant species with sufficiently big and comparable flowers (ranging from 2 to 4 cm in diameter). We avoided flowers growing in rich inflorescences so that one could easily distinguish the shape of a single flower. One exception to this rule was the members of the daisy family (*Asteraceae*) because their inflorescences are so compact that most people consider them single flowers. We resized all flowers to 3 cm and centered them. We also removed the original background from the photographs and replaced it with a neutral black one, ensuring a good contrast across different colors and unifying the viewing conditions. The original photographs had diverse backgrounds, such as green, blue, brown, or gray. For a single stimulus, we used three photographs of the same flower species from three different angles (30° to the left, en face, 30° to the right) so that the raters could adequately assess the shape of the flowers. Some species have prolonged corollas or other floral parts which are not visible from the en-face angle (see Figure 1 for examples of stimuli).

We presented each stimulus as a printed and laminated card. Each printed flower was 3 cm in diameter, and the whole card measured 13 × 4.5 cm (a detailed description of the creation and processing of the stimuli can be found in Hůla & Flegr, 2016). The whole set

Table 1

List of Flower Species Used as Stimuli

	Scientific name	Color	Color group	Symmetry	Mean Kenya	Mean Czech 1	Mean Czech 2
1	*Antirrhinum majus*	Pink	Pink	Bilateral	27.06	27.02	24.46
2	*Antirrhinum majus*	Yellow	Yellow	Bilateral	20.67	29.00	27.51
3	*Borago officinalis*	Blue	Blue/violet	Radial	15.22	16.35	13.23
4	*Calendula officinalis*	Yellow	Yellow	Radial	17.33	15.35	14.90
5	*Campanula rotundifolia*	Pink	Pink	Radial	17.98	17.06	20.10
6	*Centaurea cyanum*	Blue	Blue/violet	Radial	16.48	10.75	10.97
7	*Centaurea jacea*	Purple	Purple	Radial	25.50	23.92	25.74
8	*Cichorium intybus*	Blue	Blue/violet	Radial	16.52	12.71	11.79
9	*Cirsium palustre*	Pink	Pink	Radial	22.15	21.76	24.51
10	*Convolvulus arvensis*	Pink	Pink	Radial	21.70	19.05	23.46
11	*Crepis biennis*	Yellow	Yellow	Radial	23.26	20.65	21.05
12	*Cymbalaria muralis*	Violet	Blue/violet	Bilateral	26.02	24.94	24.13
13	*Dianthus deltoides*	White	White	Radial	14.15	16.51	18.08
14	*Dianthus carthusianorum*	Purple	Purple	Radial	16.39	15.40	11.23
15	*Dianthus superbus*	White	White	Radial	25.59	27.94	25.82
16	*Erythronium dens-canis*	Pink	Pink	Bilateral	26.72	25.24	21.46
17	*Euphrasia rostkoviana*	White	White	Bilateral	20.17	22.92	21.31
18	*Fragaria viridis*	White	White	Radial	16.15	16.76	17.64
19	*Geranium palustre*	Purple	Purple	Radial	19.17	14.89	16.21
20	*Geranium pyrenaicum*	Pink	Pink	Radial	19.46	12.54	15.23
21	*Geranium sanguineum*	Purple	Purple	Radial	14.81	18.71	17.41
22	*Impatiens glandulifera*	Purple	Purple	Bilateral	23.67	26.97	26.26
23	*Kerria japonica*	Yellow	Yellow	Radial	16.89	16.70	17.13
24	*Lamium album*	White	White	Bilateral	26.74	27.37	31.38
25	*Lamium maculatum*	Pink	Pink	Bilateral	25.83	27.56	29.08
26	*Lathyrus tuberosus*	Pink	Pink	Bilateral	19.64	21.70	22.31
27	*Lilium martagon*	White	White	Bilateral	15.83	24.68	22.87
28	*Limodorum abortivum*	Violet	Blue/violet	Bilateral	26.50	25.40	25.51
29	*Linaria vulgaris*	Yellow	Yellow	Bilateral	23.43	28.51	28.36
30	*Linum austriacum*	Blue	Blue/violet	Radial	13.93	14.65	14.28
31	*Ophrys apifera*	Pink	Pink	Bilateral	25.85	25.32	22.44
32	*Phalaenopsis* sp.	Pink	Pink	Bilateral	20.04	16.60	20.64
33	*Phalaenopsis* sp.	Purple	Purple	Bilateral	18.35	17.57	19.56
34	*Pisum sativum*	White	White	Bilateral	22.37	23.87	23.79
35	*Potentilla fruticosa*	Yellow	Yellow	Radial	20.46	15.06	14.72
36	*Santina* sp.	White	White	Radial	9.98	12.19	13.72
37	*Silene montana*	Purple	Purple	Radial	18.15	18.10	16.46
38	*Solanum lycopersicum*	Yellow	Yellow	Radial	26.11	28.05	28.28
39	*Viola biflora*	yellow	Yellow	Bilateral	21.89	21.46	20.08
40	*Viola reichenbachiana*	Violet	Blue/violet	Bilateral	20.78	18.79	16.87

Note. Color = flower color; color group = color used for the analysis of color preferences; symmetry = type of floral symmetry; Mean Kenya/Czech 1/Czech 2 = mean ranking of the species from all raters in the Kenyan/Czech 1/Czech 2 samples.

of stimuli is also available on Figshare: https://doi.org/10.6084/m9.figshare.19601911.v1.

The researcher presented to each rater the design and purpose of the study and explained that the participation is entirely voluntary, and the rater can withdraw at any time without giving a reason. Each rater gave verbal consent to take part in the study. There was no time limit for the task. Before the ranking, a researcher shuffled all 40 photographic stimuli and placed them in front of the rater. The researcher then asked the rater to "Order the flowers from the one you find the most beautiful for you personally, to the one you find the least beautiful." The rater then ranked the stimuli either by rearranging them or by forming a pile. Therefore the most preferred flowers obtained the lowest ranks and vice versa.

Participants

The participants in the Kenyan sample were random Kenyan citizens from both urban and rural areas who were asked to take part in the study by one of the researchers (Pavlína Šámalová). We only collected the most basic demographic information (gender, age, and rural/urban area of residence) because we wanted to make the experimental process as short and least burdensome as possible. We offered each participant a reward of $2 at the end of the experiment. The participants in the Czech sample were also recruited from the general public, but they were mostly students from urban areas. Unfortunately, we were not able to achieve the same demographic composition for both samples. The data collection of the Czech sample took place during the initial COVID-19 pandemic waves when traveling and in-person meetings were severely limited. However, our previous experience suggests that in the Czech population, individual differences play only a minor role in the esthetic responses to flowers.

After analyzing the Kenyan and Czech samples, we collected an additional independent Czech sample. This allowed us to gain insight into the variation in the rankings both within and across populations. For example, we could directly compare whether the

Figure 1
Examples of Stimuli

Note. The figure shows two pairs of flower species with similar shapes and different colors. It also illustrates radially and bilaterally symmetrical flowers. From the top: *Linum austriacum*, *Geranium sanguineum*, *Lathyrus tuberosus*, *Pisum sativum*. See the online article for the color version of this figure.

observed correlation between Czechs and Kenyans was comparable to the correlation between two independent Czech samples. Moreover, since approximately half of the raters in the second Czech sample consisted of professional botanists or botany students (data collection during a field excursion), we were also able to partly explore the effect of familiarity on the esthetic responses. However, we did not design the current study to test the effect of familiarity on flower preference. Therefore, we should consider any observed trends merely as an invitation for further, more rigorous inquiries.

Sample Size

The Kenyan sample consisted of 54 people (12 female and 42 male), $M_{\text{age}} = 27 + 10.8$ years. Czech Sample 1 contained 54 participants (35 female and 19 male), $M_{\text{age}} = 29 + 12.8$, while Czech Sample 2 had 48 participants (39 female and nine male), $M_{\text{age}} = 27 + 8.7$.

We were severely limited by the time allocated to the data collection in Kenya since this project was not the main purpose of the journey there. Thus, we could not increase the size of the Kenyan sample to any great extent. However, a power analysis revealed that our final data sample would be sufficient to reveal a correlation coefficient $r = .3$ or higher with a power of .8.

Statistical Analyses

The whole dataset is available on Figshare: https://figshare.com/s/a3ccb7ce64fd9f58cc4c. We used R 4.0.4 (R Core Team, 2020) and R studio 1.2.5042 (RStudio Team, 2020) for statistical analyses. We set the α level for all tests to .05. Due to the in-person collection method, there were no missing values in our data.

We visualized the ranking data via Multidimensional preference analysis and a subsequent biplot using the *mdpref* function from the package *pmr* (Lee & Yu, 2013, 2022). This technique reduces the dimensionality of the data but tries to retain their main features. It displays objects (flowers) and judges (raters) in a single plot. Each flower species is represented by a point and each rater by a vector. The projections of the points onto the vector reflect the rankings of the judge (Alvo & Yu, 2014). The points have coordinates that are the scores of the flowers on two extracted dimensions. The rater vectors start in the center of the plot and go through a point whose coordinates are the coefficients of the rater on the two extracted dimensions. The direction of the vector reflects the preference of the rater. The point which is the farthest in the direction of the vector is the most preferred by the rater. Clusters of points represent flowers with the same preference patterns across the judges. Vectors pointing in similar directions represent judges with similar preferences (SAS Institute, 2018).

To assess the absolute agreement among respondents with respect to their rankings, we used the intraclass correlation coefficient ICC(A,1) within each sample. Since we were interested in mean rankings in further analysis, we then calculated the ICC2(A,k) type of coefficient (McGraw & Wong, 1996).

We computed the mean rank of each flower species across all raters within each sample. When comparing the mean rankings between samples (two measurement variables), we used Pearson's correlation test with r as the effect size estimator. We also performed Holm–Bonferroni correction for multiple tests. We used the *paired.r* function from the R package *Psych* (Revelle, 2022) to compare whether correlation coefficients differed significantly between samples. The function performs *t* tests of the *z*-transformed *r*'s.

To explore the effect of symmetry and color on the mean ranking of flowers and their interaction with the samples of raters, we used the multifactorial analysis of variance (ANOVA) and a subsequent Tukey's post hoc test. Given the unbalanced design of our data, we performed the Type II tests. The mean ranking of each flower species served as the dependent variable, and floral symmetry (bilateral and radial), color (blue/violet, pink, purple, white, and yellow) served as the between-sample factors (each flower only has one value of symmetry and color). We used the samples of raters (Czech 1, Czech 2, and Kenya) as the within-sample factors (each flower has a mean ranking for each sample). In the exploratory part of the analysis, we proceeded analogously while exploring the interaction of symmetry and color with the familiarity of flowers.

Results

Congruence Among Raters

First, we wanted to know whether there was any agreement in the single rankings of the raters in each of our samples. The absolute agreement estimated by the ICC(A,1) was low, Kenya: ICC[A,1] = 0.12, 95% confidence interval [CI] [0.08, 0.2], $F(39, 2067) = 8.58$, $p < .0001$; Czech 1: ICC[A,1] = 0.20, 95% CI [0.14, 0.30], $F(39, 2067) = 13.8$, p ,<.0001; Czech 2: ICC[A,1] = 0.20, 95% CI [0.14, 0.30], $F(39, 2067) = 12.8$, $p < .0001$.

However, the ICC(A,k) showed a strong positive association (close to one) between the mean rankings in each set. That means that even though the absolute agreement in single ratings among raters was low, it was sensible to compare the mean ratings in further analyses, Kenya: ICC[A,54] = 0.89, 95% CI [0.83, 0.93], $F(39, 2067) = 8.58$, $p < .0001$; Czech 1: ICC[A,54] = 0.93, 95% CI [0.89, 0.96], $F(39, 2067) = 13.8$, $p < .0001$; Czech 2: ICC[A,54] = 0.92, 95% CI [0.89, 0.95], $F(39, 2067) = 12.8$, $p < .0001$.

Multidimensional Preference Analysis

To better understand the distribution of rankings, we visualized the data using the multidimensional preference analysis and a subsequent biplot. We extracted two dimensions which explained 19.3% of the variability in the Czech Sample 1, 19.5% in the Czech Sample 2, and 15% in the Kenyan sample. The plots for each set of raters show relatively similar patterns (see Figure 2). Most raters have similar preferences within each sample, although some raters differ. Raters in the Kenyan sample have less similar preference patterns than the Czech raters. Raters across samples seem to agree on which flowers are preferred and which are not (the vectors usually point toward the same species).

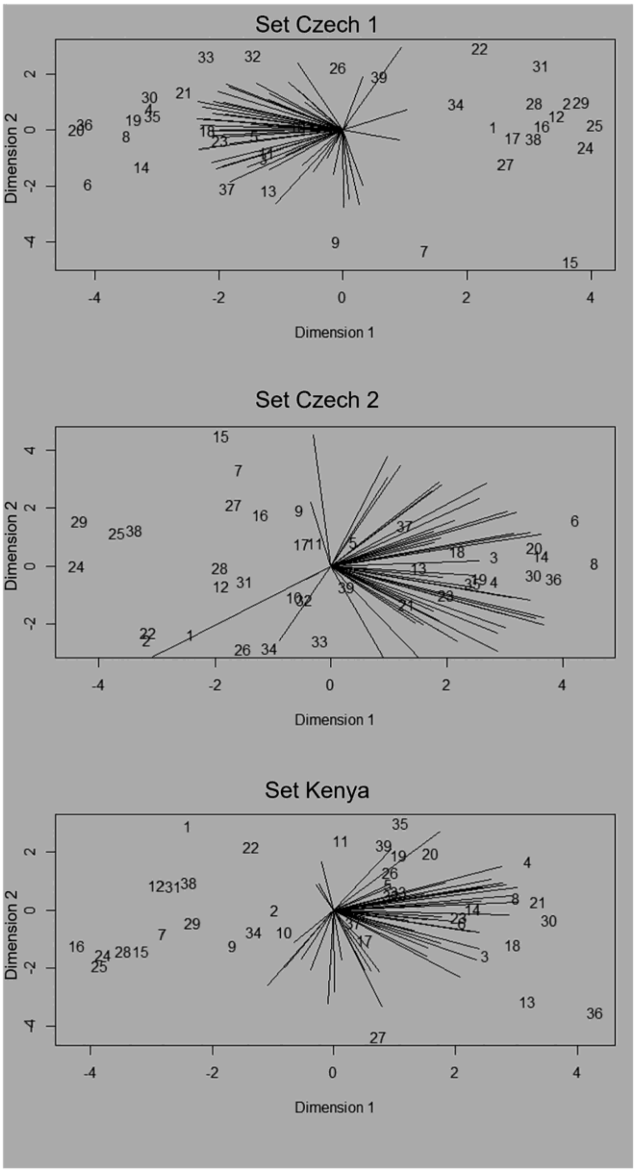
To better understand the meaning of the extracted dimensions and the clustering of the flowers, we visualized the plots in a different way, where one can see the species name abbreviations, colors, and type of symmetry (Figure 3). In the Czech Sample 1, the first dimension represents the type of symmetry. The second dimension seems to gather flowers with ragged or uneven contours at one end and with compact and smooth contours at the other. The Czech Sample 2 follows a similar pattern, although the division is less pronounced. The dimensions in the Kenyan sample are more challenging to interpret. The first dimension probably represents how close a flower is to a round, compact shape, such as a circle or sphere. The second dimension maybe show a distribution of colors (white vs. yellow). Interestingly, blue flowers tend to be clustered across samples.

Comparison of Mean Rankings Between Samples

In order to reveal if Czech and Kenyan raters ranked flowers similarly, we compared the mean ranking of each flower species between Czech and Kenyan samples. We used Pearson's correlation tests, revealing very strong positive correlations in the flowers ranking between Kenyan and both Czech samples (Kenya and Czech 1: $r = .79$, 95% CI [0.63, 0.88], $t = 7.88$, $df = 38$, $p < .0001$; Kenya and Czech 2: $r = .77$, 95% CI [0.61, 0.87], $t = 7.51$, $df = 38$, $p < .0001$; see also Figure 4). Kenyans thus ranked flowers in a similar way as Czech raters.

However, the correlation between the ranking of the two Czech samples was even higher than between Czechs and Kenyans (Czech 1 and Czech 2: $r = .92$, 95% CI [0.86, 0.96], $t = 14.67$, $df = 38$, $p < .0001$), meaning that the raters in the Czech samples agreed in their flower ranking more than Czechs and Kenyans.

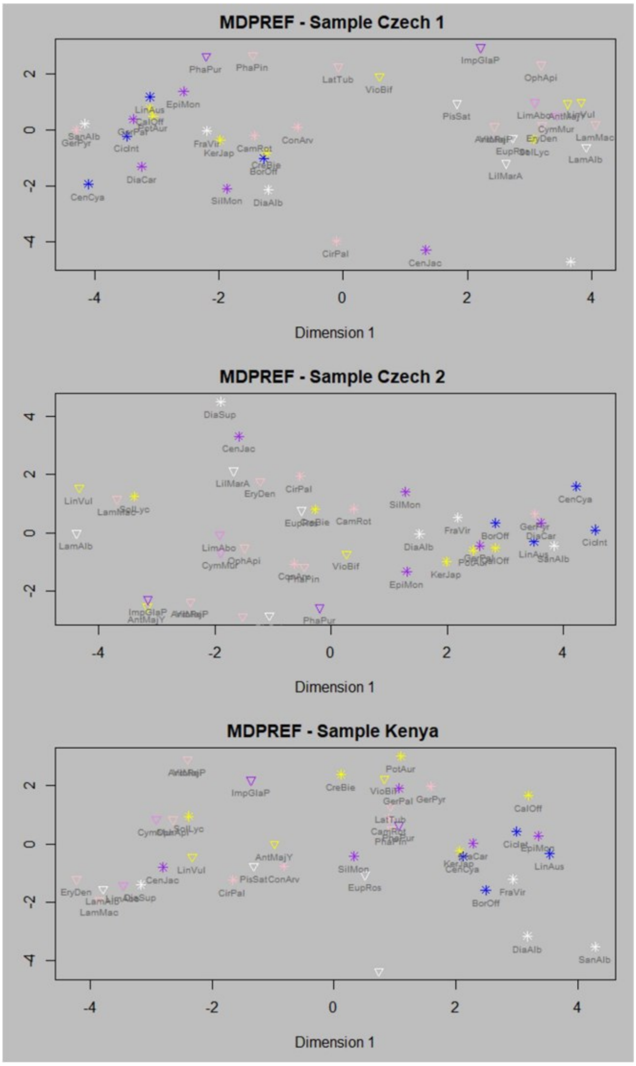
Figure 2 *The Multidimensional Preference Analysis Biplot of the Rankings of Flowers*



Note. The x and y axes represent the extracted dimensions. The numbers are the flower species (see Table 1). The lines represent the raters.

We subsequently tested whether the correlation coefficients between the three samples differed significantly using t tests on z-transformed correlation coefficients (function *paired.r*) There was no statistically significant difference between the correlation coefficients of the Kenyan sample and Czech Sample 1 versus the Kenyan sample and Czech Sample 2 ($z = 0.36, p = .72$). However, the Kenyan sample and Czech Sample 1 versus Czech Sample 1 and Czech Sample 2 differed significantly ($z = 3.69, p < .001$). In other words, these tests again confirmed that there was a higher level of agreement in the rankings between the two Czech samples than between either the Czech sample or the Kenyan sample.

Figure 3 *Plots of the Multidimensional Preference Scales With Two Extracted Dimensions*



Note. x-axis is Dimension 1, and y-axis is Dimension 2. Points are the flower species. Stars are radially symmetrical flowers, and triangles the bilaterally symmetrical ones. The colors of symbols reflect the color of the flower species. MDPREF = xxxx. See the online article for the color version of this figure.

Symmetry, Color, and Culture

We were also curious how the type of floral symmetry and flower color affect the rankings. We wanted to explore whether Kenyan and Czech raters treat shapes and colors differently (i.e., if there are interactions between symmetry or color and the sample of raters). We performed a multifactorial ANOVA (Type II), where the mean rankings of each flower species represented the dependent variable. Floral symmetry and color were the between-sample factors, and a sample of raters was the within-sample factor. The initial model showed interaction between the samples and symmetry and color. That means there were differences between Kenyans and raters in both Czech samples in how they treated flower shapes and colors. There was no interaction between the symmetry and color (see Table 2). However, there was a significant effect of floral symmetry. Please note that there could not be any effect of sample per se on the mean ranking of all flowers. Each rater ranked all flowers in his/her respective sample (from 1 to 40). Therefore, the mean rankings across all flowers were the same. We could expect the effect of a sample while observing single species (for example, how Czechs and Kenyans differ in the ranking of *Viola reichenbachiana*). However, it was not the purpose of this analysis.

A subsequent Tukey's post hoc test revealed that bilaterally symmetrical flowers were ranked significantly higher than the radially symmetrical ones (thus being less preferred because the most preferred flowers had the lowest ranks). Mean difference = −5.65, 95% CI [−7.12, −4.20], $p < .001$. See Figure 5.

The interaction between the color and sample was evident only in the case of white color. Kenyans ranked white flowers lower (liked them more) than raters from both Czech Sample 1 (mean difference = −2.66, $p = .032$) and Czech Sample 2 (mean difference = −2.95, $p = .022$). See also Figure 6.

Although ANOVA revealed a significant interaction between the sample and symmetry, a post hoc test did not show any statistically significant difference in the ranking of bilaterally and radially symmetrical flowers across samples.

Exploratory Analysis

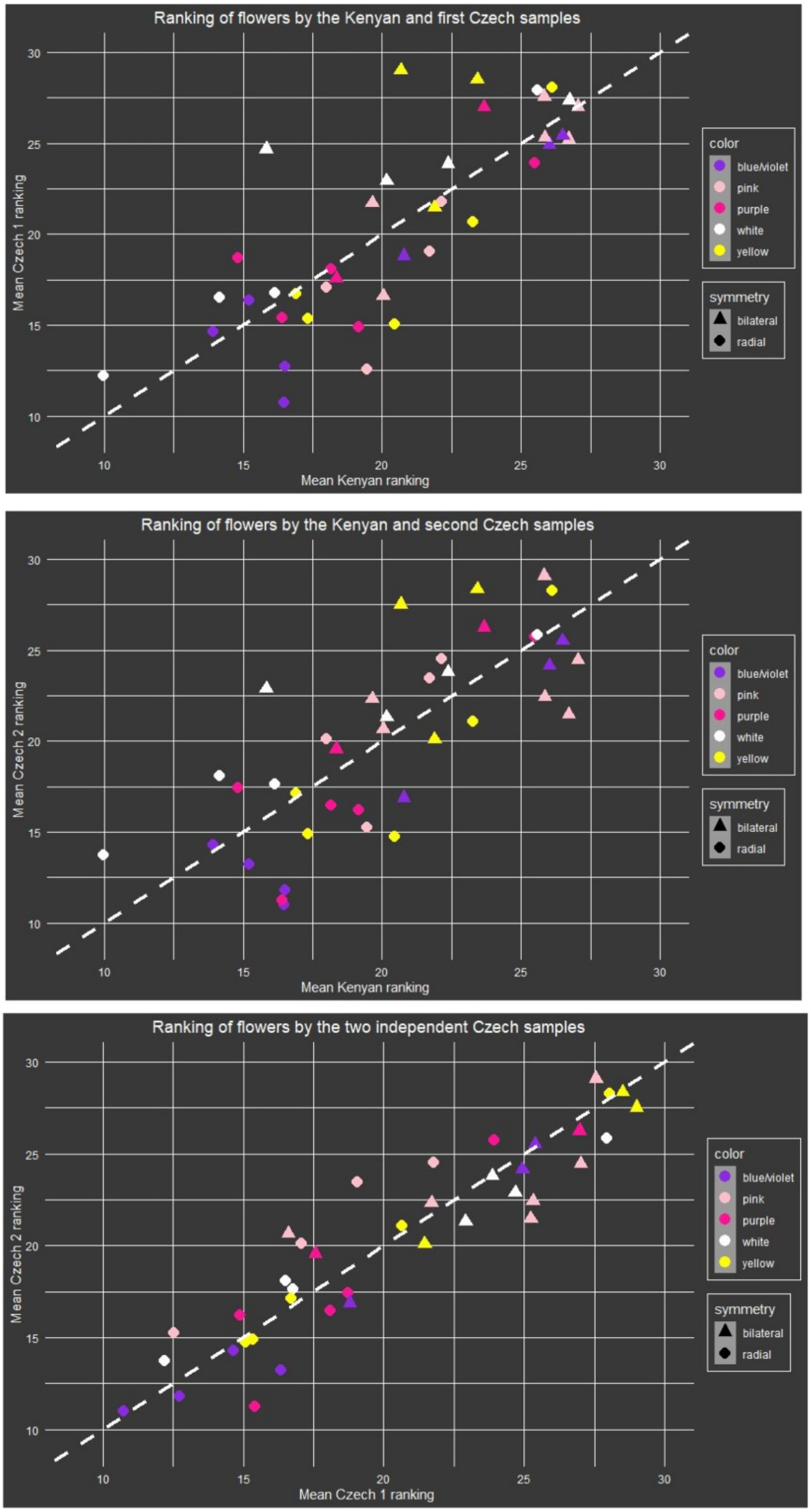
Familiarity

To address the issue of familiarity, we also divided Czech Sample 2 into a botany experts subsample ($n = 23$) and a nonexperts subsample ($n = 25$). We then correlated both subsamples with the Czech Sample 1 (in which all raters were nonexperts) as well as with the Kenyan sample. Below, we can see that in the Czech samples, the two nonexpert groups agreed on their rankings more than the nonexperts and the botanists. This difference was statistically significant ($z = 3.3, p < .001$). Although it might seem that Czech nonexperts also agreed with the Kenyan raters more than the Czech botanists and the Kenyan raters, this difference was not significant ($z = 1.08, p = .28$).

> Botany experts and Czech 1: $r = .79$, 95% CI [0.64, 0.88], $t = 7.98$, $df = 38$, $p < .0001$; nonexperts and Czech 1: $r = .97$, 95% CI [0.94, 0.98], $t = 24.70$, $df = 38$, $p < .0001$.
>
> Botany experts and Kenya: $r = .66$, 95% CI [0.44, 0.81], $t = 5.40$, $df = 38$, $p < .0001$; nonexperts and Kenya: $r = .81$, 95% CI [0.66, 0.89], $t = 8.38$, $df = 38$, $p < .0001$.

We also performed a multifactorial ANOVA (Type II) where the mean ranking of flowers represented the dependent variable, symmetry and color the between-sample factors, and familiarity the within-sample factor. We identified three levels of familiarity: low (Kenyans), moderate (Czechs without any botanical background), and high (Czech botany experts). We found a main significant effect of symmetry and a significant interaction between symmetry and familiarity (see Table 3). However, a post hoc test did not reveal any significant differences in the ranking of radially or bilaterally symmetrical flowers between raters with different levels of familiarity with the flower stimuli.

Figure 4 *Pearson's Correlations Between the Mean Rankings of Flower Preference of Top: Kenyan and Czech 1 Samples (*r = *.79), Middle: Kenyan and Czech 2 Samples (*r = *.77), Bottom: Czech 1 and Czech 2 Samples (*r = *.92)*



Note. The dashed line represents the absolute correlation (*r* = 1). Points (flower stimuli) above the line had a higher ranking in the sample on the *y*-axis, points below the line had a higher ranking in the

(*Continued on next page*)

Table 2

ANOVA Table (Type II) of the Mean Ranking of Flowers Showing Significant Interaction Between the Sample and Flower Symmetry and the Sample and Flower Color, and a Significant Effect of Symmetry on Flower Ranking

AQ18

	df	*MSE*	*F*	*p*
Symmetry	1,30	46.27	18.79	<.001
Color	4,30	46.27	18.79	.380
Symmetry: color	4,30	46.27	0.54	.709
Sample	2,60	3.44	0.00	.997
Symmetry: sample	2,60	3.44	4.41	.016
Color: sample	8,60	3.44	2.96	.007
Symmetry: color: sample	8,60	3.44	1.31	.258

Note. ANOVA = analysis of variance; *MSE* = mean square error.

We have to be highly cautious while interpreting the data on familiarity. The sample size of the subsets is small, and the study was not designed to test this issue. However, we observed some interesting trends that indicate that familiarity might have some role in flower preference. We should focus on its role in a separate and carefully prepared study.

Discussion

We found low agreement between the individual rankings of the raters in each dataset (ICC[A,1] around 0.2). It was probably caused by the high number of stimuli (40) to rank. Such a number yields difficult for the raters to reduce all features of the stimuli to a single variable (preference). However, our sample size was sufficiently large to calculate mean rankings, that showed a very good agreement among the raters within each sample (ICC[A,k] around 0.9). This means that it was sensible to look for possible differences in the mean rankings between the samples.

As expected, we found very high positive correlations in the esthetic ranking of flowers between the Kenyan and both Czech samples ($r = .79$ and .77, respectively); the correlation between the two Czech samples was even higher ($r = .92$, see Figure 4). These findings are in line with the research conducted on animals (Frynta et al., 2011; Landová et al., 2018; Lišková & Frynta, 2013) and with our expectations.

A visual inspection of the multidimensional preference analysis biplots (Figure 2) allowed us to compare the rankings of individual raters. We can see that most raters (represented by the vector lines) roughly agreed on their rankings within each sample. However, there was always a minority of raters with a very different taste. We can also see that the ranking patterns do not substantially differ across samples. Of course, there are some differences between all samples. It would be surprising not to find any. However, it is evident that there was very good agreement between the Czech and Kenyan raters on which flowers are preferred and which are not.

These findings support the notion that esthetic responses to flowers are shared by humans as a species. Of course, we cannot draw any strong conclusions from a single study performed on a limited sample, but our results clearly show that we should continue in this direction and conduct a large-scale intercultural study.

Symmetry

The results supported our expectations about the preferences for different types of symmetry, i.e., bilaterally symmetrical flowers were ranked worse than radially symmetrical ones (Figures 5 and 6). This was not surprising in the Czech population since we found the same pattern in our previous research (Hůla & Flegr, 2016). The effect of the symmetry type was large in both Czech Sample 1 (Cohen's $d = 1.58$) and Czech Sample 2 (Cohen's $d = 1.32$). We can assume that bilaterally symmetrical flowers are considered more complex and less prototypical than radially symmetrical flowers, which accounts for their lower preference. The Kenyan raters also preferred radially symmetrical flowers (Cohen's $d = 1.13$), although even though the effect was still large, it was less pronounced than in the Czech samples.

The ANOVA also found a significant interaction between symmetry and sample (see Table 2), suggesting that raters across samples rank bilaterally or radially symmetrical flowers differently. However, we did not find any significant difference when we tried to look at the differences between groups using Tukey's post hoc tests. The largest difference (1.46 ranks) was in the ranking of bilaterally symmetrical flowers between Kenyan and Czech 1 samples.

It is possible that the percentage of common bilaterally symmetrical flowers is higher in tropical Kenya than in temperate Czechia. An illustrative example is orchids (bilaterally symmetrical): there are 283 species of orchids native to Kenya, many of them commonly cultivated and with large flowers (Gateri et al., 2015). On the other hand, Czechia only has around 60 orchid species, nearly all of them rather inconspicuous, endangered, and not commonly seen (Kaplan, 2019). Bilaterally symmetrical flowers might thus seem more typical to Kenyans (and also to the botanists in Czech Sample 2), resulting in their slightly better ranking than in Czech Sample 1.

The multidimensional preference analysis also supports the importance of symmetry for the ranking of flowers. The most important extracted dimension was symmetry in all samples (see Figure 3), although other shape properties played a role in the Kenyan sample. However, the two extracted dimensions explained only around 20% of the variability, so we should not overestimate its importance.

Bilaterally symmetrical flowers often have quite complex and atypical floral compositions (Hůla & Flegr, 2016). Therefore, it is possible that the type of symmetry per se is not crucial for the flower preference. Other shape properties, which are tightly linked to the type of symmetry, but not so easily described, might play a decisive role.

Color

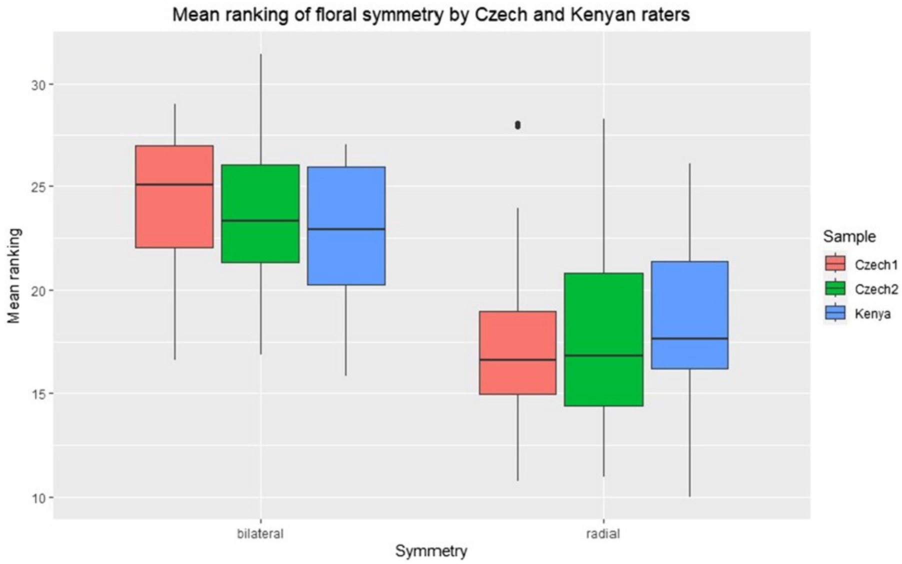
We predicted only a minor effect of color on the ranking of the flowers. Based on some of our previous findings and also on studies of general color preferences (Camgöz et al., 2002; Hůla & Flegr,

Figure 4 (*Continued*)

sample on the *x*-axis. Please note that a higher ranking means a lower preference. Circles represent radially symmetrical flowers and triangles bilaterally symmetrical ones. The colors of the points reflect the color group of each flower. See the online article for the color version of this figure.

Figure 5

Mean Ranking of Floral Symmetry by Czech and Kenyan Raters x*-Axis: Type of Floral Symmetry,* y*-Axis: Mean Ranking of Flower Species by All Participants*

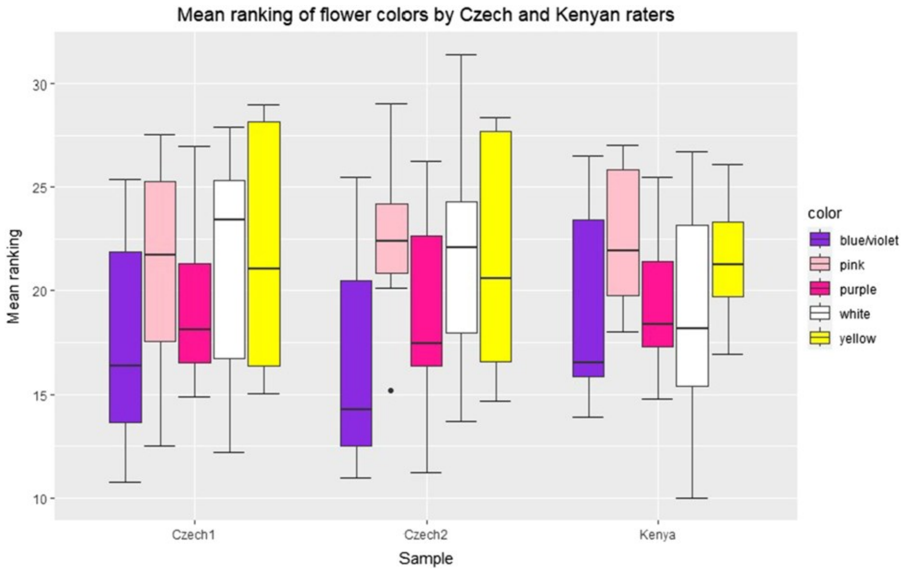


Note. Please note that a higher ranking means a lower preference. Red boxes: first Czech sample, green boxes: second Czech sample, blue boxes: Kenyan sample. See the online article for the color version of this figure.

2016; Palmer & Schloss, 2010; Schloss et al., 2012), we assumed that blue flowers would be more highly ranked compared to yellow flowers. Blue and yellow colors are consistently rated on the different sides of the preference spectrum in industrialized western countries. However, we did not observe any effect of color in a previous study focused on the preference for flowers and fruits (Hůla & Flegr, 2021). Figure 6 might suggest that blue/violet flowers were preferred slightly more than yellow and pink flowers across samples, but the

Figure 6

Mean Ranking of Flower Colors by Czech and Kenyan Raters x*-Axis: Sample of Raters,* y*-Axis: Mean Ranking of Flower Species by All Participants*



Note. Please note that a higher ranking means a lower preference. The color of boxes represents the color of flowers rated. See the online article for the color version of this figure.

Table 3

ANOVA Table (Type II) of the Mean Ranking of Flowers Showing Significant Interaction Between Familiarity and Flower Symmetry and a Significant Effect of Symmetry on Flower Ranking

	df	*MSE*	*F*	*p*
Color	4, 30	42.26	1.34	.278
Symmetry	1, 30	42.26	18.43	<.001
Color: symmetry	4, 30	42.26	0.62	.650
Familiarity	2, 60	46.27	0.00	<.999
Color: familiarity	8, 60	5.53	1.94	.071
Symmetry: familiarity	2, 60	5.53	3.21	.047
Color: symmetry: familiarity	8, 60	5.53	1.25	.285

Note. ANOVA = analysis of variance; *MSE* = mean square error.

multifactorial ANOVA did not reveal any significant differences in color rankings However, it showed a significant interaction between color and sample. A subsequent post hoc test revealed that Kenyans ranked white flowers slightly better than raters in both Czech samples (the difference is 2.66 ranks for Czech Sample 1 and 2.95 ranks for Czech Sample 2). In the multidimensional preference analysis, Dimension 2 of the Kenyan sample also suggested that white color is somehow important for the rankings. We can only speculate why Kenyans should rank white flowers better than Czechs. It can be an artifact of the stimuli selection. Also, white flowers are the most common in Czechia. It would be interesting to see the distribution of flower colors in Kenya. Maybe the difference in the rankings might be caused by the frequency of the white color among commonly seen flowers. For example, blue is one of the least common colors among Czech flowers, and it is also the most preferred (Hůla & Flegr, 2016). Of course, the Kenyan preference for white might be a purely cultural phenomenon. It would be beneficial to see if this finding would be replicated in future studies.

Our current findings illustrate again that when raters see a flower from a close distance, the effect of its color in forming an esthetic response is much lower compared to its shape properties. Conspicuous flower colors are probably more crucial when seeing flowers from a greater distance when their shape is difficult to recognize (Hůla & Flegr, 2021).

Display of Stimuli

Our results might have been influenced by the display method of the stimuli. The raters did not rate the whole plants, but only single flowers on black background. This certainly somehow decreased the ecological validity of the rankings. When creating the stimuli, we tried to find a balance between closeness to reality and a need to comparability of the stimuli. Real plants have various number of flowers and different shapes of inflorescences, they often have completely different habitus, shape of leaves, etc., which would bring unbearable amount of noise into the data. That is why we finally used only the single flowers. As we mentioned in the Methods, the flowers had similar size in reality and they were easily distinguishable from other flowers on the plant. Also, people are used to such displays since many ornamental plants in florist shops look very similar (the so-called single-stem flowers). We also chose a neutral black background, because flowers are usually seen on various backgrounds (green–leaves, blue/white–sky, brown/grey–soil or stones, etc.) and we wanted to have the same level of "realness" for all flowers. Finally, our (unpublished) data show that people rate real flowers and the photographs used in the current study very similarly.

Familiarity

The flowers used as stimuli are common in Czechia, and most of them can be easily spotted during walks through the countryside, in gardens, and even in the cities. Although we did not include any flowers known to have particularly strong symbolism for Czech culture, we can nevertheless assume that the majority of Czech raters were familiar with them to some extent. On the other hand, Kenyan raters probably had no firsthand experience with these flower stimuli. Therefore, given the high correlations in the ratings, it might seem that familiarity did not play much of a role in the esthetic responses to the flowers in our study.

However, it is possible that familiarity does not influence the pattern of the esthetic response, but rather its overall strength (e.g., considering all unknown flowers as less attractive). The ranking method did not allow us to examine this possible difference since all the stimuli were at least partly familiar to Czech raters and almost completely unfamiliar to Kenyan raters. We would have needed stimuli with mixed familiarity or a different method, such as rating flowers on a scale, to be able to address this issue in more depth.

Nevertheless, we were able to partly explore the role of familiarity at least in the Czech Sample 2, where almost half of the sample consisted of botanists. Their familiarity with the presented stimuli was obviously much higher than in the case of other respondents who were not interested in plants. When we correlated the nonexpert subset with the Czech Sample 1, we observed an almost perfect correlation in the rankings ($r = .97$). In the case of the expert subset and Czech Sample 1, the correlation was significantly lower ($r = .79$). Since there were no other substantial differences between the raters in the two subsets, the difference in the rankings was probably caused by familiarity with the stimuli (i.e., the raters knew the displayed species from real life), overall better knowledge of flowers and their morphology and ecological context, or the raters' general attitude toward flowers. Although the correlation between the Czech experts and Kenyan raters seemed lower ($r = .66$) than between Czech nonexperts and Kenyans ($r = .81$), the difference was not statistically significant.

A multifactorial ANOVA revealed a significant interaction ($p = .047$) between the familiarity level and the symmetry ranking. However, a subsequent post hoc test did not show any significant differences. The most pronounced difference (1.41 ranks) was in the ranking of bilateral flowers between the raters with moderate (Czech nonexperts) and low (Kenyans) levels of familiarity with the stimuli. The difference between the raters with low (Kenyans) and high (Czech botanists) levels of familiarity is far less pronounced (0.73 ranks). This trend might suggest that the difference in the rating of bilaterally symmetrical flowers between Czechs and Kenyans may be caused by familiarity. Kenyans do not know the Czech flowers, but they probably see bilateral flowers more often than ordinary Czech people, as do Czech botanists.

These results suggest that familiarity with the stimuli or general knowledge of flowers might influence the pattern of esthetic responses (i.e., which flowers are ranked better and which worse) at least within the Czech sample. The effect of familiarity seems to be more pronounced when comparing raters with a deep knowledge of the presented flowers to raters without any knowledge of the flowers at all, yet even in these extreme cases, there is still a substantial level of agreement between the raters.

Limitations and Prospects

Although our study revealed a strong agreement in the ranking of flowers between Czechs and Kenyans, it is severely limited by the relatively low number of participants (156 in total), especially given the ranking method of the assessment of flower preference. This paper should serve as a tentative invitation to explore the neglected, but potentially very promising area of intercultural research of esthetic responses to flowers. Although our current findings seem convincing, we need to perform a large-scale study on several cultures across the world to be able to further support and generalize our findings.

In future studies, we have to pay particular attention to the demographical composition of the raters. We should also collect more information about the raters, especially their knowledge of flowers and their attitudes toward them. For example, it would be interesting to properly examine, how gender differences interact with cultural background (although our previous research on flowers in the Czech context, as well as intercultural studies on the preference for animals, reported only minor gender differences (Frynta et al., 2011; Hůla & Flegr, 2016; Landová et al., 2018; Lišková & Frynta, 2013). In the Kenyan set, we only had a very small number of women (and a small number of men in the Czech samples), so it would not make much sense to divide our dataset into tiny subsets. A detailed study focusing on individual differences between raters (such as age, socioeconomic status, or knowledge of plants) would certainly be welcome.

In future studies, it would be beneficial to use both a rating scale and the ranking method in order to see the strength of the esthetic response, not just its pattern. This approach might help to decipher the effect of familiarity on flower preference because familiarity might possibly influence the strength of esthetic responses, but not necessarily their order.

Rating scales might also be preferable for larger sets of stimuli. Our raters ranked 40 photographs, which is more than is usually used for ranking methods. With a growing number of stimuli, it becomes difficult to reliably rank all of them because of the mental fatigue of participants and because it becomes challenging for the raters to integrate all the aspects of the presented stimuli into a single dimension. Although the level of agreement between the single rankings of our raters was low, we still observed a high level of agreement in their mean rankings. Furthermore, our set of stimuli is relatively small when compared with the number of photographs used in the abovementioned studies on animals. Frynta et al. (2010) addressed this concern and found that even with large sets of stimuli, the ranking method brings similar results and levels of agreement between raters as the rating on scales. We should, however, remain cautious and take the number of our stimuli into account.

The exploratory part of this study showed a possible effect of familiarity on the esthetic responses to flowers and might explain some of the observed differences between Czech and Kenyan raters (ranking of bilaterally symmetrical and white flowers). It should, therefore, be a focus of future research, possibly by creating a set of stimuli with mixed familiarity to the raters, using flowers from different parts of the world. A creation of several standardized and mutually comparable sets of species from various floras would give us a powerful tool for many future inquiries.

Conclusion

We found a substantial similarity in the pattern of esthetic responses toward flowers in all our samples. This strong agreement existed in spite of not only the demographical, but more importantly the ecological and cultural differences between the Kenyan and Czech raters. Despite the fact that the level of agreement in the rankings of flowers was higher between the two Czech samples, the intercultural similarity is indisputable. Czechs and Kenyans respond to flowers of different colors and different types of symmetry in a similar way. We observed, however, some differences in the rankings. Kenyans seem to rank white flowers slightly better than Czechs and are also mildly more tolerant toward (usually disliked) bilaterally symmetrical flowers. We suspect that these differences might be caused by the different levels of familiarity with the stimuli rather than by ecological or cultural factors. However, we need a new study focusing on the role of familiarity to further explore this area. Our results support those theories that consider the esthetic responses toward flowers as shared by humans as a species. However, there is a need for a large-scale intercultural study to confirm our first tentative results.

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APPENDIX 4

Symmetry, prototypicality, complexity, color, and human aesthetic response to real flowers and their photographs

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Abstract

Humans have long appreciated the beauty of flowers. The global cut flower trade exceeds €15 billion per year. Surprisingly, we have very limited knowledge of preferred floral traits and almost no empirical evidence for theories explaining the human aesthetic responses to flowers. This study aimed to confirm the results regarding the relative importance of floral color and shape properties on the rating of the beauty of flowers by independent sets of raters and stimuli. Another objective was to determine whether the ratings differ when different types of stimuli – real flowers, standardized photographs, and images from the internet – are used. In three independent experiments, we collected data from 297 Czech respondents who rated the beauty of diverse flowers, both wild and cut. First, they rated flowers under monochromatic red light (analogous to rating sepia-tone photographs), then under polychromatic yellow light. They also rated sepia-tone and color photographs of the same species of flowers in two online questionnaires. We found a strong preference for radially symmetrical and prototypical flowers with moderate levels of complexity. Blue/violet, red, and purple colors influenced the rating positively. White and yellow had no or even negative effects. Our data also show strong correlations (r ≈ 0.7) between the ratings of all types of stimuli in all three experiments. This study confirms the results of our previous research and deepens our knowledge of general human preferences for flowers. It also provides evidence that in certain conditions, photographic stimuli can serve as an adequate substitute for real flowers

Keywords

flower preference; flower beauty; aesthetic responses; symmetry; complexity; prototypicality; color; phytophilia; evolutionary aesthetics; people-plant interactions

1. Background

Humans have an ambivalent attitude toward plants and flowers. On one hand, humans have spent the vast majority of their history in a close relationship with plants, which served as the main source of food, medicine, and other essential materials. On the other hand, people in modern societies often live in environments very scarce in plants. Some authors have suggested that the human mind is so attuned to being surrounded by plants that we try to compensate for their absence by purchasing potted plants and applying floral motifs to various everyday objects (Appleton, 1996; Eibl-Eibesfeldt, 1989). Recent research attributes a crucial role to plants in shaping some of human cognitive mechanisms, such as strategies to avoid natural toxins (Rioux & Wertz, 2021; Wertz, 2019), and regards plants as drivers of human social learning (Oña et al., 2019; Wertz & Wynn, 2019; Włodarczyk et al., 2020).

People show a particularly high interest in ornamental flowers, cultivating and breeding them for millennia **(Goody, 1993)**, and creating a whole branch of worldwide industry related to cut flowers. Despite that, research on preferred flower traits is still very limited, and mostly constrained to a single flower species and its presentation to the customer **(Behe et al., 1999; Grygorczyk et al., 2019; Yue & Behe, 2010)**, but see also **(Wu et al., 2021)**.

Wildflowers and other wild plants, on the other hand, remain mostly neglected (especially when compared to animals). This phenomenon, known as plant awareness disparity (formerly plant blindness), gained attention in recent years **(Achurra, 2022; Prokop & Fančovičová, 2023; Schussler & Olzak, 2008)**. Plant awareness disparity causes a problem because the lack of interest in wild plants might cause serious problems in the ability and willingness of the public to protect endangered species and natural habitats. Some authors call for a better understanding of features that make plants more attractive to the public so that they can be used by teachers and other specialists to promote awareness of plants **(Prokop & Fančovičová, 2023)**.

A recent study **(Adamo et al., 2021)** also found that even the scientific focus on various plant species in botany depends more on the appearance of plants than on factors such as plant ecology or rarity.

A solid body of basic research that focuses on the aesthetic responses of humans to various plant features would be beneficial not only for flower sellers and breeders but also for teachers, individuals involved in nature conservation, and plant researchers. Additionally, such research could help us identify the most suitable theoretical frameworks for explaining the basis of human attraction to flowers. For instance, theories like the habitat selection theory (Heerwagen & Orians, 1995; Orians & Heerwagen, 1992) and ecological valence theory (Palmer & Schloss, 2010; Schloss et al., 2012) emphasize the importance of flower colors, each with slightly different expectations. In contrast, theories of information processing tend to focus more on shape properties, such as symmetry, complexity, or prototypicality (Reber et al., 2004; Renoult, 2016; Renoult & Mendelson, 2019).

We tried to explore the topic in our previous research **(Hůla & Flegr, 2016)** where we conducted an online study with more than 2000 participants who rated the beauty of Czech wildflowers of diverse shapes and colors. We found a strong link between floral prototypicality, complexity, and type of symmetry. Attractive flowers tended to be highly prototypical, simple, and radially symmetrical. We also found that colors influenced the beauty of flowers, but not as much as shape properties. The most preferred flower colors were blue and purple, whereas yellow was not preferred at all.

The current project should confirm and expand our previous research, thus providing more solid evidence of our results. This time, we work not only with photographs of flowers but also with real living flowers. Photographs are widely used in the research of aesthetic responses, but there is only a very limited number of studies that would compare if the photographs reflect reality. To our knowledge, there is one study on the aesthetic response to snakes **(Landová et al., 2012)**, and one study focusing on roses **(Grygorczyk et al., 2019)**. The study on snakes found a good agreement between the rating of photographs and real snakes. The study on roses did not find any correlation between the rating of real roses and their photographs. However, it is conceivable that the difference arose because the participants rated the close-up pictures of single flowers, whereas the real roses were whole potted bushes.

2. Research Objectives and Hypotheses

2.1 Primary Objective

In this project, we want to follow up on our previous research (Hůla & Flegr, 2016) and use independent sets of stimuli and raters to determine how different shapes and colors of real living flowers influence their perceived beauty. We also want to determines how flower preferences differ across various types of stimuli – reality flowers, standardized photographs, and photographs downloaded from the internet.

More specifically, we want to answer the following questions: Is shape more important than color in the rating of the beauty of flowers? How does the type of symmetry, type of color, level of prototypicality, and complexity influence the rating of flower beauty? Do the flower preferences substantially differ between the types of stimuli?

2.2 Hypotheses

Based on the results of our previous research and from the literature, we formulated the following hypotheses:

1. There will be no substantial difference between the rating of standardized photographs and photographs from the internet.

2. Real flowers will generally be considered more beautiful than the flowers in the photographs.

3. There will be a strong positive correlation ($r > 0.6$) between the rating of real flowers and their photographs.

4. There will be a strong negative correlation between the perceived prototypicality and complexity of flowers.

5. Bilaterally symmetrical flowers will have low levels of prototypicality and high levels of complexity.

6. Radially symmetrical flowers will be rated as more beautiful than bilaterally symmetrical flowers.

7. The rating of flower beauty will increase with perceived flower prototypicality.

8. The effect of perceived flower prototypicality on the overall rating of the beauty of flowers will be stronger than the effect of flower color.

9. The positive effect of color on the overall rating of flower beauty will be strongest for the red and blue/violet colors and weakest for the yellow color.

3. Materials and Methods

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

The research consisted of three consecutive studies spanning 9 months. Study A took place in August, Study B in October, and Study C in May of the following year. All studies had the same design, but different stimuli and independent raters.

The experiment had three parts. First, the participants rated the beauty of flowers on standardized photographs in an online questionnaire. The following week, we invited the participants to our laboratory, where they rated real flowers of the same species as in the photographs. Two weeks after the rating in the laboratory, the participants rated the same flower species once again, this time on photographs that we downloaded from the internet.

3.1. Participants

We were looking for participants via shareable Facebook posts in the *Labbunnies* [Pokusní králíci] group, a community of approximately 20 thousand Czech and Slovak volunteers who are willing to take part in various studies in evolutionary psychology. *Labbunnies* operates under the umbrella of a citizen science project managed by Dr. Flegr's team. We also advertised the research in several Facebook university groups and placed flyers on the university campus.

We thus recruited the participants from the public and university students. There were fewer students in Study A because it took place during the summer break. Each participant had to read information about the research and consent to take part in it. All participants were adults with normal or corrected-to-normal vision.

As a reward for taking part in the research, each participant received a commemorative badge, a mixture of meadow plant seeds, and a cut flower. In Study C, we also additionally rewarded participants with CZK 100 (approx. € 4).

3.2. Stimuli

In each study, we used three types of stimuli: fresh flowers, standardized photographs, and photographs downloaded from the internet. The photographs are available at Figshare. Study A: 10.6084/m9.figshare.24441037, Study B: 10.6084/m9.figshare.24441232, and Study C: 10.6084/m9.figshare.24441382

Real flowers

In Study A and C, we used Czech wildflowers as stimuli. We tried to use flowers of diverse colors and shapes. We always used two flowers with similar shapes and different colors. There were 36 flowers in total in both studies (18 shape types with different colors). However, the species composition was different across studies. We only included species that had easily recognizable flowers (or a compact inflorescence that seems like a single flower to a layperson, e.g., members of the daisy family). The flowers were from 1.8 to 4.6 cm in diameter, typically around 2 cm. We also included only scentless flowers. See Tables 1 and 3 for the list of species used in studies A and C.

Although we would like to have all stimuli of the same size and with evenly distributed colors across all shapes, we were severely limited by the availability of wildflowers. Since we worked with withering seasonal material, we had to choose species naturally growing in Prague or cultivated in the Charles University botanical garden. All plants used in a particular study had to be in flower at the same time for more than two weeks, ensuring we had enough time to take their standardized photographs for the online rating, and also had a consistent supply of fresh specimens for the subsequent laboratory rating. The plants also had to be available in sufficiently high numbers. This was because some flowers had to be replaced several times daily during the laboratory rating to prevent them from withering.

In Study B, we focused mainly on flower colors. Since Czech wildflowers do not have enough color variants within a single species, we used cut ornamental flowers available in florist shops. This strategy also allowed us to test the effect of red color, which does not occur among the Czech wildflowers (except for the genus *Papaver*). We used eight species with different shape properties. Each species had at least four color variants, resulting in 38 flowers in total (see Fig.2). The list of species can be found in Table 2.

Standardized photographs

We photographed the flowers as soon after we picked them as possible, usually within two hours. We took the photographs in a room with access to daylight and no artificial lights. e photographed the flowers on the same day time and under the same weather conditions. We photographed each flower against a white background. We took three photographs of each flower: a shoot *en face*, 30° to the left, and 30° to the right. We used the Canon EOS 600D camera with a 50 mm lens and additional 13 and 21mm macro rings.

We then edited the photographs in the same way as in our previous research (Hůla & Flegr, 2016): We cut the flower from the background, rescaled it so that the longer side of the flower had 150 px and placed the rescaled flower in the center of a black square, 200 x 200 px wide. We also prepared a separate set of photographs, where we transformed the flower colors into the sepia tone (50 % function sepia tone). Otherwise, it was identical to the first set. We used this set to compare the influence of color on beauty ratings. We edited the photographs in the Corel DrawX7 (removing the background) and Corel PhotoPaintX7 programs.

Photographs from the internet

We found freely available photographs of given species on the internet. We only used photographs with sufficient resolution and chose flowers in corresponding angles. The editing procedure was the same as for the standardized photographs.

The main difference from the standardized photographs was that we were not able to fully control the camera type, light conditions, and exact angles. Also, we used photographs of three different flowers for one species (one for each angle) instead of a single flower.

See Figure 1 for examples of standardized photographs and internet images.

3.3. Display

Online rating of standardized photographs

When participants enrolled in our research, we sent them a link for an online questionnaire built in the Qualtrics environment. First, they consented to fill in the questionnaire (by clicking on a button: "I agree and continue"). Then they indicated their age and gender and proceeded directly to the rating of flowers.

The display was identical to our previous research (Hůla & Flegr, 2016). Each flower species was displayed by three horizontally adjacent photographs starting with the 30° to the left, the *en face* photograph in the center, and the 30° to the right as the last one (See Fig.1). Above the photographs, there was a statement: „The flower in the pictures is very beautiful." The participants expressed their agreement with the statement on a six-point rating scale, where 0 meant "strongly disagree," and 5 meant "strongly agree." The participants rated the set of colored flowers. The flowers appeared in randomized order.

Rating of real flowers in the laboratory

Several days (from three to seven) after the first online rating, the participants came to our laboratory to rate real flowers. We wanted to ensure at least several days of delay between the two ratings to prevent participants from remembering how they had rated the stimuli. However, we had to take into account the flowering period of the plant species that served as stimuli. That is why the delay between the ratings could not be longer.

The experiment had three parts – a rating of stimuli under red light, a computer questionnaire, and a rating of stimuli under normal yellow light.

We first instructed the participants about the upcoming experiment and received their written consent to take part in it.

The rating took place in a windowless room. The only sources of light were two table lamps placed above the stimuli. This setting assured controlled light conditions independent of daytime or weather. The first lamp emitted monochromatic red light (60W LED bulb, T = 1000 K, OBI brand "colored LED"), and the second lamp emitted polychromatic yellow light (46W halogen bulb, 700 lm, T = 2700 K, R_a = 100, OSRAM Classic 64543 A). The color rendering index (R_a = 100) of the yellow bulb provided a color representation identical to sunlight.

We placed each stimulus (a single flower) into a glass jar filled with water. The jars were identical and covered by a black lid with a hole in its center. The flower itself thus remained uncovered, but its stem had access to water to slow down the withering. We covered the lid with the flower with a white plastic cup and wrote a number on it. We then put all the jars on three rotating plates and placed the plates next to each other on a table (see Fig. 3).

The participants received a paper form with printed statements and the beauty rating scales (identical to the online rating). We wrote the stimuli numbers next to the scales. The order of stimuli numbers on each form was unique, and randomly generated in the R program. The participants rated the stimuli from the top scale to the bottom scale. They looked at the number next to the scale, found a cup with a corresponding number, and uncovered the jar. When they decided on the rating of the stimulus, they encircled a desired number on the scale, placed the cup back on the jar, and proceeded to the following stimulus. There was no time limit for the rating. The participants could also rotate the plates to see the stimuli from different angles, if necessary. There was only one participant present during the rating. A researcher was also present in the room. However, the area with stimuli was separated from the rest of the room by a curtain.

Each participant started with the rating under a red light. It was impossible to distinguish flower colors during this rating. We later used it in the analysis of the effects of colors on the beauty of flowers. After this rating, the participant approached the computer to fill in an electronic questionnaire. The questionnaire contained questions about basic demographic information, attitude to and knowledge of plants, some psychological characteristics, and questions about health. Most of the questions were not relevant to this research. An important objective of the computer questionnaire was to distract the participants between the two ratings. After the questionnaire, the participant proceeded to the second rating, this time under yellow light. The researcher rotated all three plates before the second rating and provided the participant with a new rating sheet (with a different order of stimuli numbers).

It was necessary to rate the stimuli under red light first so that the participant could not recall their colors during the second rating.

Online rating of photographs from the internet

Two weeks after the laboratory experiment, we sent the participants a second online questionnaire. We expected that the participants would not remember their ratings from the previous experiment after such time.

In the second questionnaire, the participants first rated the beauty of the sepia-toned set of standardized photographs and then the set of colored photographs from the internet. The flowers in each set appeared in a randomized order.

3.4. Complexity and prototypicality questionnaire

We also prepared two questionnaires, where two independent sets of raters recruited from the *Labbunnies* Facebook group rated the perceived complexity and prototypicality of the flowers used in beauty ratings (only the colored ones). The raters chose on a six-point scale how they agreed with the statement: “This is how I imagine a COMPLEX flower.” or “This is how I imagine a TYPICAL flower.”

Each rater was randomly assigned to only one option (complexity/prototypicality). The flowers appeared in a randomized order. At the beginning of the questionnaire, we explained what we meant by complexity and prototypicality, and we provided examples and images of birds and butterflies that people generally consider as having a low/high complexity/prototypicality.

In the first questionnaire, the participants rated the flowers from studies A and B, and in the second questionnaire, they rated the flowers from study C.

We used the ratings to compare, how perceived complexity and prototypicality of flowers influence their beauty ratings.

Fig.1

Fig.2

Fig.1: Examples of flower stimuli (wildflowers). Top: *Geranium palustre*, **middle:** *Lathyrus tuberosus*, **bottom:** *Cerastium tomentosum*. The first row of each species represents the standardized photographs and the second row represents the internet images.

Fig.2: Examples of flower stimuli (ornamental plants) and their colors. **Top:** *Dianthus sp*., **bottom:** *Phalaenopsis sp.,* **Colors from left**: white, yellow, pink, purple, red.

Fig. 3: Experimental room. Left: rating under red light, **right:** rating under normal yellow light. **Top:** situation during rating. All flowers are covered by numbered cups and placed on rotating plates. Participants only uncover and rate one flower at a time. **Bottom:** illustrative setting with all flowers uncovered. Flower colors are indistinguishable under red light.

3.5. Sample size

Because of the flowering period of the stimuli, we were able to conduct the laboratory experiment only for one week per set of stimuli. Each participant's ratings took approximately 30 minutes. This fact severely limited the possible number of participants. In the case of online complexity and prototypicality ratings, we were able to obtain a larger sample size.

To determine a minimal necessary sample size, we used the datasets from our previous study (Hůla & Flegr, 2016). They contained ratings of photographs of flower species similar to the current study. We calculated a corridor of stability (Schönbrodt & Perugini, 2013) where the mean ratings of beauty (resp. complexity and prototypicality) of each flower stimulus served as inputs. We set w to 0.2 and ran 1000 simulations per stimulus. The mean prototypicality and complexity ratings converged in more than 95% of cases when at least 100 participants rated the stimuli. The ratings of flower beauty required a larger sample size. However, when at least 80 participants rated the stimuli, we could easily and reliably distinguish groups of very beautiful, moderately beautiful, and not very beautiful flowers. We thus decided to collect data from at least 80 participants during each of the laboratory ratings.

3.6. Statistical analysis

We used p-values and effect sizes (Cohen‘s d for t-tests, η^2 for ANOVAs, R^2 for LMs) to make inferences. We set the alpha level for all statistical tests to 0.05. Due to the high number of hypotheses, we describe each statistical method together with the results. We think it will increase the clarity of the text.

We decided to exclude all suspicious data (e.g. too low age, short duration, or wrong answers to two questions checking the attention of participants in the online questionnaires) as well as data that showed no variance in the ratings. We also excluded data where participants rated less than 90 % of the stimuli.

We did not replace the missing values. After each participant‘s rating in the lab, we checked the quality of the stimuli. When we noticed that some of the flowers withered during the rating, we discarded the original rating of the given flowers and replaced them with a missing value (and replaced the withered flower with a fresh one).

In Study A, some flowers were prone to quick withering, and two flower stimuli were missing during one of the rating days because the locality where they were growing was unexpectedly mowed. When a flower stimulus was rated by less than 90% of the raters, we marked it as „withered“ and took it into account in further analyses. In total 10 flowers were considered „withered“. We did not encounter this issue in the other two studies.

3.7. Participants

90 participants enrolled in Study A, but only 81 arrived at our lab and completed the whole experiment. We had to remove 9 more participants from the analysis due to a high number of missing values in their ratings, resulting in 72 participants in total (66F, 16M, mean age = 29.8 ± 9.3 years). The number of participants was lower than the minimal sample size set by the corridor of stability. Moreover, due to the withering, some flowers were rated by even fewer participants. However, we decided to analyze the data anyway, but we were cautious in interpreting the results.

102 participants enrolled in Study B, but only 82 rated the flowers in the lab and completed the whole experiment. 2 more participants had to be removed from the analysis because of the missing values in their ratings. The final sample thus consisted of 80 participants (51F, 29M, mean age = 24.9 ± 5.8 years).

158 participants enrolled in Study C, 134 completed the whole experiment, and 7 had to be removed because of the missing values in their ratings. The final sample consisted of 127 participants (98F, 29M, mean age = 26.7 ± 8.1 years).

In the complexity and prototypicality questionnaires, we managed to get answers from 260 participants (206F, 54M, mean age = 33.3 ± 11.1 years) for studies A and B, and from 241 participants (173F, 68M, mean age = 38.2 ± 13.1 years) for study C.

4. Results

To test hypotheses 1 and 2:

1. there will be no substantial difference between the rating of beauty of the standardized photographs and photographs from the internet

2. real flowers will generally be considered more beautiful than the flowers in the photographs

we calculated a one-way repeated measures ANOVA, where the mean ratings of the beauty of flower species by all respondents served as the dependent variable, and the type of stimulus (real flower, standardized photograph, and image from the internet) served as the factor. We used the repeated measures method because each flower species was rated by the same respondents three times, first as a standardized photograph, then in real, and finally as an internet image. We used post-hoc pairwise t-tests with Bonferroni correction to identify differences between groups.

Study A
There was a statistically significant difference in the rating of different stimuli types ($F_{(1.31,\ 45.72)} = 7.57$, $p = 0.005$, generalized $\eta^2 = 0.087$). the post hoc test revealed a statistically significant difference ($p = 0.005$) only between the mean rating of beauty of real flowers (3.482 points) and standardized photographs (3.064 points). There was no statistically significant difference between the mean rating of beauty of internet images (3.20 points) and real flowers or standardized photographs (3.064 points).

Study B
There was a statistically significant difference in the rating of different stimuli types ($F_{(2,\ 74)} = 5.93$, $p = 0.0040$, generalized $\eta^2 = 0.023$). The post hoc test revealed a statistically significant difference ($p = 0.012$) only between the mean rating of beauty of real flowers (3.324 points) and standardized photographs (3.154 points). There was no statistically significant difference between the mean rating of beauty of internet images (3.172 points) and real flowers or standardized photographs (3.154 points).

Study C
There was a statistically significant difference in the rating of different stimuli types ($F_{(2,\ 70)} = 3.936$, $p = 0.024$, generalized $\eta^2 = 0.022$). the post hoc test revealed a statistically significant difference ($p = 0.026$) only between the mean rating of the beauty of real flowers (3.38 points) and internet images (3.21 points). There was no statistically significant difference between the mean rating of beauty of standardized photographs (3.23 points) and real flowers (3.38 points) or internet images (3.21 points).

We can conclude that there were no substantial differences between the rating of beauty of the internet images and standardized photographs. Also, real flowers were generally considered slightly more beautiful than the standardized photos (studies A and B) and internet images (study C).

To test the hypothesis 3:

3. there will be a strong positive association between the rating of real flowers and their photographs,

we performed Pearson's correlation tests between the mean ratings of the beauty of flower species by all respondents across all three types of stimuli (real flowers, standardized photographs, and internet images).

Study A
We observed a strong positive correlation between the mean rating of beauty of real flowers and standardized photographs (t = 4.71, df = 34, p-value < 0.0001, r = 0.629, 95% C.I. [0.378; 0.793]), as well as internet images (t = 4.69, df = 34, p-value < 0.0001, r = 0.626, 95% C.I. [0.375; 0.791]). There was an even stronger positive correlation between the standardized photographs and the internet images (t = 9.04, df = 34, p-value < 0.0001, r = 0.840, 95% C.I. [0.707; 0.916]).

Study B
We observed stronger positive correlations than in Study A across all stimuli types: Real flowers and standardized photographs (t = 9.74, df = 36, p-value < 0.0001, r = 0.775, 95% C.I. [0.606; 0.878]), real flowers and internet images (t = 6.416, df = 36, p-value < 0.0001, r = 0.730, 95% C.I. [0.535; 0.851]), and standardized photographs and internet images (t = 9.657, df = 36, p-value < 0.0001, r = 0.849, 95% C.I. [0.727; 0.919]).

Study C
Also in study C, we observed strong positive correlations between all types of stimuli: Real flowers and standardized photographs (t = 6.166, df = 34, p-value < 0.0001, r = 0.727, 95% C.I. [0.523; 0.852]), real flowers and internet images (t = 7.089, df = 34, p-value < 0.0001, r = 0.772, 95% C.I. [0.595; 0.878]), and standardized photographs and internet images (t = 4.644, df = 34, p-value < 0.0001, r = 0.623, 95% C.I. [0.370; 0.790]).

In studies A and B, the strongest correlation was between the standardized photographs and internet images whereas in Study C, this correlation was the weakest (but still over 0.6). See also Fig. 4.

We were also interested in which portion of the variability in the ratings can be explained by the ratings of other stimuli types. We constructed generalized linear models where one type of stimuli was the dependent variable, and another one the explanatory variable. In the case of real flowers, we also added the flower size as another explanatory variable (all flowers in the photographs and internet images had the same size, but the real flowers differed across species). In study A, we also added the variable „withered“ (flowers rated by fewer participants because they withered very quickly) into the model, to control for its possible effect.

Study A
In the case of real flowers, the withered flowers had no effect and were removed from the final models. Flower size had a significant, but low positive effect on the overall rating in both models (coefficient estimate = 0.03). The model with standardized photographs as an explanatory variable had $R^2 = 0.575$ ($F_{2,33} = 22.33$, $p<0.0001$), and the model with internet images had $R^2 = 0.585$ ($F_{2,33} = 23.24$, $p<0.0001$). When we compared the standardized photographs and internet images, the internet images explained 70% of the variability in the ratings of standardized photographs ($F_{1,34} = 81.76$, $p<0.0001$, $R^2 = 0.706$).

Study B

In study B, the flower size had no effect and was removed from the final models. Standardized photographs explained 60% of the variability in the ratings of real flowers ($F_{1,36}$ = 54.29, p<0.0001, R^2 = 0.601). The internet images explained 53% of the variability in the ratings of real flowers ($F_{1,36}$ = 41.17, p<0.0001, R^2 = 0.533) and 72% of the variability in the ratings of standardized photographs ($F_{1,36}$ = 93.27, p<0.0001, R^2 = 0.722).

Study C

In study C, there was a statistically significant positive, but weak effect of the flower size on the rating of beauty (coefficient estimate = 0.02). 66% of the variability in the ratings of real flowers was explained by the rating of standardized photographs ($F_{2,33}$ = 31.68, p<0.0001, R^2 = 0.657) and 65% by internet images ($F_{2,33}$ = 30.75, p<0.0001, R^2 = 0.650). Only 39% of the variability in the ratings of the standardized photographs was explained by the ratings of internet images ($F_{1,34}$ = 21.57, p<0.0001, R^2 = 0.388).

We tested the hypothesis 4:

> **4. there will be a strong negative correlation between the perceived prototypicality and complexity of flowers,**

by a Pearson's correlation test, where we compared the mean ratings of perceived complexity and prototypicality of flowers.

We observed very strong negative correlations between the perceived complexity and prototypicality of flowers in study A (t = -12.968, df = 34, p-value < 0.0001, r = -0.912, 95% C.I. [-0.955; -0.833]) and study C (t = -10.039, df = 34, p-value < 0.0001, r = -0.865, 95% C.I. [-0.930; -0.749]), and a strong negative correlation in study B (t = -5.029, df = 34, p-value < 0.0001, r = -0.642, 95% C.I. [-0.798; -0.406]). See also Fig. 5.

for hypothesis 5:

> **5. bilaterally symmetrical flowers will have low levels of prototypicality and high levels of complexity,**

We used two-sample t-tests, where the perceived prototypicality/complexity served as dependent variables and flower symmetry as a grouping factor. We performed a Bonferroni correction to the p-values due to a high number of tests. We list the p-values after the correction. See also Fig. 5.

Typicality

Bilaterally symmetrical flowers were perceived as less prototypical than radially symmetrical flowers across all studies: Study A (t = 4.00, df = 32, p< 0.001, Cohen's d = 1.43, mean radial = 2.96, mean bilateral = 1.64, 95% C.I. of the difference: [0.65;2.00]), study B (t = 6.91, df = 36, p< 0.0001, Cohen's d = 2.24, mean radial = 3.29, mean bilateral = 1.73, 95% C.I. of the difference: [1.10;2.01]). Study C (t = 5.81, df = 34, p< 0.0001, Cohen's d = 1.97, mean radial = 3.56, mean bilateral = 1.99, 95% C.I. of the difference: [1.02;2.12]).

Complexity

Bilaterally symmetrical flowers were rated as more complex than radially symmetrical flowers in all three studies. Study A: t = -3.71, df = 32, p< 0.001, Cohen's d = 1.33, mean radial = 2.00, mean bilateral = 3.34, 95% C.I. of the difference: [-2.08;-0.60], study B: t = -4.71, df = 36, p< 0.001, Cohen's d = 1.53, mean radial = 2.27, mean bilateral = 3.01, 95% C.I. of the difference: [-1.05;-0.42], study C: t = -3.61, df = 34, p < 0.001, Cohen's d = 1.22, mean radial = 1.96, mean bilateral = 3.17, 95% C.I. of the difference: [-1.90;-0.531].

To test the hypotheses 6, 7, 8 and 9:

> **6. radially symmetrical flowers will be rated as more beautiful than bilaterally symmetrical flowers,**
>
> **7. the rating of flower beauty will increase with perceived flower prototypicality,**
>
> **8. the effect of perceived flower prototypicality on the overall rating of the beauty of flowers will be stronger than the effect of flower color,**
>
> **9. the positive effect of color on the overall rating of flower beauty will be strongest for the red and blue/violet colors and weakest for the yellow color,**

we constructed generalized linear models, where the mean ratings of the beauty of real flowers represented the dependent variable, and the perceived prototypicality and complexity, flower symmetry, flower size, and flower color served as the explanatory variables. Each color was used as a separate binary variable with values 0 (not present) and 1 (present). For study A, we included the variable "withered" in the model. We used the step-wise backward elimination method for the reduction of the models.

Study A

The flowers in Study A had four different colors: blue/violet, purple, white, and yellow. We merged the blue and violet colors into one group because of their low numbers. Because of a very strong correlation between perceived prototypicality and complexity (r = -0.91), we included only the variable prototypicality in the model.

For the real flowers, the initial full model explained 66% of the variability in the ratings (AIC = 35.04). The final reduced model explained 57% of the variability ($F_{4,31}$ = 10.3, p< 0.0001, R^2= 0.57, AIC = 35.1)

	Coefficient estimate	Standard Error	t value	p-value
Intercept	2.373	0.294	8.076	< 0.0001
prototypicality	0.171	0.054	3.192	0.00323
yellow	-0.421	0.153	-2.748	0.00989
white	-0.393	0.144	-2.723	0.0105
flower size	0.0303	0.00831	3.642	0.000976

Study B

The flowers in Study B had five different colors: pink, purple/violet, red, white, and yellow. We merged the purple and violet colors into one group because of their low numbers. The full initial model explained 83% of the variability in the ratings (AIC = 15.01). The final reduced model explained 79% of the variability ($F_{5,32}$ = 24.68, p< 0.0001, R^2 = 0.794, AIC = 12.61).

	Coefficient estimate	Standard Error	t value	p-value
Intercept	3.934	0.280	14.070	< 0.0001
bilateral	-2.509	0.326	-7.688	< 0.0001
prototypicality	-0.210	0.0811	-2.566	0.0152
purple/violet	0.427	0.108	3.941	<0.001
red	0.356	0.112	3.162	0.00342
bilateral:prototypicality	1.172	0.127	9.210	<0.0001

Study C

The flowers in Study B had five different colors: pink, purple, blue/violet, white, and yellow. We merged the purple and violet colors into one group because of their low numbers. The full initial model explained 60% of the variability in the ratings (AIC = 47.90). The final reduced model explained 40% of the variability ($F_{3,32}$ = 7.22, p< 0.001, R^2 = 0.4036, AIC = 48.19).

	Coefficient estimate	Standard Error	t value	p-value
Intercept	1.850	0.360	5.144	< 0.0001
prototypicality	0.207	0.0673	3.075	0.00429
blue/violet	0.463	0.211	2.195	0.0356
flower size	0.0285	0.00867	3.286	0.00247

The models differed in the portion of variability explained. While the model in Study B accounted for more than 80% of the variability of the ratings, the model in Study A explained 60%, and in Study C only 40% of the variability.

We observed a minor positive effect of flower size on the overall rating of beauty of wildflowers in studies A and C. There was also a positive effect of perceived prototypicality. In Study A, we found a negative effect of yellow and white colors on the rating of beauty, and this effect was stronger than the effect of prototypicality. In Study C, we observed a positive effect of blue/violet color, also stronger than the effect of prototypicality. There was no effect of flower symmetry on the rating of flower beauty in studies A and C.

Study B revealed different results. Red and purple/violet colors had a positive effect. However, we observed a negative effect of prototypicality. Moreover, there was a strong negative effect of bilateral symmetry on the rating of flower beauty. The significant interaction between the bilateral symmetry and prototypicality indicates, that the rating of beauty of bilateral flowers improved with their perceived prototypicality.

We further examined the hypothesis 9:

9. the positive effect of color on the overall rating of flower beauty will be strongest for the red and blue/violet colors and weakest for the yellow color,

by controlling for the shape properties of the flowers and testing only the effect of color. All participants first rated the flowers under red light, which prevented them from distinguishing flower colors. We used the difference between their ratings of flower beauty under normal yellow light and red light as the dependent variable and flower colors as factors in the analysis of variance. Since the number of flowers of each color was unbalanced, we used Welch's ANOVA and a subsequent Games-Howell post hoc test to distinguish the differences between groups.

We found a significant effect of color in study A ($F_{3,17,52} = 5.890$, $p = 0.006$), with a difference between purple and white (mean difference = -0.216, 95% C.I. [-0.376;-0.056], p adj. = 0.007), and purple and yellow (mean difference = -0.202, 95% C.I. [-0.360;-0.044], p adj. = 0.011).

In study B, we also found a significant effect of color ($F_{4,16.20} = 7.667$, $p = 0.001$), specifically between white and red (mean difference = 0.511, 95% C.I. [0.135;0.886], p adj. = 0.008), yellow and red (mean difference = 0.644, 95% C.I. [0.238;1.050], p adj. = 0.002), and yellow and purple (mean difference = 0.485, 95% C.I. [0.071;0.899], p adj. = 0.019).

In study C, however, we observed no effect of color ($F_{4,13.754} = 1.179$, $p = 0.363$).
See also Fig. 6.

There were some outliers in all studies, and after their removal, the trends in the data only became more pronounced – there was a bigger difference between purple and white and purple and yellow in Study A, Study C remained insignificant, and

in Study B, the ratings for yellow color became significantly worse than for all other colors.

5. Discussion

5.1. Real flowers, standardized photographs, and internet images

One of the aims of our studies was to explore whether we can use photographs of flowers as substitutes for real flowers in the research of aesthetic responses to flowers. Moreover, we wanted to see, if carefully selected and edited internet images of flowers can serve as equivalents of standardized photographs. We expected that there would not be a substantial difference between the ratings of standardized photographs and internet images and that we would observe a strong positive association in the ratings of all three types of stimuli. However, a 2D representation of flowers on screen cannot fully capture all their properties, therefore, we expected the ratings of the beauty of real flowers to be higher than the ratings of photographs and internet images.

Our results suggest that there was no difference between the mean rating of standardized photographs and internet images of flowers. The ratings of real flowers were slightly higher than the ratings of standardized photographs in studies A and B, but not in study C. Real flowers also scored slightly higher than internet images in study C, but not in studies A and B. When we take a closer look at the statistically significant differences, we can see that the effect sizes of the observed differences between real flowers and standardized photographs were small ($\eta^2 = 0.02$) in study B and medium (η^2

= 0.09) in study A. The mean differences in the ratings were close to 0.15 points for the small effect, and close to 0.4 for the medium effect (out of the maximal difference of 5 points). The only statistically significant difference between the ratings of real flowers and internet images (study C) also had a small effect ($\eta^2 = 0.02$) and the mean difference between the ratings was close to 0.15 points.

We can conclude that when we look at the absolute ratings of different types of stimuli, there are no differences between the standardized photographs and internet images. Moreover, the differences between real flowers and internet images are also nonsignificant or very small. In the case of real flowers and their standardized photographs, there is a small difference between ornamental flowers (study B) and ambiguous results for wildflowers (medium effect for study A and no effect for study C). Since study A had a lower number of participants and some problems with withering flowers, the results of study C should be taken more seriously.

Even more interesting is to look not only at the absolute differences in the ratings (which flower got which score) but also at the relative differences (which flower scored better than another). The relative differences tell us more about the suitability of photographs or internet images as substitutes for real flowers because we are usually comparing the aesthetic responses to different flowers. Therefore, we used the correlation test to see the strength of the association between the ratings of different types of flower stimuli. We found strong positive correlations in the ratings of real flowers and their standardized photographs (A: $r = 0.63$, B: $r = 0.78$, C: $r = 0.73$), as well as their internet images (A: $r = 0.63$, B: $r = 0.73$, C: $r = 0.78$). We also found strong positive correlations between the rating of standardized photographs and internet images (A: $r = 0.84$, B: $r = 0.85$, C: $r = 0.62$). See also Fig. 4.

Generalized linear models also showed that a substantial amount of variability in the ratings of real flowers can be explained by the ratings of standardized photographs (A: $R^2 = 0.58$, B: $R^2 = 0.60$, C: $R^2 = 0.66$), as well as by the internet images (A: $R^2 = 0.59$, B: $R^2 = 0.53$, C: $R^2 = 0.65$). Internet images also explained more than 70 % of the variability in the ratings of standardized photographs in studies A and B, but only 39 % in study C (A: $R^2 = 0.70$, B: $R^2 = 0.72$, C: $R^2 = 0.39$).

Our results are similar to those of Landová and colleagues (Landová et al., 2012), who directly compared the ratings of beauty of living organisms (snakes) with the rating of beauty of their photographs. In their case, the $r = 0.78$ and $R^2 = 0.61$. We have to take into account that in their study the participants ranked the snakes from the most to the least beautiful and did not use scales. However, another research focusing on the rating of the beauty of parrots showed that both ranking and rating on scales yield very similar results (Frynta et al., 2010).

We expected to find the strongest association among stimuli types between standardized photographs and internet images because they are more similar to each other than to real flowers. Indeed, this was the case in studies A and B. Study C, however, showed a strong association between real flowers and both photographs and internet images, but a relatively weak between photographs and internet images. The way the photographs and images were taken, edited, and presented did not differ across studies. Stimuli in study C had a similar ratio of bilaterally symmetrical flowers as in the other two studies, also they did not contain any unique colors (such as red in study B) or entirely different shapes. Both studies A and B took place during the growth season, and the participants were recruited from the same background. The observed result thus remains intriguing.

In conclusion, we observed very low differences in the absolute ratings of flower beauty across different types of stimuli. The relative ratings strongly positively correlated and a substantial amount of variability of ratings of real flowers was explained by the ratings of standardized photographs or internet images (and flower size). The results were in line with previous research conducted on animals (Landová et al., 2012). We can thus say that standardized photographs, as well as carefully chosen and edited internet images, can serve as good substitutes for real flowers in the research of aesthetic responses.

5.2. Prototypicality, complexity, and symmetry

Based on our previous research (Hůla & Flegr, 2016), we expected to find a strong association between symmetry and the perceived prototypicality and complexity of flowers. Flowers rated as very prototypical would be rated as simple, and highly complex flowers would be rated as unusual. Radially symmetrical flowers would score high in prototypicality and low in complexity when compared with bilaterally symmetrical flowers. Our results confirmed this expectation. Bilaterally symmetrical flowers had low levels of prototypicality (A: mean difference = 1.32, d = 1.43; B: mean difference = 1.56, d = 2.24; C: mean difference = 1.57, d = 1.97. Maximal possible difference was 5 points) and high levels of complexity (A: mean difference = 1.34, d = 1.33; B: mean difference = 0.74, d = 1.53; C: mean difference = 1.21, d = 1.22). There was also a very strong negative correlation between the mean rating of perceived prototypicality and complexity of flowers (A: r = -0.91; B: r = -0.87; C: r = -0.64).

The negative correlation between complexity and prototypicality might appear intuitive, but it is not self-evident. For example, a prototypical butterfly (such as the peacock butterfly) would probably have colorful patterns on the wings and would be therefore more complex than a dull and simple, yet less prototypical flour moth. When flowers are concerned, however, it seems that simple flowers are mostly rated as prototypical. If we look at the graphs (Fig. 5), there are seldom simple and unusual flowers (only *Cyclamen* in study B). More often, we encounter complex and prototypical flowers, especially in study C, which might account for its weaker (but still strong) correlation than in the other two studies. The prototypical, yet complex flowers seemed to have one common feature. They had an overall simple shape, but they were composed of many parts. Some were double-flowered (had extra petals) – *Kerria, Santina* – and some were polyandrous (had extra stamens) – *Fragaria, Potentilla*.

The strong association of bilateral flowers with low prototypicality and high complexity was not caused by the symmetry itself, because there were exceptions to this trend. The most complex and unusual flowers had usually fused floral parts (*Lamium, Antirrhinum*) or were drooping (*Aquilegia, Cyclamen*), and therefore, were bilaterally symmetrical. On the other hand, there were some simple bilateral flowers (*Rhododendron, Calibrachoa*).

Many studies found that symmetry, prototypicality, and complexity influence the aesthetical responses of humans to various objects and organisms (see for example (Reber et al., 2004). Our previous research on flowers (Hůla & Flegr, 2016) also found an effect of all these three features on the rating of flower beauty, when they were tested separately. When testing for their relative importance, we found that prototypicality played the most important role by encompassing both complexity and symmetry. Our current results also found prototypicality to affect the ratings of beauty, with coefficient estimates of the linear models around 0.2, and no effect of complexity or symmetry (studies A and C). In study B, we observed a strong negative effect of bilateral symmetry (coefficient estimate around -2.5), and also a negative effect of prototypicality (-0.2). However, there was a significant interaction between bilateral symmetry and prototypicality (1.2), so in general, the presence of bilaterality lowered the rating of beauty by 2.5 points, but for each point of prototypicality, it improved the rating by 1.2 points. This result illustrates, that prototypicality might be crucial when rating very unusual vs normal flowers, and not very beneficial when rating normal flowers vs very typical flowers. On the other hand, we observed this interaction only in study B, where there were only 8 different genera (4 bilateral), so the effect might have been caused by a specific flower stimulus rather than by symmetry.

Based on our previous experiences, we also expected the effect of prototypicality on the ratings of beauty to be more important than the effect of colors. Prototypicality indeed influenced all flowers, but when there was an effect of color, it was stronger.

5.3. Beauty and colors

Our previous research conducted on internet images of flowers (Hůla & Flegr, 2016) predicted only the positive effect of blue color (coefficient estimate 0.34) on the rating of flower beauty when we did not control for shape properties. In another study, exploring aesthetic responses to various flowers and fruits, we found red and pink colors to have the highest ratings. However, there were no blue or violet flowers and fruits in the study (Hůla & Flegr, 2021). Now, we found a positive effect of blue/violet (0.46) in study C, a positive effect of purple/violet (0.43) and red (0.34) in study B, and negative effects of yellow (-0.42) and white (-0.39) in study A.

When the shape properties were filtered out in our previous research (Hůla & Flegr, 2016), blue (0.37), purple (0.22), and pink (0.20) colors had a positive effect, and yellow had a negative effect (-0.20).
In the current studies, we also controlled for the shape features of the stimuli by looking at the difference between the ratings of flowers under normal light and red light (Fig. 6). In study C we observed no statistically significant differences between the ratings of different colors, but purple flowers were rated as more beautiful under normal light than under red (monochromatic) light. In study B, red and purple/violet flowers had higher ratings than yellow flowers, and red also scored higher than white. Red and purple/violet flowers scored higher under normal light, but yellow flowers got better ratings under red light (when their color was not visible). In study A, purple flowers scored higher than yellow and white flowers and purple and blue/violet flowers also got better ratings under normal light. We should pay attention especially to the results of study B, where the stimuli had low diversity of shapes and each flower species was present in at least four color variants.

From our results, we can see a clear trend where blue/violet, red, and purple have an overall positive effect on the rating of the beauty of flowers, and yellow and white have a neutral or negative effect. These results are in line with our previous research conducted on flowers. Moreover, red was reported to be preferred among customers purchasing flowers in shops (Behe et al., 1999; Yue & Behe, 2010), and among students rating the attractiveness of fruits (Prokop & Fančovičová, 2012). Red was preferred also in a study focusing on the beauty of trees (Kaufman & Lohr, 2002), but another study found the opposite results, with red being the least preferred color, and blue the most preferred (Muderrisoglu et al., 2009). Research on the beauty of snakes also reported a positive effect of red (Maresová et al., 2009). Studies focusing on birds found mostly the positive effect of blue, but not red (Lišková et al., 2015), and of blue and yellow (Frynta et al., 2010; Lišková et al., 2015), the latter being the least preferred in our sample. The preference for colors is highly context- and object-dependent (Ben-You and Ling-Li, 2011), so what applies to birds or snakes might not apply to flowers.

5.4. Limitations and Future Prospects

We encountered practical problems during the data collection, which affected Study A. Withering flowers, unexpectedly destroyed source areas for flower stimuli, and participants who did not arrive at the lab considerably lowered the number of raters per flower. However, the results of study A showed similar trends as the other two studies.

Another issue typical for the research of aesthetic responses to flowers is a relatively lower number of men among the participants, which makes it difficult to generalize our results.. It is thus difficult to examine possible sex differences in the ratings. Our previous research showed, however, that differences between men and women are only minor, and mostly in absolute ratings, not in the relative ratings (men rated all flowers slightly less beautiful than women, but the order of their ratings was the same).

We also need to point out that the ratings of complexity and typicality were performed online on the standardized photographs. They were rated by an independent set of participants, who did not see the real flowers. The ratings of real flowers might be different. On the other hand, there were no substantial differences between real flowers and photographs in the ratings of beauty, so we might still consider the prototypicality and complexity scores reliable.

We found that the aesthetic responses of Czech participants to flowers are stable. A logical next step is to conduct a large-scale intercultural study to examine if the features affecting the rating of the beauty of flowers are the same across cultures. We might also focus on the familiarity with flowers and their role in the ratings. Another promising approach that might help us to understand, if the patterns of aesthetic responses to flowers are shared by all humans, is to work with infants, who are not yet affected by the cultural influences.

6. Summary and Conclusion

Our results suggest that both standardized photographs and internet images of flowers might serve as substitutes for real flowers in the research of aesthetic responses. Of course, a careful selection and editing of images is necessary. However, the possibility to use internet images not only greatly simplifies the logistics of experiments, but also opens many possibilities in the research of the effect of familiarity of flowers, it might help to conduct intercultural studies and incorporate a more diverse set of flowers into stimuli samples.

We also confirmed and expanded the results of our previous research on independent sets of raters and stimuli, showing that at least among Czech raters, the features affecting the rating of flower beauty remain stable in time and across stimuli. We confirmed the strong negative relationship between prototypicality and complexity. We also confirmed that bilaterally symmetrical flowers score low in prototypicality and high in complexity. However, our data suggest that the bilateral symmetry itself is not responsible for these scores, it is more probably just a by-product of some atypical and complex floral features, such as fused or drooping corollas. Furthermore, we confirmed that prototypicality is more important than complexity or type of symmetry in the rating of flower beauty. It had a positive effect by itself (studies A and C), or a positive modulating role on bilateral flowers (study B).

According to our expectations, blue/violet and purple colors had a positive influence on the rating of beauty, whereas white and yellow had neutral or even negative effects. Unlike the previous research, the effects of colors here were stronger than the effects of prototypicality. However, they were not present in all studies. For the first time, we also explored the effect of red color on the rating of flower beauty, and it was positive.

Our results provide a more robust basis and offer new options for conducting future research on aesthetic responses to flowers, especially in intercultural contexts.

7. Acknowledgments

We would like to thank Tereza Bezděková and Hana Vršecká for their help with the purchase of ornamental flowers, Vojtěch Zíka for help with the digitalization of the data, and Tomáš Macháček for the propagation of the experiment. This research was supported by the Charles University (GAUK n.: 1494217).

Fig. 4: Relationship between the mean rating of beauty across different types of stimuli. X-axis/y-axis: mean rating of beauty of a given flower stimulus from all participants (in points, min = 0, max = 5). **A/Z** = radially (actinomorphic)/bilaterally (zygomorphic) symmetrical flowers. **B/V** = blue/violet, **Pi** = pink, **P/Pr** = purple, **R** = red, **W** = white, **Y** = yellow. Flowers above the dashed line had higher rating on the y-axis and the flowers below the line had a higher rating on the x-axis.

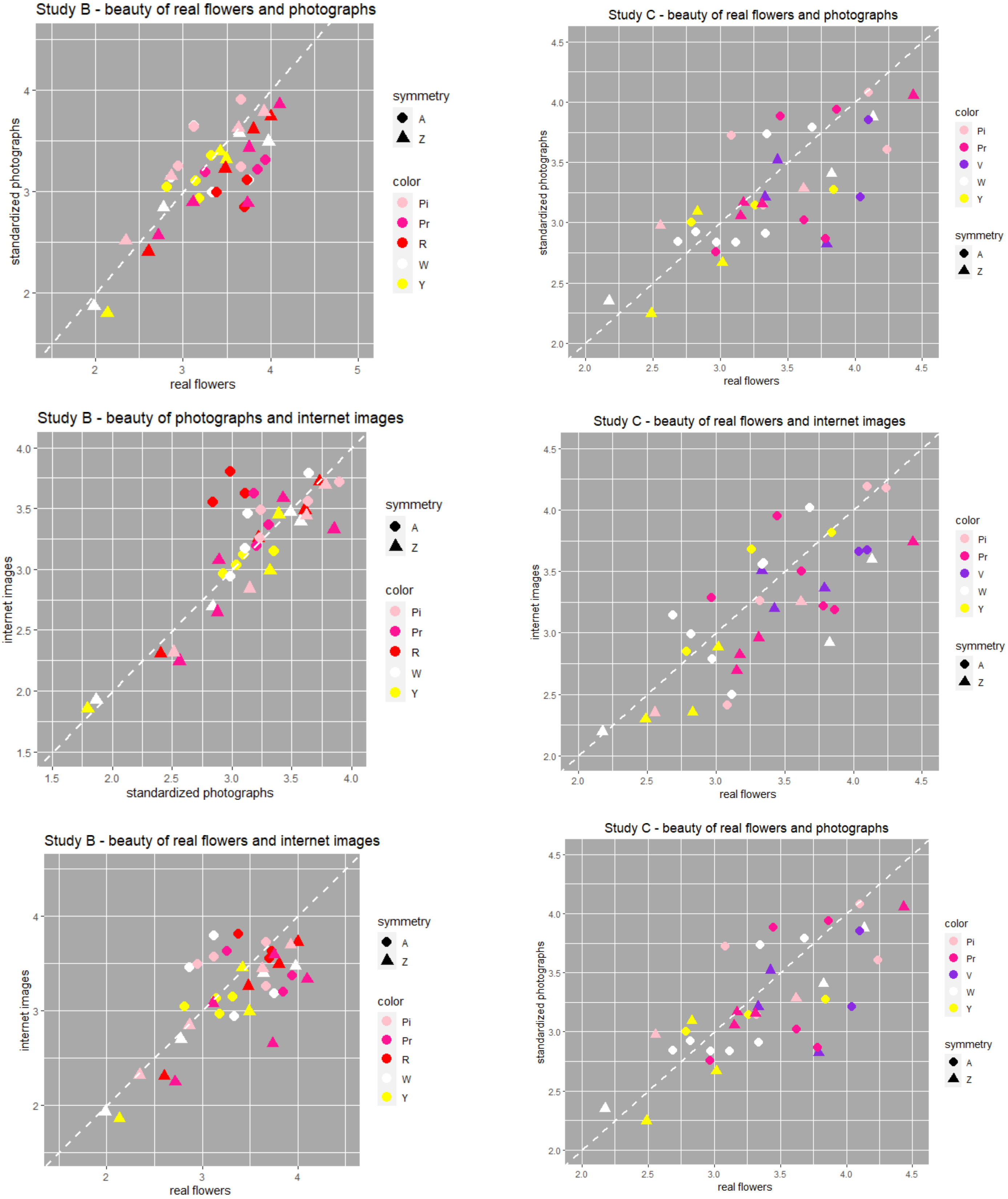
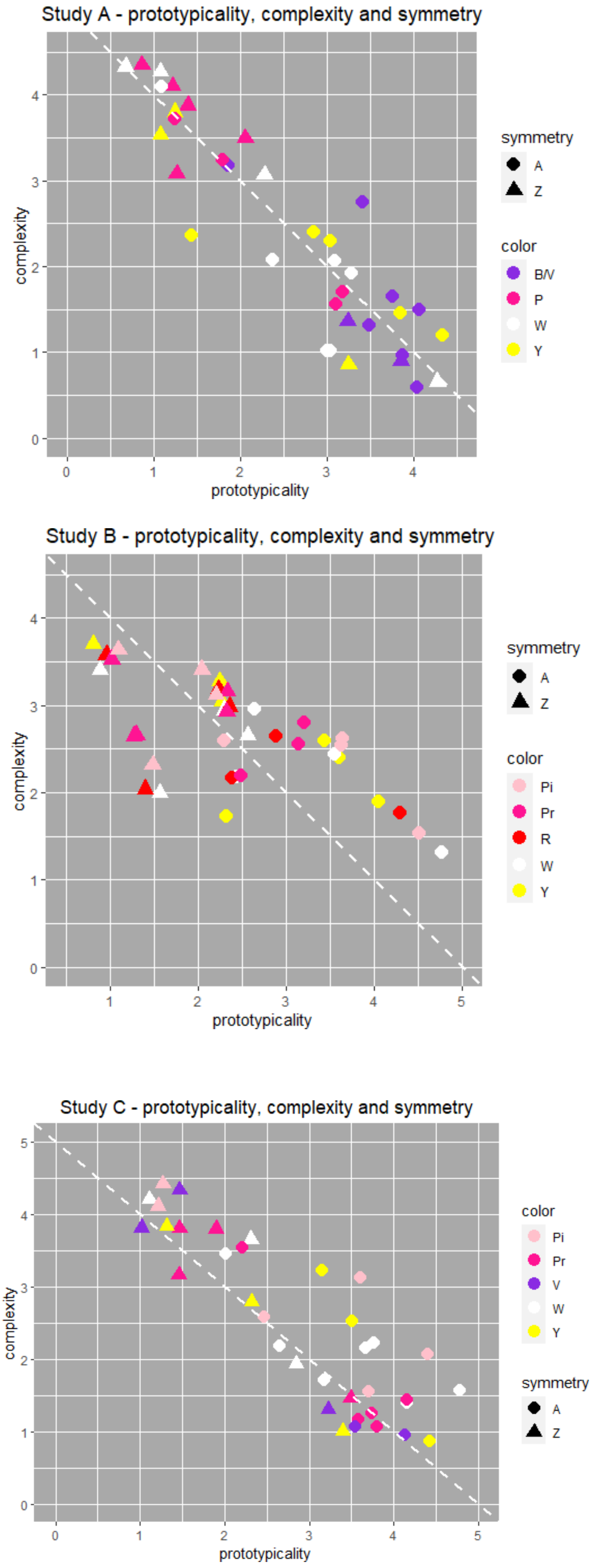
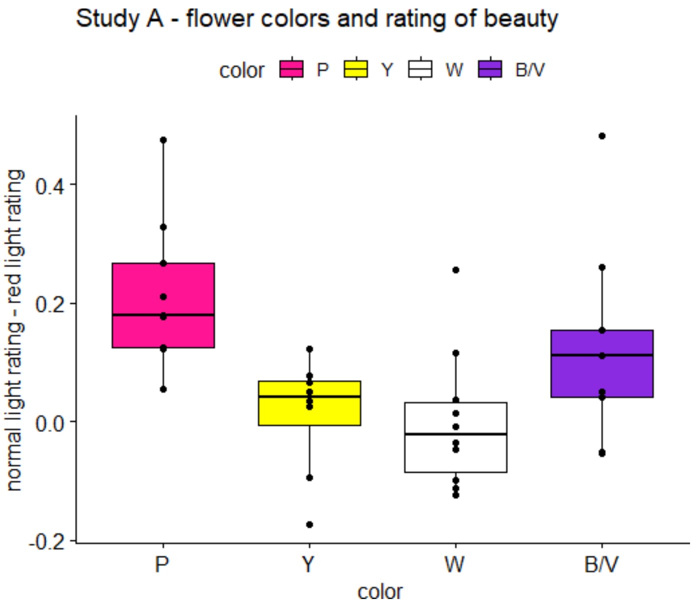
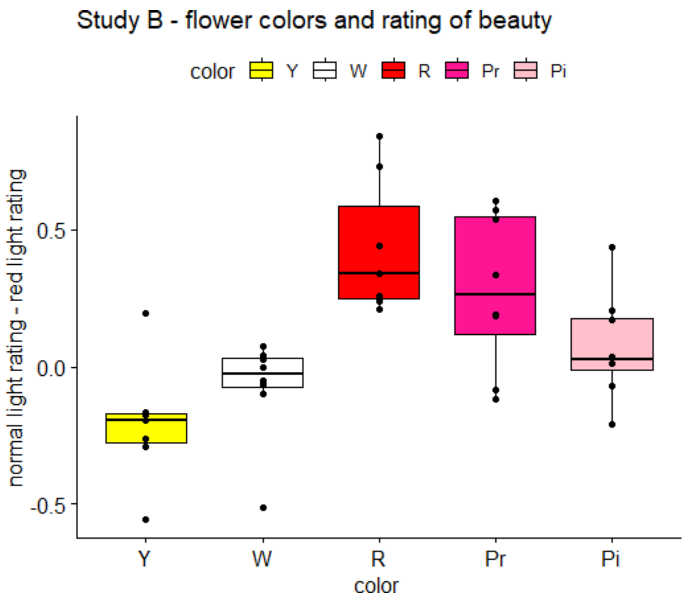


Fig. 5: Relationship between the perceived prototypicality and complexity, and floral symmetry. X-axis/y-axis: mean rating of prototypicality/complexity of a given flower stimulus from all participants (in points, min = 0, max = 5). **A/Z** = radially (actinomorphic)/bilaterally (zygomorphic) symmetrical flowers. **B/V** = blue/violet, **Pi** = pink, **P/Pr** = purple, **R** = red, **W** = white, **Y** = yellow.







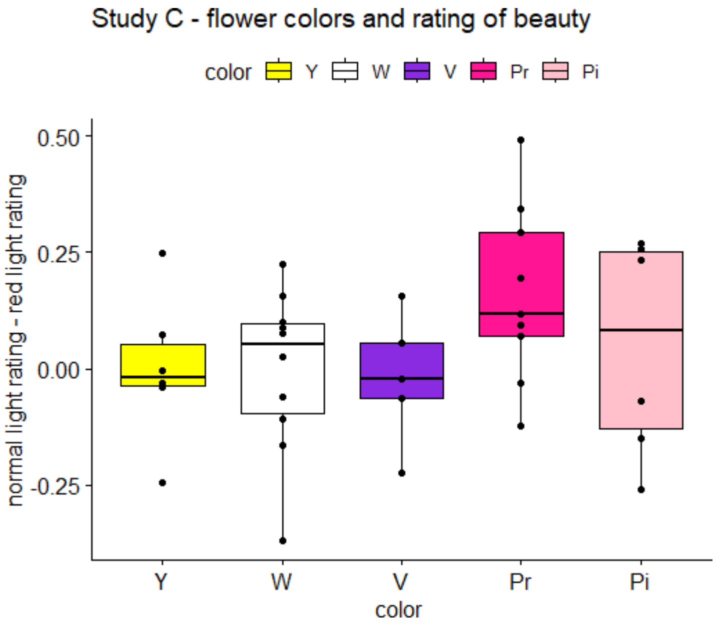


Fig. 6: The effect of color on the difference between the rating of beauty under normal and red light. x-axis = flower colors, y-axis = the difference between the mean rating of beauty of flowers under normal light and red light. The values above 0 indicate that flowers of a given color had a higher rating when their color was distinguishable.

ID	scientific name	flower size (mm)	symmetry	color	real flower	photograph	internet	complexity	prototypicality	real red	difference light	withered
11	*Lathyrus tuberosus*	20	bilateral	purple	3,44	2,96	2,85	3,08	1,27	2,96	0,48	no
12	*Colutea arborescens*	23	bilateral	yellow	2,86	2,51	2,42	3,53	1,08	2,81	0,05	no
13	*Lamium album*	18	bilateral	white	2,47	2,03	2,07	4,33	0,68	2,46	0,01	no
14	*Lamium maculatum*	18	bilateral	purple	2,75	2,58	2,00	4,35	0,87	2,63	0,12	no
15	*Impatiens glandulifera*	39	bilateral	white	3,48	2,29	2,13	4,27	1,08	3,22	0,26	yes
16	*Impatiens glandulifera*	38	bilateral	purple	3,73	2,68	2,63	4,10	1,22	3,55	0,18	yes
17	*Phalaenopsis sp.*	38	bilateral	purple	4,39	3,80	3,61	3,50	2,06	4,33	0,05	no
18	*Phalaenopsis sp.*	38	bilateral	white	4,29	3,76	3,31	3,07	2,28	4,33	-0,05	no
19	*Calibrachoa sp.*	25	bilateral	yellow	3,23	2,81	3,06	0,86	3,24	3,33	-0,09	no
20	*Calibrachoa sp.*	27	bilateral	blue/violet	4,18	3,08	3,54	1,36	3,24	4,14	0,04	no
21	*Antirrhinum majus*	43	bilateral	purple	3,46	2,71	2,39	3,87	1,39	3,25	0,21	no
22	*Antirrhinum majus*	40	bilateral	yellow	3,12	1,89	2,15	3,80	1,24	3,00	0,12	no
23	*Sutera cordata*	20	bilateral	blue/violet	3,85	2,97	3,40	0,89	3,85	3,74	0,11	no
24	*Sutera cordata*	20	bilateral	white	2,65	3,34	3,32	0,65	4,27	2,66	-0,01	yes
25	*Calendula officinalis*	34	radial	yellow	4,33	3,51	3,76	1,20	4,33	4,31	0,02	no
26	*Symphyotrichum sp.*	30	radial	blue/violet	3,56	3,56	3,92	1,49	4,06	3,40	0,16	no
27	*Crepis biennis*	30	radial	yellow	3,13	3,03	3,28	1,45	3,84	3,05	0,08	no
28	*Cichorium intybus*	35	radial	blue/violet	3,83	3,44	4,31	1,65	3,76	3,57	0,26	no
29	*Fragaria viridis*	22	radial	white	3,23	2,94	3,46	1,92	3,28	3,26	-0,04	yes
30	*Potentilla fruticosa*	31	radial	yellow	3,75	3,14	3,76	2,30	3,03	3,71	0,03	no
31	*Hypericum perforatum*	26	radial	yellow	3,03	3,43	3,29	2,40	2,84	3,20	-0,17	no
32	*Rubus fruticosus*	36	radial	white	3,29	2,81	2,78	2,07	3,09	3,17	0,12	yes
33	*Phlox paniculata*	37	radial	blue/violet	4,11	3,81	3,71	0,59	4,03	4,00	0,11	no
34	*Saponaria officinalis*	23	radial	white	3,43	2,32	2,83	1,02	3,03	3,39	0,04	no
35	*Convolvulus arvensis*	25	radial	white	3,07	3,47	3,44	1,02	2,99	3,17	-0,10	yes
36	*Campanula persicifolia*	28	radial	blue/violet	3,85	3,63	3,85	1,31	3,48	3,90	-0,05	no
37	*Solanum lycopersicum*	20	radial	yellow	2,69	2,87	2,58	2,36	1,44	2,62	0,07	no
38	*Borago officinalis*	23	radial	blue/violet	3,69	3,37	3,83	3,17	1,86	3,64	0,05	yes
39	*Dianthus sp.*	25	radial	white	3,08	3,29	3,21	2,08	2,37	3,19	-0,11	no
40	*Dianthus carthusianorum*	21	radial	purple	4,06	3,72	3,92	1,56	3,09	3,94	0,13	no
41	*Centaurea jacea*	40	radial	purple	3,40	2,68	3,55	3,24	1,80	3,13	0,27	no
42	*Centaurea cyanum*	33	radial	blue/violet	4,09	4,17	4,40	2,75	3,41	3,60	0,48	yes
43	*Geranium pratense*	35	radial	blue/violet	4,18	3,75	3,64	0,97	3,87	4,24	-0,05	yes
44	*Epilobium montanum*	25	radial	purple	3,25	2,94	3,64	1,71	3,18	2,92	0,33	yes
45	*Arctium tomentosum*	25	radial	purple	3,28	2,73	2,72	3,71	1,25	3,10	0,18	no
46	*Virga pilosa*	23	radial	white	3,09	2,30	2,46	4,09	1,09	3,21	-0,12	no

Tab. 1: Study A – list of stimuli. ID = identification number of the flower stimulus, **scientific name** = scientific name of the flower, **flower size (mm)** = diameter of the flower in mm, **symmetry** = type of floral symmetry, **color** = color of the flower, **real flower** = mean rating of the beauty of real flowers by all participants, **photograph** = mean rating of the beauty of standardized photographs of the flowers by all participants, **internet** = mean rating of the beauty of flowers in internet images by all participants, **complexity** = mean rating of the perceived complexity of flowers by all participants, **prototypicality** = mean rating of perceived prototypicality of flowers by all participants, **real red** = mean rating of the beauty of real flowers under red light by all participants, **difference light** = difference in the mean rating of the beauty of flowers under normal yellow light and red light by all participants, **withered** = was the flower rated by less than 90% of participants due to withering (yes = rated by less than 90% of participants, no = rated by more than 90% of participants). All ratings are in points (min = 0, max = 5). Please note that the symmetry of some flowers is not strictly botanical, but it reflects the appearance of the flower to the non-botanical public. *Crepis, Cichorium, Centaurea, Arctium*, and *Virga* are inflorescences of zygomorphic flowers but they form pseudanthia (flower heads) that look like single radial flowers.

ID	genus	flowerSizeMm	symmetry	color	real flower	photograph	internet	complexity	prototypicality	real red	difference light
11	*Alstroemeria*	70	bilateral	pink	3,93	3,78	3,69	3,41	2,05	3,89	0,04
12	*Alstroemeria*	60	bilateral	red	3,80	3,61	3,49	3,18	2,23	3,56	0,24
13	*Alstroemeria*	70	bilateral	purple	3,75	3,43	3,59	3,16	2,33	3,84	-0,08
14	*Alstroemeria*	65	bilateral	white	3,98	3,49	3,47	2,65	2,56	4,03	-0,05
15	*Alstroemeria*	70	bilateral	yellow	3,42	3,39	3,45	3,04	2,27	3,98	-0,56
16	*Antirrhinum*	45	bilateral	pink	2,35	2,51	2,32	3,64	1,10	2,18	0,17
17	*Antirrhinum*	44	bilateral	purple	2,72	2,56	2,24	3,53	1,02	2,11	0,60
18	*Antirrhinum*	45	bilateral	red	2,60	2,40	2,30	3,57	0,96	1,76	0,84
19	*Antirrhinum*	45	bilateral	white	1,99	1,87	1,93	3,40	0,89	1,99	0,00
20	*Antirrhinum*	45	bilateral	yellow	2,14	1,79	1,85	3,70	0,81	1,94	0,20
21	*Cyclamen*	30	bilateral	pink	2,86	3,15	2,84	2,31	1,48	2,43	0,44
22	*Cyclamen*	30	bilateral	purple	3,11	2,89	3,07	2,65	1,27	2,54	0,57
23	*Cyclamen*	30	bilateral	red	3,48	3,22	3,26	2,04	1,40	2,75	0,73
24	*Cyclamen*	30	bilateral	violet	3,74	2,88	2,65	2,66	1,30	3,20	0,54
25	*Cyclamen*	30	bilateral	white	2,78	2,84	2,70	1,99	1,57	2,70	0,08
26	*Dianthus*	40	radial	pink	3,67	3,90	3,72	2,54	3,63	3,88	-0,21
27	*Dianthus*	40	radial	purple	3,94	3,30	3,37	2,55	3,14	3,75	0,19
28	*Dianthus*	40	radial	red	3,73	3,11	3,62	2,65	2,88	3,29	0,44
29	*Dianthus*	40	radial	white	3,75	3,11	3,17	2,95	2,64	3,71	0,04
30	*Dianthus*	40	radial	yellow	3,32	3,35	3,15	2,59	3,43	3,61	-0,29
31	*Freesia*	43	radial	pink	3,67	3,23	3,26	2,59	2,29	3,46	0,20
32	*Freesia*	43	radial	red	3,70	2,84	3,55	2,17	2,39	3,36	0,34
33	*Freesia*	43	radial	purple	3,85	3,21	3,20	2,20	2,49	3,66	0,19
34	*Freesia*	43	radial	white	3,33	2,99	2,94	2,17	2,44	3,40	-0,07
35	*Freesia*	43	radial	yellow	3,19	2,93	2,96	1,72	2,33	3,36	-0,18
36	*Phalaenopsis*	39	bilateral	pink	3,63	3,62	3,44	3,12	2,20	3,70	-0,07
37	*Phalaenopsis*	39	bilateral	purple	4,10	3,85	3,33	2,92	2,33	3,76	0,34
38	*Phalaenopsis*	39	bilateral	red	4,00	3,73	3,72	2,98	2,36	3,79	0,21
39	*Phalaenopsis*	39	bilateral	white	3,64	3,57	3,39	2,94	2,30	3,61	0,03
40	*Phalaenopsis*	39	bilateral	yellow	3,49	3,32	2,99	3,27	2,25	3,69	-0,19
41	*Chrysanthemum*	35	radial	pink	2,95	3,24	3,49	1,53	4,52	2,94	0,01
42	*Chrysanthemum*	35	radial	red	3,38	2,99	3,80	1,77	4,29	3,13	0,26
43	*Chrysanthemum*	35	radial	white	3,12	3,65	3,79	1,31	4,77	3,64	-0,51
44	*Chrysanthemum*	35	radial	yellow	2,81	3,04	3,04	1,90	4,05	3,08	-0,26
45	*Santina*	40	radial	pink	3,12	3,63	3,56	2,62	3,64	3,11	0,01
46	*Santina*	40	radial	purple	3,26	3,18	3,62	2,80	3,20	3,38	-0,12
47	*Santina*	40	radial	white	2,86	3,13	3,46	2,44	3,55	2,96	-0,10
48	*Santina*	40	radial	yellow	3,15	3,10	3,12	2,40	3,61	3,31	-0,16

Tab. 2: Study B – list of stimuli. **ID** = identification number of the flower stimulus, **genus** = genus of the flower stimulus, **flower size (mm)** = diameter of the flower in mm, **symmetry** = type of floral symmetry, **color** = color of the flower, **real flower** = mean rating of the beauty of real flowers by all participants, **photograph** = mean rating of the beauty of standardized photographs of the flowers by all participants, **internet** = mean rating of the beauty of flowers in internet images by all participants, **complexity** = mean rating of the perceived complexity of flowers by all participants, **prototypicality** = mean rating of perceived prototypicality of flowers by all participants, **real red** = mean rating of the beauty of real flowers under red light by all participants, **difference light** = difference in the mean rating of the beauty of flowers under normal yellow light and red light by all participants. All ratings are in points (min = 0, max = 5). Please note: *Cyclamen* is a radial flower, but because it is drooping, it appears bilateral.

ID	scientific name	flower size (mm)	symmetry	color	real flower	photograph	internet	complexity	typicality	real red	difference light
11	*Fragaria viridis*	22	radial	white	2,69	2,84	3,14	2,22	3,77	3,05	-0,37
12	*Potentilla fruticosa*	31	radial	yellow	3,26	3,15	3,68	2,52	3,51	3,29	-0,03
13	*Antirrhinum majus*	46	bilateral	purple	3,15	3,05	2,69	3,80	1,47	2,86	0,29
14	*Antirrhinum majus*	42	bilateral	yellow	2,49	2,25	2,30	3,84	1,31	2,49	0,00
15	*Calibrachoa sp.*	23	bilateral	yellow	3,02	2,67	2,88	1,01	3,40	3,06	-0,04
16	*Calibrachoa sp.*	27	bilateral	violet	3,79	2,82	3,36	1,31	3,23	3,85	-0,06
17	*Lamium album*	18	bilateral	white	2,17	2,35	2,20	4,20	1,11	2,15	0,02
18	*Lamium maculatum*	18	bilateral	pink	2,56	2,98	2,35	4,11	1,21	2,29	0,27
19	*Phalaenopsis sp.*	41	bilateral	purple	4,43	4,05	3,74	3,80	1,90	4,32	0,12
20	*Phalaenopsis sp.*	39	bilateral	white	4,13	3,88	3,60	3,66	2,31	4,19	-0,06
21	*Aquilegia officinalis*	32	bilateral	violet	3,43	3,52	3,20	4,33	1,47	3,27	0,16
22	*Aquilegia officinalis*	44	bilateral	pink	3,62	3,28	3,25	4,42	1,27	3,77	-0,15
23	*Leucanthemum sp.*	30	radial	white	3,68	3,79	4,02	1,57	4,78	3,79	-0,11
24	*Leucnanthemum sp.*	35	radial	pink	4,24	3,60	4,18	2,07	4,41	3,98	0,26
25	*Weigela sp.*	33	radial	pink	3,08	3,72	2,41	1,55	3,70	3,15	-0,07
26	*Weigela sp.*	30	radial	white	2,97	2,84	2,79	1,71	3,18	2,82	0,16
27	*Phlox paniculata*	25	radial	violet	4,10	3,85	3,67	0,96	4,13	4,12	-0,02
28	*Phlox paniculata*	20	radial	purple	3,87	3,94	3,19	1,07	3,81	3,77	0,09
29	*Cerastium tomentosum*	18	radial	white	3,35	3,73	3,57	1,40	4,16	3,26	0,09
30	*Geranium pyrenaicum*	18	radial	purple	3,45	3,88	3,95	1,44	4,15	3,57	-0,12
31	*Kerria japonica*	37	radial	yellow	3,84	3,28	3,82	3,22	3,15	3,77	0,07
32	*Santina sp.*	41	radial	pink	4,10	4,08	4,19	3,12	3,61	3,87	0,23
33	*Lathyrus tuberosus*	20	bilateral	purple	3,17	3,17	2,82	3,16	1,46	2,68	0,49
34	*Babtisia australis*	25	bilateral	violet	3,33	3,21	3,50	3,81	1,02	3,28	0,06
35	*Diaanthus sp.*	21	radial	pink	3,32	3,15	3,26	2,59	2,46	3,58	-0,26
36	*Dianthus sp.*	33	radial	white	2,82	2,92	2,99	2,19	2,65	2,75	0,08
37	*Ranunculus acris*	20	radial	yellow	2,79	3,00	2,85	0,87	4,43	3,03	-0,24
38	*Geranium sanguineum*	37	radial	purple	3,62	3,02	3,50	1,17	3,58	3,65	-0,03
39	*Rhododendron sp.*	29	bilateral	white	3,83	3,41	2,92	1,93	2,85	3,60	0,23
40	*Rhododendron sp.*	35	bilateral	purple	3,31	3,16	2,96	1,46	3,49	3,24	0,07
41	*Nemesia sp.*	22	bilateral	yellow	2,83	3,09	2,35	2,79	2,32	2,58	0,25
42	*Trifolium pratense*	32	radial	purple	2,97	2,76	3,28	3,54	2,21	2,77	0,20
43	*Vinca major*	44	radial	violet	4,04	3,21	3,66	1,07	3,55	4,26	-0,22
44	*Primula rosea*	33	radial	purple	3,78	2,87	3,22	1,26	3,74	3,44	0,34
45	*Allium schoenoprasum*	38	radial	white	3,34	2,91	3,56	3,46	2,01	3,50	-0,16
46	*Rubus fruticosus*	36	radial	white	3,12	2,84	2,50	2,16	3,67	3,02	0,10

Tab. 3: Study C – list of stimuli. **ID** = identification number of the flower stimulus, **scientific name** = scientific name of the flower, **flower size (mm)** = diameter of the flower in mm, **symmetry** = type of floral symmetry, **color** = color of the flower, **real flower** = mean rating of the beauty of real flowers by all participants, **photograph** = mean rating of the beauty of standardized photographs of the flowers by all participants, **internet** = mean rating of the beauty of flowers in internet images by all participants, **complexity** = mean rating of the perceived complexity of flowers by all participants, **prototypicality** = mean rating of perceived prototypicality of flowers by all participants, **real red** = mean rating of the beauty of real flowers under red light by all participants, **difference light** = difference in the mean rating of the beauty of flowers under normal yellow light and red light by all participants. All ratings are in points (min = 0, max = 5). Please note that the symmetry of some flowers is not strictly botanical, but it reflects the appearance of the flower to the non-botanical public. *Leucanthemum, Santina*, and *Trifolium* are inflorescences of zygomorphic flowers, and *Aquilegia* has radial symmetry, but it appears to be bilateral because its flower is drooping.

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He contributed to the study design, data collection, statistical analyses, manuscript writing, and subsequent revisions.

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