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Analysis of Factors Affecting Human Preferences and Thus Effort Given to the Conservation of Animal Species

Ph.D. Thesis

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V Praze, dne Silvie Lišková

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Abstract

Recently, it was reported that humans treat animals that they perceive as aesthetically attractive unequally to the “ugly” ones, turning more attention to them and setting more conservation programs for their protection. The aim of this thesis was to investigate the issue focusing around animal beauty in more detail by examining human preferences towards one of the most popular animal taxon, the birds.

In three subsequent studies, we assessed human preferences towards selected bird species: all members of the order of parrots, randomly selected representatives of all non-passerine bird families, and all members of the vividly colored passerine family Pittidae. The first study revealed that the preferred parrots were kept in zoos in higher numbers, regardless of their conservation priority (IUCN status). We discussed possible consequences of this finding and the benefits that may arise in the light of animal conservation if this bias in species preferences was to be considered by conservation specialists. We also found that people preferred long-tailed parrots possessing blue and yellow colors over green ones, which were probably perceived as dull and uninteresting as the majority of the parrots are fully or partially green.

In the next two studies, we found that shape, pattern, and overall lightness are the main determinants of the respondents’ choice. The respondents liked birds with long tails, short necks and legs, and large eyes, as well as birds with more complex patterns with wavelet-decorated bellies. The effect of colors was weaker, but still significant, and revealed that people liked blue, yellow, and green birds. The results suggest that the processes according to which human aesthetic preferences are formed originated far in the history of nocturnal mammals when achromatic properties of environment presented the only utilizable visual clues. We found no significant role of the color red, the perception of which was acquired relatively recently in evolution, in human preferences of birds. We propose that its role is rather in communication and attention grabbing than in the evaluation of bird beauty.

Abstrakt

V posledních letech se ukazuje, že lidé na zvířata, která považují za atraktivní, pohlíží poněkud odlišně, než na zvířata “ošklivá”. Ta krásná se těší větší pozornosti a vyšším počtem ochranářsky zaměřených projektů. Cílem této studie proto bylo prozkoumat fenomén zvířecí krásy do detailů, a to na příkladu populárního zvířecího taxonu – ptáků.

Ve třech po sobě jdoucích studiích jsme změřili lidské preference vůči různým skupinám ptáků: prvně to byli všichni zástupci papoušků, dále náhodně vybraní reprezentanti ze všech nepěvčích čeledí, a nakonec pity, pestrobarevná skupina pěvců čeledi Pittidae. První studie ukázala, že papoušci, které lidé považují za krásné, jsou v zoologických zahradách chováni ve vyšších počtech, nezávisle na statutu jejich ohrožení (status IUCN). V článku diskutujeme možné následky této skutečnosti a také výhody, kterých je možno dosáhnout, pokud budou ochranáři brát v potaz důležitost krásy jakožto faktoru zasahujícího do problematiky ochrany zvířat. Dále jsme zjistili, že lidé preferují zejména dlouhoocasé papoušky, kteří jsou modře či žlutě zbarvení. Zelená barva naopak papouškům na kráse ubírala, což vysvětlujeme tím, že většina papoušků je zelená a tudíž může respondentům připadat nezajímavá.

V následujících dvou studiích se ukázalo, že lidské preference ptáků jsou ovlivněny hlavně tvarem, vzorem a celkovou světelností. Respondentům se líbí ptáci dlouhoocasí, s krátkým krkem a nohama a velikýma očima, kteří na sobě mají komplexní vzor v podobě vlnkovaného břicha. Efekt barev se ukázal být mnohem méně významný, ale přesto signifikantní a potvrdilo se, že se lidem líbí ptáci modří a žlutí, ale také zelení. Tyto výsledky jsou v souladu s hypotézou, že původ lidských estetických preferencí sahá daleko do evoluční historie nočních savců, pro které achromatické vlastnosti prostředí tvořily hlavní vizuální podněty. Červená barva, kterou primáti začali být schopni rozlišovat relativně nedávno, neměla na lidské preference téměř žádný vliv. Její funkce bude pravděpodobně hlavně v komunikaci a schopnosti přitáhnout pozornost.

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1 Introduction

1.1 Aims and focus of the thesis

The thesis consists of two publications in peer reviewed journals (PLoS ONE, $IF_{5\text{-year}}$ = 4.244, Anthrozoos, $IF_{5\text{-year}}$ = 1.419), a submitted manuscript, and a summarizing book chapter. Within the thesis, the included papers are referred to by roman numerals. For their full list, please see the index.

The following part of the introduction summarizes the aims of the thesis. It is followed by a review of the literature focused around the topic of animal beauty and its implication in conservation, discussing the results of the study in this light. It consists of four subchapters, seemingly very distant in topics; however, its aim is to review the most important issues forming the phenomenon of animal beauty more closely and to answer some questions that may rise in the mind of a reader of the papers included in the thesis.

Nowadays, mankind covers about 83% of the Earth's land surface (Sanderson et al. 2002). The lives of humans have a massive impact on the Earth's course, which, in the modern age, consequentially leads to the destruction of habitats of many animal species. However, such a great potential of humans to change the Earth may lead not only to destruction, but also to the protection of the species that suffer from habitat loss or other human-inflicted damage, e.g., massive hunting. Financial limits do not allow support to all needful species and a selection must be made to decide which species are a priority to protect. Many authors have pointed to an existing bias in this selection. To select just a few, e.g., Seddon et al. (2005) have shown that large species of birds and mammals, especially ungulates, carnivores, Galloanseres, Falconiformes and Gruiformes, are over-represented in the reintroduction projects worldwide. Metrick and Weitzman (1996, 1998) showed a similar bias in the funding decisions of the US government that preferentially supports large and attractive animals rather than the endangered ones. Gunnthorsdottir (2001) has also pointed out that the public support is higher for species perceived as attractive.

Since humans are the ones to make the changes, it is of an extreme importance to ask which factors affect human decision making in which species to protect. The studies of Jana Marešová and colleagues (Marešová 2012) were the first to deal with the actual human aesthetic preferences of animals and their connection to conservation in more detail. Not only did they find that various animal taxa are paid greater attention to (are kept in zoos in greater numbers and thus have a higher chance of protection) when perceived as beautiful (Frynta et al. 2009), but also they found that the perceived beauty of animals (model snakes) was shared among very different cultures of people from the Czech Republic and Papua New Guinea (Marešová et al. 2009a), as well as people from the five main inhabited continents (Frynta et al. 2011). Such finding is alarming, showing that the morphological traits of an animal may further determine its chances of survival on the Earth. Also, because the base preferences are shared among mankind, the drive that moves these chances may be really strong. Because of that, it is of an utmost importance to pay a special attention to this phenomenon, and to further examine the properties of the morphological traits that make an animal "ugly" or "beautiful", as perceived by humans.

The presented dissertation thesis extends the issue of human-perceived aesthetics of animals into even more detail. My colleagues and I have adopted the already established method of testing human preferences of animals by showing printed picture cards to human respondents, but we extended it to computer presentation of animal pictures using the Internet. The two methods were compared and their benefits and disadvantages were discussed (**I**). We then selected a different model taxa (the parrots, Psittaciformes) to repeat the analysis of the effect of animal aesthetics to zoo population size on a larger scale. The aesthetic preferences of all extant species of parrots (n = 367) were examined in this study (**I**) which confirmed the previous results gained from other animal taxa analyzed on the family level.

In two other papers (**II**, **III**), we focused on the traits of the animals that are responsible for the determination of human preferences. First, we selected two random species of each extant non-passerine bird family and analyzed whether it was the color or shape of the bird that formed human aesthetic preferences (**II**). Later on, we extended this study with a more detailed analysis of the effect of colors and pattern on human preferences of morphologically uniform birds, the pittas of the family Pittidae (**III**). Both of the papers generated very surprising results revealing that color is much less important for the determination of human aesthetic preferences of colorful birds than one would expect, especially when there is such a high scientific evidence of the importance of color in the shaping of human emotional feelings (Ball 1965; Crozier 1997; Kaya and Epps 2004), attention (Ioan et al. 2007), and performance (Hill and Barton 2005; Elliot et al. 2007).

Last but not least, in the short review included in the Encyclopedia of Quality of Life and Well-Being Research (**IV**), we summarized the current knowledge of the issue as a whole. In nine pages, we reviewed and summarized the agreement in human cross-cultural perception of animals, its implication in animal conservation, and the basic findings about the specific bodily traits that are responsible for the animals to be perceived as attractive or unattractive.

In summary, the main aims of the thesis were: (a) to confirm the results of previous studies that zoos worldwide keep aesthetically attractive animals prior to animals with conservation needs on a larger, species-level scale (all parrot species); (b) to compare two commonly used methods of testing human preferences and to further refine the overall methodology; (c) to examine the factors that determine human preferences of birds, and (d) to examine the degree of the effect of these factors, namely colors, shape, and pattern.

1.2 Zoos' role in conservation: Why is the perceived animal attractiveness important?

Zoological gardens worldwide represent facilities with an enormous amount of resources that can be devoted to the conservation of wildlife. One of the most apparent roles of zoos is keeping of large animal collections and the preservation of genomes of a meaningful number of species. In response to this, Soulé et al. (1986) formed the concept of zoos serving as modern "Noah's Arks": They proposed the role of zoos in restoring natural populations of animals that become extinct or damaged once the degradation of nature caused by mankind stabilizes in 500-1000 years. This idea has many limitations, e.g., the required size of the populations kept for such a long time without loss of genetic variability being too large (Soulé 1980; Frankham et al. 2002; Reed et al. 2007; Lees & Wilcken 2009), and as such has been questioned by many authors (e.g., Roberts 1988; Snyder et al. 1996, Fischer & Lindenmayer 2000; Mathews et al. 2005). Nevertheless, some evidence for a realized success in the contribution of zoos in the ex-situ conservation exists. For example, the red wolf (*Canis rufus*) was considered Extinct in the Wild by 1980 on the IUCN Red List of Threatened Species. After the restoration program had been managed from 1987 to 1994, the population restored to the Critically

Endangered status (Gusset and Dick 2012). As of 2002, twenty packs (approximately 100 individuals) of wild-born red wolves inhabited the restoration area (Philips et al. 2003). The Critically endangered California condors (*Gymnogyps californianus*) have been successfully returned to the wild after being bred by AZA zoos under a Species Survival Plan (WAZA 2005). Other good examples of successfully maintained zoo animal populations released back into the wild are the Przewalski horse (*Equus ferus przewalskii*; Volf 2009), the American bison (*Bison bison*; Freese et al. 2007), the European wisent (*Bison bonasus*; Ahrens 1921; Tokarska et al. 2009), Arabian oryx (*Oryx leucoryx*; Stanley Price 1989), and the black-footed ferret (*Mustela nigripes*). The ferret recovered from a very small population of only eighteen remaining individuals (Dobson and Lyles 2000). The following animals with the "Extinct in the Wild" status on the IUCN Red List are actively bred in zoos, managed in a studbook-based breeding program, and are being reintroduced (Gusset and Dick 2012): Wyoming toad (*Anaxyrus baxteri*), Père David's deer (*Elaphurus davidianus*), Guam rail (*Gallirallus owstoni*), and Scimitar-horned oryx (*Oryx dammah*). Another 29 animals with the same status are actively bred, and their future reintroduction is possible.

In summary, zoological gardens are capable of contributing to the conservation of animal species with the ex-situ breeding effort. In spite of zoos' animal collections being very large, the number is still quite scant when compared to the number of extant animal species (for a review, see Frynta et al. 2009). In this light, animals that are kept in zoos have a higher possibility of survival through ex-situ breeding when their natural populations decline. Thus, to be valuable for conservation, the selection of animals to be included in the worldwide zoo collections should not be random; it should reflect the conservation needs and the status of threat of the given species. Marešová and Frynta (2008) and Frynta et al. (2009) analyzed the factors affecting the size of the worldwide zoo collections of various animal taxa (boid snakes, selected groups of mammals, birds and reptiles) and found that the body size and human-perceived beauty of the animals are significantly contributing to the higher population sizes of species in zoos. Our following studies have confirmed these results in parrots (I) and almost all mammalian families (Frynta et al. 2013). In a recent study, we also found that brain size (reflecting the intelligence or complex behavior of the animals) positively affected the inclusion of the mammalian family in the collection. All of these findings further emphasize the importance of conservation specialists and zoo curators alike to pay special attention to human-perceived and judged characteristics of animals, as these can in turn affect the effectiveness of animal conservation.

The captive breeding and reintroduction using the ex-situ breeding of maintained populations of endangered species is only one of the many roles a zoo can play in the conservation of wildlife. The zoos' large potential to contribute to the conservation can also be realized through scientific research, public education and in-situ conservation. All of these major roles are, in fact, connected to the issue of animal attractiveness. Scientific research allows us to acquire vital information about rare animals' needs, their behavior, and reproductive biology. The African elephant (*Loxodonta africana*) may serve as an example: Most research about its breeding biology has been examined in captivity and now we have detailed knowledge about its oestrus cycle, physiology of the reproductive system, and chemical signals or nutritional needs, all of which can be used in wildlife contexts in the in-situ conservation programs (Smith and Hutchins 2000). Additionally, zoos providing a lot of exotic species for research allow for the recruitment of various specialists such as nutritionists, physiologists, veterinarians, and reproductive biologists. Their presence may be vital for ex-situ conservation programs constructed when urgent needs arise, for example if an unexpected crisis decimates a natural population of a given species. However, the research held by zoos focuses mainly on the most attractive mammalian taxa: The Primates, Carnivora and Artiodactyla (Maple and Bashaw 2010; see Frynta et al. 2013 for the attractiveness assessment). The apparent bias towards attractive mammalian taxa may be caused simply by the availability of the animals, as the most attractive taxa are present in zoos more often and in larger numbers, as mentioned earlier in the chapter (Frynta et al. 2013). Once again, this bias to the attractive species may lower the chances of the survival of non-attractive species.

The assessment of the attractiveness of the species, however, may also serve good purposes when a "beautiful" species is intentionally selected to promote conservation programs through public education and fund-raising. According to WAZA (World Association of Zoos and Aquariums), about 600 millions people visit zoos annually (WAZA 2005), and this number keeps growing: in 2013, the number of annual zoo visits reached above 700 millions visitors (www.waza.org). Both special educational programs of zoos and the visitors' free-choice learning could raise the awareness of conservation needs of many species and their habitats and influence many people to change their behavior (Zimmermann 2010). Unfortunately, some authors report a minimal impact of zoo education programs to behavioral changes of the visitors (Adelman et al. 2000;

Balmford et al. 2007; but see Mallapur et al. 2008), as they are rather interested in seeing the animals than learning facts about them (Ryan and Saward 2004). However, it has been noted that it is easier to promote learning through subjects in which the learner has a personal interest (Rennie and Johnston 2004) or an emotional affinity (Ballantyne and Packer 2005). Moss and Esson (2005) suggested that the attractiveness of animals may also raise the effectiveness of learning. If this is true, an effective strategy would be an intentional selection of an attractive species to exhibit for the purposes of well-planned educational programs.

The main contribution of zoos to the in-situ conservation is through fund-raising. According to a three-year review of British and Irish zoos held in 1997-2000, the zoos spent over 5 million GBP (approximately 150 million CZK) on field conservation and the Wildlife Conservation Society based at Bronx Zoo, NY, spends about 32 million USD (approx. 6 billions CZK) on in-situ conservation projects each year (WAZA 2005). These sums are definitely not negligible; however, to be able to donate such amounts, the zoos depend on the income generated by zoo visitors through gate takings, corporate sponsorship, foundation or government grants, and also contributions made by zoo visitors to specific conservation projects. The decisions of which species are worth protecting by an individual are often measured through their willingness to pay (WTP), analyzed through various surveys. It has been found that the WTP to support biodiversity conservation strongly correlates with the perceived attractiveness of the species (93%, Martín-López et al. 2007). The scientific considerations (e.g., the degree of taxonomic uniqueness, distributional uniqueness, ecological role on ecosystems functioning, or endangered status) are much less important than the affective factors (the respondent's individual attitude towards the animals) when the decisions are made (Martín-López et al. 2008). Thus, regardless of the species' real conservational value, it can be used as a "representative" of a conservational program when considered attractive by the public to gain more financial support.

There are at least four terms in common use when considering single species conservation management: The "keystone", "indicator", "umbrella", and "flagship" species. Although the definitions of these terms may vary throughout publications, the authors usually agree that in the case of the "flagship species", its value lies in its attractiveness for the public and is chosen to raise public awareness, action and fund-raising (Leader-Williams and Dublin 2000). A reasonable definition of flagship species was proposed by Verissimo et al. (2011, page 2): "*A species used as the focus of a* *broader conservation marketing campaign based on its possession of one or more traits that appeal to the target audience.*" In contrast, the other terms are used for the management of species based on their ecological or strategic roles. In short, the "keystone" species is a species that has a vital role in the ecosystem, disproportionally larger relative to its abundance; the "indicator" species reflects the quality and changes in environmental conditions and community composition; and the umbrella species is a species that has such demanding habitat requirement that saving it automatically leads to saving other species, bringing these under its protection (Leader-Williams and Dublin 2000). The meanings of these terms should not be mistaken or exchanged for the "flagship" species' role that highlights the importance of the attractiveness of the selected species.

The benefits of using the flagship species in conservation have already been proven; one of the first such projects was the restoration of the golden lion tamarin status in Brazil in the mid-1980s (Dietz et al. 1994). Other projects using a flagship species include the African and Asian elephants, black and white rhinos, kakapos, mountain tapirs, lemurs, etc. (for a review, see Leader-Williams and Dublin 2000). However, each animal is perceived differently by the public and as such its value as a flagship may vary. The study of White et al. (1997) of the public WTP for the conservation in Great Britain demonstrated that people were willing to donate more funds to otters than to water voles. It is not very surprising as the family Mustelidae in which the otters belong are considered to be much more "beautiful" by the respondents than the water voles family Muridae (Frynta et al. 2013). Moreover, the people were willing to pay less money for the conservation of the otters and water voles when lumped together into one conservation program than they were willing to donate for the otters alone (White et al. 1997). This may be explained either by the sole presence of the unattractive animal in the program, which pushes the respondents back, or by the raising complexity of the message that was presented to the respondents. Either way, using one attractive species as a flagship to promote a conservation program proved to be an effective strategy. The message is simple and it emotionally touches the target public, raising their awareness and WTP. In summary, the importance of the attractiveness of the species should not be taken lightly. But what exactly is the term "attractiveness of the species" referring to, and how much is this attractiveness linked to the actual *beauty*?

1.3 Aesthetics, beauty, attractiveness and attitude

The terms “beauty”, “aesthetics” (or aesthetic preferences), and attractiveness are often confused as synonyms in literature (e.g., Geldart et al. 1999; Richards 2001; Jacobsen et al. 2006). However, their meanings differ in detail. To let you better understand the concept of human preferences as studied in our papers, it is necessary to review the definitions of these terms as used in psychological studies. Aesthetics seem to have by far the most ambiguous meaning. It is connected to human aesthetic judgment of objects with aesthetic properties, leading to an aesthetic experience through emotional feeling. There is no simple definition of what an aesthetic property is; Levinson describes it as follows in “The Oxford Handbook of Aesthetics” (Levinson 2005, page 6):

> *…there is a substantial convergence in institutions as to what perceivable properties of things are aesthetic, as this open-ended list suggests – beauty, ugliness, sublimity, grace, elegance, delicacy, harmony, balance, unity, power, drive, élan, ebullience, wittiness, vehemence, garishness, gaudiness, acerbity, anguish, sadness, tranquility, cheerfulness, crudity, serenity, wiriness, comicality, flamboyance, languor, melancholy, sentimentality – bearing in mind, of course, that many of the properties on this list are aesthetic properties only when the terms designating them are understood figuratively.*

The description of aesthetic experience then follows, not giving us much more clues of what to find beyond its meaning (Levinson 2005, pages 6-7):

> *Aesthetics conceived as the study of certain distinctive experiences or states of mind, whether attitudes, perceptions, emotions, or acts of attention, similarly requires some conception of when a state of mind or mental activity is an aesthetic one. Among the marks that have been proposed as distinguishing aesthetic states of mind from others are: disinterestedness, or detachment from desires, needs and practical concerns; non-instrumentality, or being undertaken or sustained for their own sake; contemplative or absorbed character, with consequent effacement of the subject; focus on an*

> *objects form; focus on the relation between an objects form and its content or character; focus on the aesthetic features of an object; and figuring centrally in the appreciation of works of art.*

In summary, aesthetics connect to a human's mind, emotions, and ability to judge perceived objects from many perspectives – *beauty* being one of them, but including also the value of an object that is determined by its practical use, rarity, and the experience of the observer with the object, etc.

Eysenck (1972) has formed a hypothesis that there are "general factors" determining the aesthetic judgment of a person, calling it "good taste." These factors divide people into categories of differing aesthetic preferences according to bright/subdued colors, complexity/simplicity, or people preferring modern/old-fashioned art. He points out that human respondents differ in their aesthetic preferences, especially when artists and non-artists are surveyed, and criticizes many papers that state otherwise for being statistically incomplete. However, in our papers of Frynta and colleagues dealing with animal *beauty*, the preferences seem consistent among very different cultures (Marešová et al. 2009a, Frynta et al. 2011), and mostly among both sexes of the respondents (**I**, **II**, **III**). The reason of this may be that aesthetic preferences are based on many factors, as mentioned above (e.g., personal experience and memory, Leder et al. 2004), with the *beauty of the object* being just one of them. *Beauty* is the element of aesthetics that is perceived as preferred, liked, and positively affecting human emotions and state of mind; it is "*the best, most appealing, or most satisfying aspect of something*" ('beauty, n.', OED 2013).

Now we may ask: which traits are perceived positively in order to be called beautiful? Birkhoff (1933) tried to measure the aesthetics (in the sense of *beauty* as described here) as a ratio between an order (or symmetry) of an object and its complexity, stating that the aesthetic measure is directly proportional to its order and inversely proportional to its complexity. This rule was not widely applicable though, as it was later found that human respondents prefer moderately complex objects (Davis 1936; Leder et al. 2004), and Berlyne (1971) suggested the aesthetics (again in the meaning of *beauty*) to be connected with pleasant feelings elicited in the brain when the respondent is exposed to moderate stimuli.

It would seem much less surprising to find an agreement in "what is beautiful" among respondents worldwide if *beauty* was affected rather by the perceptual "prerequisites" of human being, potentially shared with our ape or monkey ancestors, than personal taste and experience. Ramachandran and Hirstein (1999) proposed a list of properties that are perceived as beautiful in art, supplying the list with a biologically relevant explanation of the preferences. They called them the "rules of artistic experience", describing the "peak shift principle" as the first rule. Long known in animal ethology (Tinbergen 1969), a super-normal stimulus, expressed usually as a caricature in art, has a stronger effect on the observer than a normal stimulus. If there is something we like and it is exaggerated, we like it even more. The second-listed rule is described as "grouping and binding." When seeing a cluster of splotches, our brain is trying to identify these as an object. A primate's brain consists of many visual pathways, each specialized in motion, color, depth, form, etc. The visible splotches are processed along the way, clustered as a possible key to finding an object, until the brain finally identifies the object in a pleasant "aha" sensation (Ramachandran and Hirstein 1999). This can be very useful especially when breaking trough camouflages, and it can be processed either spontaneously or consciously in ambiguously "translated" images, for example, when seeing a goblet or two profile faces in the famous "goblet illusion" picture (Rubin 1921). Another rule described by Ramachandran and Hirstein is "contrast extraction": contrasting patches are perceived as aesthetically pleasing as the retinal cells, lateral geniculate body, and visual cortex mainly respond to sharp changes in luminance (edges), but not to homogenously colored surfaces. Chromatic and motion contrast are perceived positively as well. The cells recognize the edges as interesting and this in turn interests the whole organism; it allows the observer to recognize objects through analysis of different, but closely positioned, patches (as opposed to the "grouping and binding rule" which helps to identify similar patches positioned farther from each other), and to focus attention to an object that stands out from the background, leading to the fourth rule described by Ramachandran and Hirstein as "isolating a single module and allocating attention." When human observers focus attention on a single source of information (object), they can better notice other "enhancements" introduced by the artist and that leads to an amplified limbic activation. Ramachandran and Hirstein (1999) name other rules, namely the preferences for symmetry (symmetry may be perceived as having good health by human respondents, Rhodes et al. 2001) or "Bayesian logic of perception" with preferences for pictures that show scenes that are more probable to happen in reality; e.g., a flock of birds on a wire should rather be depicted as sitting randomly positioned from each other than sitting in periodical distances from each other; this rule seems to contrast with the "symmetry" rule. It is because the brain processes the information into a more probable situation, e.g., two occluded objects translates as an occlusion rather than two distinct objects of strange shapes. All of these rules determining *beauty* are somewhat connected to the physiological and cognitive processing and thus, agreement among very different respondents is likely to be expected.

When surveying human respondents about their preferences, it is therefore needed to be careful about the actual questions they answer (Eysenck 1972). If asked to evaluate depicted objects according to the perceived beauty or aesthetic value, the answers may generate very different results!

The term "attractiveness" is usually confused with *beauty* which is very often used as a synonym for "physical attractiveness" in studies of sexual preferences in humans (e.g., Dion et al. 1972; Grammer and Thornhill 1994; Rhodes et al. 2001; Fink and Neave 2005). In The Cognitive Structure of Emotions (Ortony et al. 1990), attractiveness (or attraction) is described as a positive or negative reaction (an interest) towards an object or a person. As the definition suggests, it includes negative attractions such as hatred. A person can be interested in "ugly," conspicuous, or strange (uncommon or unknown) objects or animals out of curiosity, and these objects of interest in turn may profit from the received attention for being attractive despite being perceived as "ugly" otherwise. Lang et al. (1993) found a positive correlation of interest with arousal and both pleasant and unpleasant pictures.

Attitude is an evaluative stance towards any concrete object or abstractive issue (Delamater 2003). It has been long assumed that attitude was the key to understanding human behavior, and although early literature disputed the degree of relationship between human attitude and behavior (Ajzen and Fishbein 1977), more recent research is consistent in asserting that behavior is influenced by attitude (Luzar and Cosse 1998).

In the conservation field, it has been reported that the attitude of respondents affects their WTP (Martín-López et al. 2007, 2008). Human attitude towards animals can be divided into two distinct groups: an emotionally-affective view and utilitarian (economic and pragmatic) consideration (summarized in Serpel 2004). The inclination for each group is then affected by various factors: animal attributes (e.g., the animals' physical appearance; Plous 1993), individual human attributes (e.g., the people's familiarity with the species; Martín-López et al. 2007), and cultural factors. There are substantial intercultural differences in attitudes to animals, determined by history, cultural/religious beliefs and values, culturally defining practices, and cultural representations (Kellert 1993; for a review see Serpell 2004).

In conclusion, the terms “aesthetics,” “attractiveness,” and “attitude” refer to states or actions that are influenced by many variables, and thus may significantly vary among different people or groups of people. *Beauty*, in contrast, refers to one of the factors that affect each of these states, being determined rather by perceptual and cognitive functions.

In our studies (**I**, **II**, **III**, **IV**), the term *beauty* is somewhat inconveniently confused with the terms “aesthetic attractiveness” and “human preferences for animals,” and this thesis follows the usage. However, for a deep understanding of the issue, it is necessary to keep in mind that we are concerned with *beauty*, as the respondents were always asked to evaluate the perceived *beauty* of the animals in all of the papers included in the thesis. This task performed by the respondents usually includes other evaluative stances, e.g., categorization of the species into similar clusters (Marešová et al. 2009b; Landová et al. 2012), which is done unconsciously and resembles the task recognized as unsupervised human categorization by some authors (Pothos and Chater 2002; Pothos and Close 2008). We will focus on this issue in our other studies to present a possible explanation for the cross-cultural agreement in ethnic classifications of animals as reported by ethnozoologists (Berlin and Stevens 1994).

1.4 Methods of attractiveness testing

The studies of human preferences for visual art trace back into the 19th century when the first experiments surveying people’s judgments about the “pleasantness” of various objects were carried out (Berlyne 1971). Ever since, the empirical studies of aesthetic preferences bloomed, developing diverse and more and more sophisticated methods of testing. One of the most common procedures for obtaining these judgments is through using the Likert scale (Likert 1932): The respondents are asked to select a number representing the degree of preference or liking for each ranked object (Halberstadt and Rhodes 2003; Martín-López 2007; Glocker et al. 2009; Archer and Monton 2011). As a variation of this method, the subjects may simply select the objects they like, which in fact corresponds to rating every object in the collection on a two-point scale (preferred/non-preferred; Berlyne 1971).

The method that we use the most in our experiments is the rank-ordering procedure: the subjects are asked to rank-order a collection of photos from the most to the least preferred (e.g., Marešová 2012, **I**, **II**, **III**). A variation of this method is the commonly used paired comparison, in which the respondents are presented two objects at the same time and select the one they prefer. The objects can also be presented in triads; in this method, the respondents are tasked to select the one they prefer the most and one they prefer the least. These two methods correspond to the rank-ordering of two and three objects at once, respectively (Berlyne 1971).

Next to the opinion surveys, the degree of pleasantness of pictures can be measured through physiological correlations of heart rate, skin conductance, and facial electromyography. It has been reported that the heart rate accelerates when the respondents observe "beautiful" (pleasant) pictures and decelerates when watching "ugly" (unpleasant) pictures (Greenwald et al 1989; Lang et al. 1993), and this is also true when smelling pleasant and unpleasant odors (Bensafi et al. 2002). Skin conductance, determined by activity in the sympathetically innervated sweat glands, is reported to increase with arousal and both pleasantness and unpleasantness of presented pictures (Bradley et al. 1990). Facial electromyography shows that the tension of the corrugator muscle (the "frowning muscle", responsible for the expression of "suffering") is highest when seeing unpleasant pictures and lowest when seeing pleasant pictures, and the tension of the zygomatic muscle is highest when seeing pleasant, none when seeing neutral, and low when seeing unpleasant pictures (Greenwald et al 1989; Bradley et al. 1990; Lang et al. 1993). These relationships suggest that for measuring the degree of "beautifulness" of a picture through physiology, the heart rate and activity of the corrugator muscle seem to be the best choice, while skin conductance and tension of zygomatic muscle would serve better for testing attention or interest through arousal.

In our paper testing human preferences towards parrots (**I**), we used the rank-order method for the evaluation of human preferences in smaller sets consisting of up to 40 pictures: a mixed set of parrots (40 pictures), amazons (34), and macaws (17). The rank-order method maximizes the informative content of the respondents' judgment by covering the full ordination scale. However, it requires a simultaneous presentation of all pictures to the respondent to allow for relative comparisons, so it is hardly applicable to large picture sets. Thus, in a consecutive experiment in which we assessed human preferences for all 367 extant parrot species (supplemented by distinctively colored subspecies), we turned to the Likert scale method of testing (five-point scale). For a more detailed description of the testing procedure, please see (**I**, **II**, **III**). However, to compare the results coming from both methods, we additionally tested one set of the 40 selected parrots using a seven-point scale evaluation. In all cases, the respondents were tasked to rank-order/assign numbers to the pictures according to their preferences of beauty, which allowed us to compare the results coming from both testing methods. The correlation was significantly high ($r^2 = 81.9\%$; $p < 0.0001$), confirming the suitability of both methods for this kind of research (see Fig. 1a).

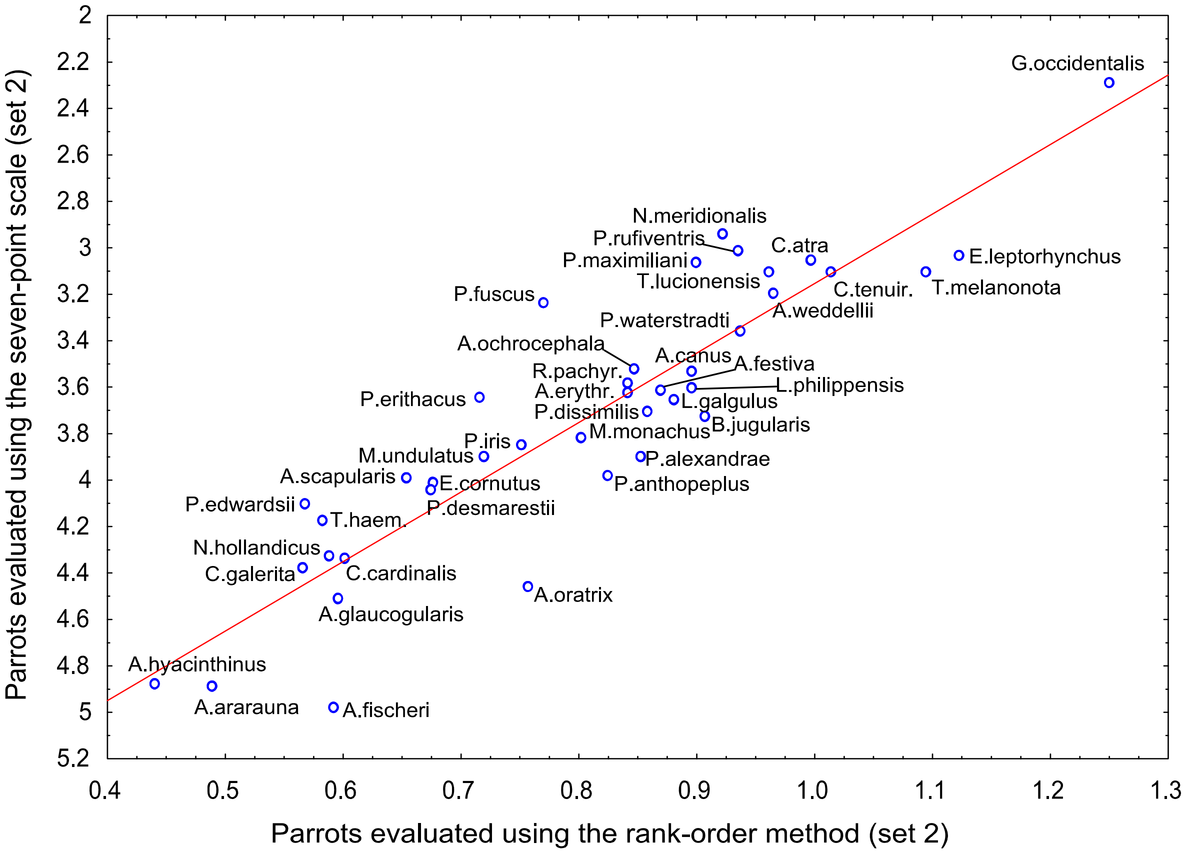

Figure 1b. Correlation of the results obtained from the order-rank and the Likert seven-point scale methods of evaluation of human preferences. A set of 40 painted pictures of parrots was evaluated using the two methods by different respondents. For a detailed description of both of the methods and the selection of species, see (I). The correlation coefficient $r^2 = 81.9\%$ and $p < 0.0001$. Note that the lower the rank, the higher is the attractiveness of the given species.

To further confirm the reliability of the Likert scale method even when testing a large amount of pictures, we extracted the same species as selected in the reduced 40 picture set tested by rank-ordering and compared the results. The comparison revealed even higher correlation ($r^2 = 85.4\%$; $p < 0.0001$, see Fig. 1b), showing that the respondents were able to evaluate as large amount of pictures as 367 without becoming expressively exhausted during the process.

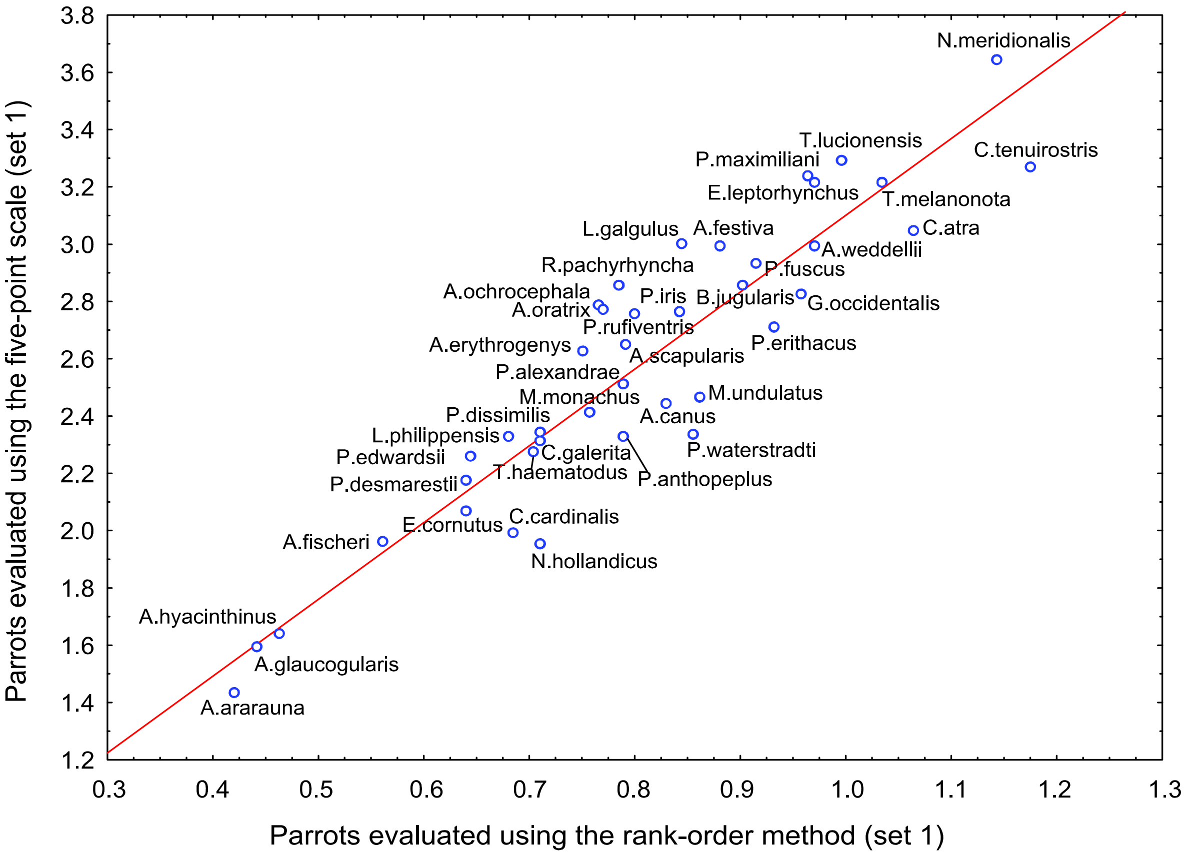

Figure 1b. Correlation of the results obtained from the order-rank and the Likert five-point scale methods of evaluation of human preferences. The order-ranked set consisted of painted pictures of 40 selected parrot species, while the set ranked on a five-point scale contained all extant 367 species. The 40 corresponding parrot species were extracted after ranking was completed to compare the results with the order-ranking method. For a detailed description of both of the methods and the selection of species, see (I). The correlation coefficient $r^2 = 85.4\%$ and $p < 0.0001$. Note that the lower the rank, the higher is the attractiveness of the given species.

A question rises when assessing human preferences toward animal species: What is the reliability of the usage of pictures in place of the real animals? Fortunately, a few studies have already confirmed the validity of using photographic representations to assess perception of nature (Kaplan and Kaplan 1989) and animals (snakes, Landová et al. 2012). To further examine the reliability of the usage of animal paintings as representatives of the real animals, we used three different paintings of each species in the reduced set of 40 parrots (**I**), creating three different sets of pictures. The sets were rank-ordered by different Czech respondents (30 males and 40 females each) and the results analyzed. The mean transformed ranks computed for individual variants were mutually fairly correlated (r^2 =61.2%; 39.5%; and 55.0%; all $p<0.0001$) and Manova revealed a small, but significant effect of the set ($F_{78,332}$= 5.76; $p<0.0001$). Thus, reliability of pictures may represent a possible methodological pitfall that potentially decreases the precision of human preference estimates. However, the parrots in our sets were painted by different artists, scanned under different conditions, and the resulting pictures were not standardized for displaying the same colors in the sense of hue, saturation, and brightness. Since these factors are known to affect human preferences (Gorn et al. 1997; Manav 2007; Labrecque and Milne 2012), a higher correlation between the sets could be attained by controlling for these factors. Also, using photographic representations of the species whenever possible (for example when studying preferences for common species of which suitable photos exist) may further decrease the differences in evaluation. Still, using pictures in human preference assessments is a widely accepted method (e.g., Gunnthorsdottir 2001; Halberstadt and Rhodes 2003; Martín-López et al. 2007) and presents an optimal solution when real animals are not available for exhibit.

1.5 Visual perception and an evolutionary interpretation of the results

Visual perception consists of several sub-processes; an object's form, color, depth, movement or texture processed separately within the visual brain pathways (Livingstone and Hubel 1987). We can expect one or more of these features to play a primary role in the determination of human preferences. Thus, in our studies, we examined the role of color, shape (**II**), lightness, and pattern (**III**) in the evaluation of bird beauty by human respondents. We found there to be a major effect of shape, lightness, and pattern, while colors affected human preferences only slightly. To better understand a possible explanation of this finding, it is useful to review the literature about visual brain pathways in humans and the processing of color, form, and pattern.

Human retinas contain four different types of photoreceptors. One of these are rods, which are active in dim light. Their absorption spectrum peaks at about 495 nm (Kraft et al. 1993). Much more important for our discussion are the other three photoreceptors, the cones, which are active in daylight. Their absorption spectra peak at about 560, 530, and 420 nm for L-, M-, and S-cones, respectively (Conway 2009). These cones are sometimes also referred to as "red," "green," and "blue," although this is not accurate because all types of cones are sensitive to a large range of wavelengths. L- and M-cones are sensitive to whole visible spectrum, with the L-cones peaking under light that would appear yellowish in the neutral viewing conditions. The S-cones peak at light appearing violet, thus, it is better to refer to the cones as L (for long wavelength), M (for medium), and S (for short; Gegenfurtner and Kiper 2003).

The retinal cone cells then project information to specific ganglion cells leading into three independent channels: (a) black-and-white axis, (b) red-green axis, and (c) blue-yellow axis (Livingstone and Hubel 1987; Casagrande 1994; Gegenfurtner and Kiper 2003). The **magnocellular pathway**, responsible for the perception of the black-and-white channel or the luminance contrast, leads through parasol ganglion cells which receive additive input from L and M cones (L+M; it is suggested that S cones, in a minority, add to this input as well; Chatterjee and Callaway 2002). The **parvocellular pathway**, generating the red-green channel, receives input from midget ganglion cells, which in turn receive chromatically opponent input from L and M retinal cells (L-M). The third, the **koniocellular pathway,** leads through bistratisfied ganglion cells which receive chromatically opponent input S-(L+M), generating the blue-yellow channel (Dacey and Lee 1994; Gunther and Dobkins 2002; Szmajda et al. 2008). The chromatically opponent input allows for recognition of chromatic contrast, and this has been widely studied especially using the better-known parvocellular pathway.

Through various psychophysical tasks, it was possible to find the differences in perception of form, pattern, color, movement, and depth between the magno- and parvocellular pathways (the koniocellular pathway was described relatively recently and is used far less often in such studies; Casagrande 1994). This is usually done by presenting stimuli that differs in the degree of luminance and chromatic contrast to respondents. When a stimulus reaches its equiluminant value, the performance of the tasks processed through the magnocellular (luminance contrast-sensitive) pathway fails completely or is fairly reduced. Equiluminance is reached when the sum of L and M excitation inputs of one color equals the sum of L and M excitation inputs of another color and thus the object is perceived as having equal luminance contrast, differing only in chromatic contrast. However, reaching equiluminance is problematic as the inputs depend on the ratio of L and M cones present in the human retina, which highly differs within individuals (the ratio of L:M was found to reach differences from 1.1:1 to as much as 16.5:1; Bowmaker et al 2003; Hofer et al 2005). Thus, the value of equiluminance is different for each person, and it also differs for each hue and eccentricity (peripheral distance; Livingstone and Hubel 1987).

Regardless of the difficulties, very interesting findings were obtained using the equiluminant stimuli: At equiluminance, the respondents experienced the loss of depth perception from stereopsis, loss of apparent movement and movement direction, colors blending during flicker tasks, loss of some optical illusions based on linear orientation and angles, loss of depth perception deduced from 2D depiction of shades, texture and movement, and loss of the ability to link similar features of an object (occlusion, depth from perspective; Ramachandran and Gregory 1978; Livingstone and Hubel 1987; Troscianko 1987; Lindsey and Teller 1990; Yeshurun 2004). Thus, even though the pathways intermingle in the primary visual cortex (Sincich and Horton 2005) and the processing of each is not easily separable, these psychophysical studies (together with morphological and other evidence) support the view that the magnocellular pathway is mainly responsible for the perception of movement and depth and the identification of the objects' position ("where" it is), while the parvocellular system focuses on the recognition of objects ("what" it is) and its colors (Preuss 2007).

Apparently, both developmental and evolutionary cues indicate that the magnocellular system is older and more primitive than the parvocellular system (Livingstone and Hubel 1987). There are homologies of the three systems found within many mammals, in which the konio- and magnocellular layers (called W and Y in non-primate mammals) of dorsal lateral geniculate nucleus dominate, while the proportion of parvocellular (called X) layer is small. In contrast, the primates' parvocellular layer dominates, forming about 80 percent of the ganglion cells (Kaas 2004). A correlation between the number of neurons in the parvocellular layer and brain size in primates was found, suggesting that visual properties of the parvocellular neuronal stream, i.e., high visual acuity, detailed object recognition, and color discrimination played a major role in primate evolution (Barton 1998).

We found that achromatic components of colorful bird species, mainly the shape in the form of a black silhouette (**II**), pattern, and overall lightness (**III**), are the main determinants of human aesthetic preferences. This implies that the roots of human aesthetic preferences (or their main determinants) may reach far into the ancestry of non-primate mammals, which were small and nocturnal creatures with color vision reduced to dichromatic state (Zhao et al. 2009, Heesy and Hall 2010). For small nocturnal species, the intensity of luminance contrast might have been the only available visual clue. The importance of achromatic properties for object recognition persisted in modern primates including humans, who are able to identify and categorize objects even if presented in a grayscale at a very low luminance contrast (Macé et al. 2005). Rapid-presentation experiments show that humans' recognition of sketched shapes of objects is as good as their recognition of high quality colorful photographs (Biederman and Ju 1988). While shape and grayscale pattern provide primary information for human perception, color contributes to cognitive interpretation and memory processing of an already recognized object (Mapelli and Behrmann 1997, Yip and Sinha 2002, Therriault et al. 2009), and this primary role of achromatic components seems to project into human perception of beauty as well. In conclusion, human evaluation of beauty seems to be mainly dependant on the more ancestral magnocellular pathway processing the recognition of achromatic properties of objects.

Although the effect of colors on human preferences of birds was much smaller than the effect of shape, lightness, and pattern, it was still revealed as significant in all cases (**I**, **II**, **III**). We found that the respondents' preferences for parrot species are positively associated with the presence of yellow, orange, and blue. The color green affected the respondents' evaluation negatively; this may be because the green is predominantly present in most of the parrots, and thus, it could have lowered the interest of the respondents. When evaluating bird representatives (randomly selected) of all non-passerine families, the respondents again showed preferences for yellow and blue (**II**). The effect of red and purple was significant as well; however, using different settings of the GLM analyses or inclusion of more or less factors in the analyses easily lead these colors out of the threshold of significance and thus, the strength of their effect is dubious and should be treated with caution. In another study, human respondents preferred blue and green when evaluating morphologically uniform and colorful species of the avian family Pittidae (**III**). When summarized, short-to-middle wavelength colors of birds (blue, green, yellow) are more or less preferred, while the longest wavelengths perceived as red color have little to no effect on human preferences.

Our finding of preferences for blue and green colors (and also white and black colors through overall lightness) is in agreement with the study of Madden et al. (2000) who surveyed respondents from eight different countries on four continents (East Asia, Europe, North America, and South America). In their study, all countries placed blue, green, white or black in the top three colors, except for people from Taiwan who placed purple on the third position. Red color followed as fairly preferred. When the respondents were supposed to associate colors with emotions, the colors blue, green, and white clustered together, as did black and brown, but red was not clustered with any other color. Although the specific associations differed across countries, the clustering of blue, green, and white remained stable, as well as the distinctive position of red. The dual position of short-wavelength colors versus long-wavelength colors (with yellow mingling into both sides) is long known. Longer wavelength hues (yellow, orange, red) induce states of arousal and excitement (Walters et al. 1982) and are cross-culturally associated with negative emotions as opposing to short wavelength hues (blue, green) that are associated with good and calming emotions (D'Andrade and Egan 1974). Why is there such a striking distinction?

The so-called warm-cool spectra discrimination, recognizing the short-wave spectrum on one side and long-wave spectrum on the other side, is consistent with dichromatic vision ancestral in Eutherian mammals (Jacobs 2009). These early mammals possessed only two opsin genes, SWS1 (short wavelength class sensitive in the violet–ultraviolet) and LWS (long wavelength class sensitive in the red–green), the latter of which duplicated and diversified into M and L opsin genes with different spectral sensitivities in primates. This duplication allowed for true trichromtic vision independently in Old World primates (*Catarrhine*) and New World howler monkeys (*Alouatta;* Osorio and Vorobyev 2005). The origin of the newly acquired opsin with sensitivity shifted towards the longer wavelengths (red) is approximated to occur at about 35 MYA (Gegenfurtner and Kiper 2003), meaning it formed relatively recently when compared to the long evolutionary history of mammals (Martin and Ross 2005). Thus, human preferences for blue, green, and yellow colors (together with their preferences for achromatic colors and clues) further support the hypothesis that the processes according to which human aesthetic preferences are formed originated far in the history of dichromatic mammals. Moreover, the preference for blue and green color has also been found in non-human primates. Chimpanzees and gorillas preferred to manipulate blue and green objects instead of red ones (Wells et al. 2008), and macaques were also reported to prefer blue colors (Humphrey 1972). Sharing of this preference for the color blue with our monkey and ape relatives suggests that this character is deeply rooted in the ancestry of humans.

The position of the red color in human aesthetics forms a very interesting question. The little to no effect of red on human aesthetic preferences of birds may be explained by a relatively short history of the color's recognition in primates. Red is known to play an important role in primate communication (Setchell et al. 2006) and food gathering (Dominy and Lucas 2001; Surridge, et al. 2003). It is recently a matter of discussion whether trichromatic primates have any advantage over the dichromatic ones (Hiramatsu et al. 2008), but phylogenetic studies show that trichromatism in primates evolved most likely in the context of foraging performance (Fernandez and Morris 2007). Once evolved, the ability to see the color red gained its importance in the selection of red-colored sexual traits and communication (Waitt et al. 2003, 2006). In humans, a similar role of red in communication was reported: men connect red colors with a woman's sexual attractiveness and desirability (Elliot and Niesta 2008). Various human studies also showed that the color red evokes anger and hatred (Mahnke 1996; Kaya and Epps 2004), causes excitement and arousal (Wilson 1966; Wolfson and Case 2000; Elliot and Maier 2007), enhances human performance in contests (Hill and Barton 2005), and functions as a distracter (Ioan et al. 2007), lessening a person's concentration and performance (Elliot et al. 2007). Rather than having an important role in human aesthetic preferences, the color red's primary function seems to be in its communication value and its ability to catch attention.

These results can also be interpreted in the light of Kay's (Kay et al. 2010) hypothesis that describes a universal pattern of emergence of color terms in human languages, stating that some colors are named and thus recognized prior to others across all human cultures. Since this pattern quite fairly corresponds to the evolutionarily hypotheses described above, I avoid discussion of this issue in detail here in the thesis introduction. For more detailed description of the topic, please see (**III**).

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3 List of publications/manuscripts

Copies of the published articles are included in the Appendix. Due to copyright restrictions, the copies of the papers numbered II, III and IV are not included in the online version of the thesis. For access to the articles, please follow the links listed in the List of appendices.

(I) Frynta D., Lišková, S., Bültmann, S., & Burda, H. (2010): **Being attractive brings advantages: the case of parrot species in captivity.** *PLoS ONE* 5, e12568. doi:10.1371/journal.pone.0012568

(II) Lišková, S., & Frynta, D. (2013): **What determines bird beauty in human eyes?** *Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals*, 26, 27–41. doi:10.2752/175303713X13534238631399

(III) Lišková, S., Landová, E., & Frynta, D. **Human preferences for colorful birds: vivid colors or pattern?** Submitted.

(IV) Frynta, D., Landová, E., & Lišková, S. (2014): **Animal beauty, cross-cultural perceptions.** In: Michalos, A. C. (ed.), *Encyclopedia of Quality of Life and Well-Being Research*. Dordrecht, The Netherlands: Springer.

4 Summary of the results

In summary, the aim of the thesis was to analyze more closely the main determinants of human preferences towards bird species and to examine the consequences of the unequal preferences to wildlife conservation. We found that the shape of the birds, namely long tail, short neck and legs, and large eyes, together with the complexity of achromatic pattern, positively determined human preferences. Color hues were found to have much weaker, yet still significant effects, on human beauty assessment. The respondents preferred mainly blue, yellow, and green hues. The results suggest that the processes according to which human aesthetic preferences are formed originated far in the history of nocturnal mammals, when achromatic properties of the environment presented the only utilizable visual clues. We found no significant role of the color red, the perception of which was acquired relatively recently in evolution, in human preferences of birds. We propose that its role is rather in communication and attention grabbing than in the evaluation of bird beauty.

In the study of all parrot species, we found that the preferred species were kept in zoos in higher numbers, regardless of their conservation priority (IUCN status). We discuss possible consequences of this finding and the benefits that may arise in the light of animal conservation if this bias in species preferences were to be considered by conservation specialists.

By points, the results of the thesis can be summarized as follows:

- The sizes of zoo populations of parrots are affected by their preference (beauty) ranks, while their status of endangerment (IUCN listing) has no effect. This result is in agreement with results previously found in other animal taxa and it further unfolds the importance of "animal beauty" as a factor to be considered in setting up conservation programs.
- The aesthetic judgment of bird beauty can be assessed both by rank-ordering of pictures simultaneously presented to the respondents and by assigning numbers to consecutively appearing pictures on a computer screen. However, varying illustrations of the same species may lead to slightly different ranking by the respondents. When substituting real animal stimuli for their illustrations, special attention needs to be paid to the saturation, lightness, hue, and other possible variables that can affect the respondents' judgment of beauty of the depicted animals.
- Achromatic properties of the depicted bird, i.e., shape, pattern, and overall lightness, are the main determinants of human aesthetic preferences of birds. The respondents liked species with long tails, short neck and legs, and large eyes, as well as species decorated with more complex patterns (wavelet-patterned bellies). This finding suggests that human aesthetic judgment of beauty might have formed a very long ago, still within the ancestry of nocturnal mammals who utilized mainly achromatic visual cues of luminance contrast.

- The small yet significant effect of colors on human preferences revealed that the respondents like mainly blue, green, and yellow-colored birds. This finding further supports a deeply rooted ancestry of aesthetic judgment of beauty within dichromatic mammals/primates.
- The color red is reported in literature to play a very specific role in human behavior, emotions and communication, but we found no significant effect of red on the determination of human preferences for birds.

5 List of appendices

Appendix 1

Prohlášení spoluautorů/Declaration of the co-authors

Appendix 2

(I) Frynta D., Lišková, S., Bültmann, S., & Burda, H. (2010): **Being attractive brings advantages: the case of parrot species in captivity.** *PLoS ONE* 5, e12568. doi:10.1371/journal.pone.0012568

For online access of the article, see:

http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0012568

Appendix 3

(II) Lišková, S., & Frynta, D. (2013): **What determines bird beauty in human eyes?** *Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals*, 26, 27–41. doi:10.2752/175303713X13534238631399

For online access of the article, see:

http://dx.doi.org/10.2752/175303713X13534238631399

Appendix 4

(III) Lišková, S., Landová, E., & Frynta, D. **Human preferences for colorful birds: vivid colors or pattern?** Submitted.

Online version of the article will be available upon publishing.

Appendix 5

(IV) Frynta, D., Landová, E., & Lišková, S. (2014): **Animal beauty, cross-cultural perceptions.** In: Michalos, A. C. (ed.), *Encyclopedia of Quality of Life and Well-Being Research*. Dordrecht, The Netherlands: Springer.

Online version of the book chapter will be available upon publishing at:
http://www.springerreference.com/docs/navigation.do?m=Encyclopedia+of+Quality+of+Life+Research+%28Humanities%2C+Social+Sciences+and+Law%29-book267

Or as a part of the printed book at:
http://www.springer.com/social+sciences/wellbeing+%26+quality-of-life/book/978-94-007-0752-8

Appendix 6

The appendix of the thesis is supplemented by additional publications co-authored by the author of this thesis (a PLoS ONE publication and a book chapter). The following publications, listed in the Appendix 6, are not an explicit part of the thesis, but complement the thematic focus of the study and are included for illustrational purposes only.

Frynta, D., Marešová, E., Landová, E., Lišková, S., Šimková, O., Tichá, I., Zelenková, M., & Fuchs, R. (2010): *Are Animals in Zoos Rather Conspicuous than Endangered?* Nova Science Publishers, Inc., New York.

Frynta, D., Šimková, O., Lišková, S., & Landová, E. (2013): Mammalian collection on Noah's Ark: the effects of beauty, brain and body size. *PLoS ONE*, 8, e63110. doi:10.1371/journal.pone.0063110

For online access of the article, see:
http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0063110

Prohlášení spoluautorů:

Jménem svým i ostatních spoluautorů do disertace Silvie Liškové potvrzuji, že autorský podíl jmenované doktorandky odpovídá počtu spoluautorů a jejich pořadí. Potvrzuji též, že se Silvie Lišková podílela na všech fázích přípravy těchto publikací, včetně sběru a správy dat, statistického zhodnocení a formulaci výsledků, sepisování vlastního textu rukopisů a nakonec i finálních úpravách v průběhu recenzního a publikačního procesu.

V Praze dne

Daniel Frynta

Appendix 2

OPEN ACCESS Freely available online

PLoS one

Being Attractive Brings Advantages: The Case of Parrot Species in Captivity

Daniel Frynta[1]*, Silvie Lišková[1], Sebastian Bültmann[2], Hynek Burda[2]

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Abstract

Background: Parrots are one of the most frequently kept and bred bird orders in captivity. This increases poaching and thus the potential importance of captive populations for rescue programmes managed by zoos and related institutions. Both captive breeding and poaching are selective and may be influenced by the attractiveness of particular species to humans. In this paper, we tested the hypothesis that the size of zoo populations is not only determined by conservation needs, but also by the perceived beauty of individual parrot species assessed by human observers.

Methodology/Principal Findings: For the purpose of data collection, we defined four sets of species (40 parrots, 367 parrots, 34 amazons, 17 macaws). Then, we asked 776 human respondents to evaluate parrot pictures of the selected species according to perceived beauty and we analyzed its association with color and morphological characters. Irrespective of the species set, we found a good agreement among the respondents. The preferred species tended to be large, colorful, and long-tailed.

Conclusions/Significance: We repeatedly confirmed significant, positive association between the perceived beauty and the size of worldwide zoo population. Moreover, the range size and body size appeared to be significant predictors of zoo population size. In contrast, the effects of other explanatory variables, including the IUCN (International Union for Conservation of Nature) listing, appeared insignificant. Our results may suggest that zoos preferentially keep beautiful parrots and pay less attention to conservation needs.

Citation: Frynta D, Lišková S, Bültmann S, Burda H (2010) Being Attractive Brings Advantages: The Case of Parrot Species in Captivity. PLoS ONE 5(9): e12568. doi:10.1371/journal.pone.0012568

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Introduction

Parrots are attractive, colorful birds [1], capable of vocal learning [2] and extraordinary cognitive skills [3–6], including numerical competence [7], tool use [8], and imitation [9,10]. Consequently, parrots belong to the most frequently kept and bred bird order in captivity (cf. [11]). In contrast, natural populations of many parrot species are considerably endangered – 27% species of parrots are listed as threatened and an additional 11% as nearly threatened [12]; cf. [13]. Captive keeping and breeding increases the risk of poaching for the illegal pet market [14–18]. In contrast, if properly managed by conservational institutions and respectable private breeders, supporting backup populations are potentially important in the time of unexpected crisis in nature. Parrots raised in captivity can be successfully reintroduced [19–21], but see [22]. The potential usefulness of parrots kept by breeders for possible rescue programs is, nevertheless, limited by extremely skewed representation of individual species in both institutional and private collections. Moreover, most private breeders are not interested in keeping endangered, but unattractive, species without commercial value that provide no prospect for sustainable funding of the breed [23]. Because of this, rescue programs involving captive breeding managed mostly by zoos and related institutions contribute substantially to the survival of some species (e.g., *Amazona versicolor*, [24]). Successful reintroduction of Puerto Rican parrots (*Amazona vittata*) may serve as an example [25–27]. Parrots kept by zoos and other public institutions are of fundamental importance and the size of worldwide zoo populations may be treated as a simplified measure of ex situ conservation effort. However, long-term captive management of endangered animals is limited by space available for breeding programs in zoos, and single species compete for their share [28]. To be effective, the selection of captive species should take into account case-specific factors such as the availability of habitat for reintroduction of the particular species, their status on the IUCN (International Union for Conservation of Nature) red list, and their capability of breeding in captivity. Still, zoos seem to preferentially shelter species that are large and attractive, even if they are expensive to keep, breed relatively poorly, and are hard to return to the wild [29]. Financial reasons could lead zoos to make such choices to attract visitors who prefer charismatic megafauna [30], but the investment to the exhibits of larger animals make no greater returns than for those of smaller animals [31,32]. Thus, it seems that it is the very human preference for attractive animals that decides the species selection for captive breeding.

The aim of this paper was to test the hypothesis that the size of zoo populations is not only determined by conservation needs, but predominantly by human aesthetic preferences towards particular species. For this purpose we (1) selected different sets of parrot pictures and asked human respondents to evaluate perceived beauty of each species, (2) analyzed the effect of morphological traits, such as coloration, body size and shape, on these estimates of human preferences, and finally (3), attempted to explain worldwide zoo population size by a set of factors including both perceived beauty and conservation status.

Materials and Methods

Ethics Statement

The experiments were performed in accord with the European law and were approved by The Institutional Review Board of Charles University, Faculty of Science. All respondents provided us a written informed consent and agreed to participate in the project voluntarily.

The aesthetic attractiveness of the species was examined by presenting pictures of individual parrot species to human respondents. For the purpose of data collection, we defined the following four sets of species:

1) Reduced set consisting of only 40 species was adopted to avoid eventual habituation of the respondents and thus maximize precision of the assessment. In order to choose species covering the whole range, from the most represented to those absent in zoo collections, we selected them as follows. First, we divided all parrots into eight groups, according to their numerical representation in zoos: 1,000 and up, from 201 to 1,000, from 101 to 200, from 51 to 100, from 26 to 50, from 11 to 25, from 1 to 10, and 0 individuals. In each group, 5 species were randomly selected using True Random Numbers Generator [33], but inclusion of more than one species belonging to a single genus within the category was avoided. In addition, as only 5 species were kept in numbers exceeding 1,000 individuals, they were all included in the reduced set.
2) Complete set consisting of 367 extant species/subspecies was adopted to maximize taxonomic resolution. It is based on the full list of parrot species [34], supplemented by 11 subspecies characterized by coloration apparently contrasting with that of nominotypic subspecies. Three additional taxa recognized by zoos were included (*Barnardius barnardi*, *Platycercus flaveolus*, *Trichoglossus rubritorquis*) and another two taxa were merged with its sister forms (*Cyanoramphus forbesi*, *Cyanoramphus malherbi*).
3) A set of amazons was introduced to examine morphologically and ecologically homogenous group of parrots. It consists of 34 taxa belonging to the genera *Amazona* (33 taxa) and *Alipiopsitta* (*A.xanthops*), covering all extant species of amazons including those subspecies characterized by a distinct coloration.
4) Macaws: 17 extant species of five genera (*Ara*, *Orthopsittaca*, *Primolius*, *Anodorhynchus*, *Cyanopsitta*, *Diopsittaca*) were included because of similar reasons as the amazons; moreover, this small group exhibits considerable color variation (see Fig. 1), and encompasses species highly represented in zoos as well as those that are kept rarely.

The parrot pictures of the reduced set were adopted alternatively from Forshaw and Knight ([35]; further referred as variant 1), Juniper & Parr ([36]; variant 2) and del Hoyo et al. ([1]; variant 3); the second source was also used for the complete set. In order to avoid possible effects of body position, size, and background on rating, the pictures were adjusted with white background, turned right, and resized so that the pictured parrots were of a similar relative size. In the case of amazons and macaws, the pictures were repainted (by S. L.) to fit the precisely identical silhouettes to remove the effects associated with body position, "facial expression", and shape (Fig. 1). Juniper & Parr [36] served as a reference for the paintings.

Because the number of included species differed considerably among the examined sets, we employed two alternative strategies for the assessment of human preferences. The first one, which we further refer to as Ranking [37,38], maximizes the informative content by covering the full ordination scale. It requires simultaneous presentation of all pictures to the respondent to allow relative comparisons, so it is hardly applicable to large sets. In contrast, the second assessment strategy, further referred to as Scoring, provides only limited scoring scale. But it benefits from the possibility to present pictures to the respondent consecutively. Such a presentation enables evaluation of extensive sets of pictures.

The reduced set was assessed by both procedures mentioned above, to verify their mutual correspondence. The respondents of the Ranking procedure were Czech citizens, mostly 19–29 years old. Each person was exposed to one set, i.e. 40 pictures, placed on a table in a random assemblage. Then we asked them: "Please, stack the photographs in an order corresponding to the beauty of the depicted parrot, from the most beautiful to the least beautiful one." The order of the photograph in the pack was then coded by numerals from 1 (the most beautiful one) to 40, further referred to as ranks. Although no explicit time limit was given, all the respondents performed the task within a few minutes. Altogether, we gathered data from 210 respondents; each of the three picture set variants was evaluated by 30 males and 40 females.

Alternatively, Open-Source Software LimeSurvey [39], running on a web server, was used to collect data from 316 respondents (133 men and 183 woman), mainly the students and employees of the Duisburg-Essen University (in Germany). Each respondent was shown the set of 40 parrot pictures (variant 1) in a set order, assigning each of them numbers from 0 (the least attractive) to 6 (the most attractive). Later on, we inverted this seven point scale to obtain values conforming polarity of the other data sets. Furthermore, the respondents were asked to indicate whether they know the pictured parrot or not. The total number of "yes" answers in each species was evaluated as the percentage of knowledge of the parrot. To analyze the effect of the order in which the illustrations were shown, we included one species (*Agapornis fischeri*) twice – in the fourth and forty-first sequence of the screening.

The complete set of species was evaluated by 112 respondents in the Czech Republic (56 men and 56 women). Each respondent was asked to evaluate each of 367 parrot species presented on a computer screen in a random order. At the beginning of the session, the first block of 35 species appeared on the screen as thumbnails arranged six by six on consecutive screens, to provide the respondent with basic information about variance in appearance of evaluated parrots. Then, the respondent was asked to score larger pictures (360×540 pixels), appearing one after another on the screen, on a five point scale (1 corresponding to the best). The timing of presentation was determined by the respondents themselves as the picture on the screen was replaced by another one when they successfully entered the score. The process was repeated until the last species was scored. Next, we standardized raw scores by subtracting respondent's mean score

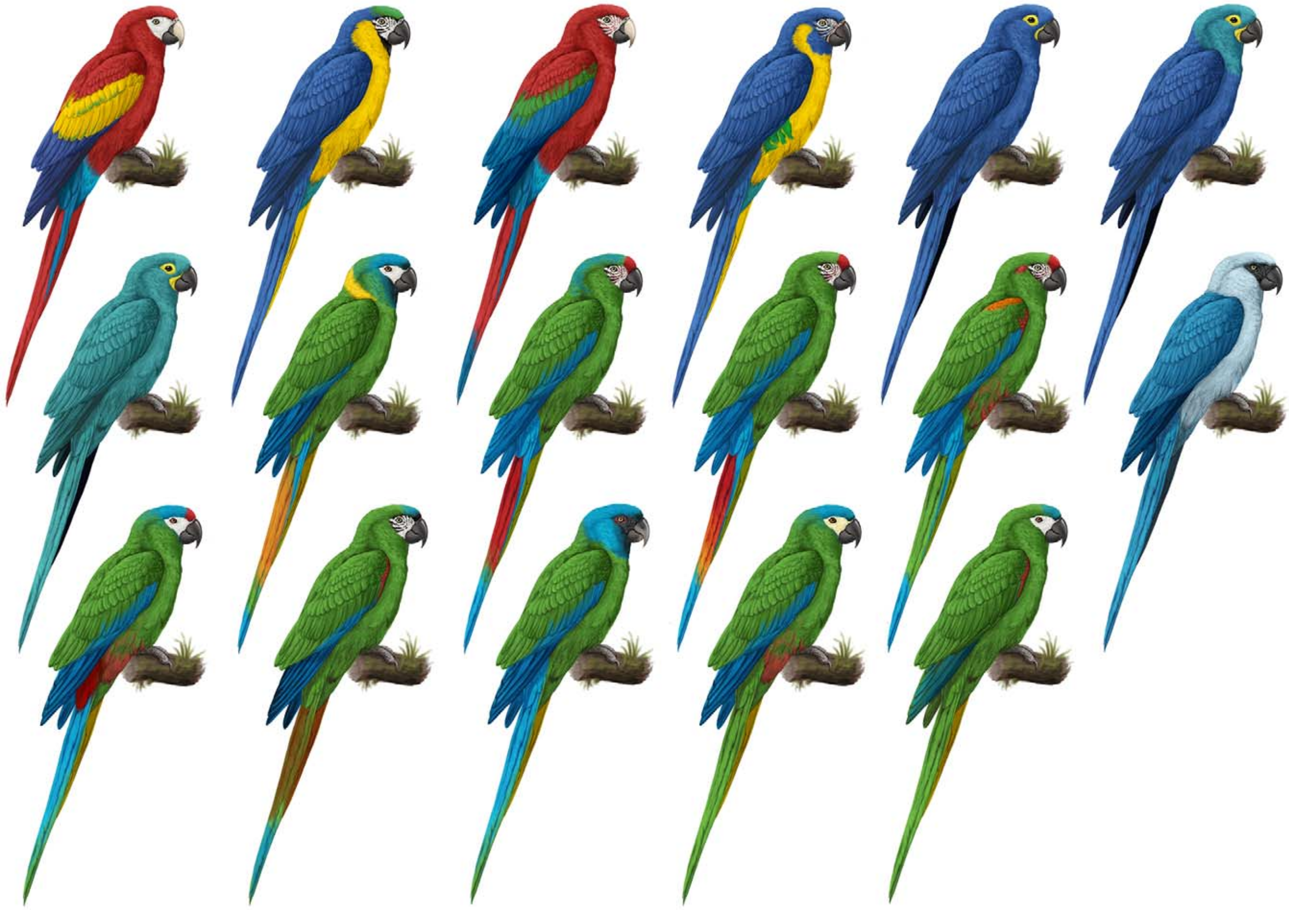

Figure 1. The standardized pictures of 17 macaw species. They are arranged in rows according to perceived attractiveness from the most preferred (top left) to the least preferred (bottom right) species by human respondents.
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and dividing by its standard deviation. Because species means of raw scores were highly correlated with standardized ones ($r^2 = 99.5\%$, $p < 0.0001$), we further analyzed the raw variables as they were more intuitive.

The sets of amazons and macaws were evaluated by 65 (30 men and 35 women) and 73 (32 men and 41 women) respondents by ranking method.

All respondents agreed to participate in the project voluntarily. Each subject provided a written informed consent and additional information about gender, age, experience with parrots, and knowledge of the presented species.

Information about the numbers of individuals of each particular parrot species kept in zoos worldwide was obtained from the ISIS [40] online database (http://www.isis.org), accurately covering [41] more than 700 zoos and aquariums from 72 countries.

Listing of species in the IUCN categories "Nearly Threatened", "Vulnerable", "Endangered", and "Critically Endangered" ([34], cf. IUCN website http://www.iucnredlist.org.), was coded as "present on the list", while the category "Least Concern" was coded as "not present". The number of species inside each parrot genus was used as a simplified measure of taxonomic uniqueness of the species. Standard body measurements (total, wing, tail, beak, and tarsus length) of each species were taken from Juniper and Parr [36], del Hoyo et al. [1], and/or Arndt [42]. We extracted principal components from these log transformed traits. The first component, accounting for 88.8% of variation, is further referred as body size, while the second one (7.7%), which may be interpreted as relative tail length, as body shape. Supplementary information was obtained from Robiller [43]. The sizes of species ranges (further referred to as range size) were extracted from graphical maps in Juniper and Parr [36]. The presence/absence of the following colors on parrot bodies was recorded: blue, green, red, orange, yellow, purple/pink, black, and white.

Statistical analyses

In order to quantify and test congruence in species ranking provided by different respondents, we adopted Kendall's Coefficient of Concordance. Prior further analyses, the raw ranks were transformed as follows: each value was divided by the number of evaluated species (40) and square-root arcsin transformed. The variables showing lognormal distribution (number of individuals kept in zoos, body measurements, taxonomic uniqueness, range size) were transformed by natural logarithm prior to the analyses. Principal Component Analysis (PCA) was performed to visualize the multivariate structure of the data sets. ANOVA/MANOVA, Hotelling tests, GLMs and/or Multiple regression analysis were applied to test the effects of independent explanatory variables. Mann-Whitney test was used as a non-parametric alternative for variables deviating from normality (raw sores).In order to partially control the effects of phylogeny, we divided the studied species into 10 clades (Nestor-Strigops; Cacatuidae; Psittrichas; Psittacini; amazons and allies of Arini; macaws and allies of Arini;

Psittaculini; Loriinae, main branch of Platycercini; Neophema-Agapornis and allies) and introduced clade as a random factor into GLMs. The clades were defined according to Wright et al. [44]; putative phylogenetic position of the remaining genera was set according to conventional taxonomy [1]. Three species suspected to be actually extinct (*Anodorhynchus glaucus, Charmosyna toxopei, C.diadema*) were excluded from all analyses dealing with size of zoo populations. We performed most calculations in Statistica 6.0. [45] and SPSS v.16.0 [46].

Results

Agreement among respondents and methods

Reduced set. The results of the ranking procedure revealed considerable congruence among the respondents in all variants of the reduced set consisting of 40 species. Kendall's Coefficients of Concordance W were 0.258, 0.239, 0.231, and 0.197 for the variants 1, 2, 3, and pooled data, respectively (all $p<0.001$). Mean transformed ranks computed for individual variants were mutually highly correlated ($r^2 = 61.2\%$, 39.5%, and 55.0% for 1 vs 2, 1 vs 3, and 2 vs 3 respectively; all $p<0.0001$). The correlations between mean transformed ranks provided by male and female respondents were even higher: $r^2 = 85.2$ (70.9, 88.4 and 73.4 for variants 1, 2 and 3, respectively).

Nevertheless, Manova revealed small, but significant effect of both variant ($F_{78,332} = 5.76$, $p<0.0001$) and gender ($F_{39,166} = 1.81$, $p = 0.0056$). Separate ANOVAs performed in individual parrot species (Bonferoni corrected $Ps<0.05$) revealed no effect of gender, but confirmed the effect of the variant in 13 species. Post hoc tests revealed that *Nymphicus hollandicus* and *Chalcopsitta cardinalis* were more preferred in variant 1 than in variant 3, while the opposite was true for *Enicognathus leptorhynchus*, *Ara glaucogularis*, *Psephotus dissimilis*, *Geopsittacus occidentalis*, *Touit melanonota*, and *Eunymphicus cornutus*. When variants 2 and 3 were compared, *Agapornis canus*, *A. fischeri*, and *Loriculus philippensis* were more preferred in the former while *Pionus fuscus*, *Touit melanonota*, and *Eunymphicus cornutus* in the latter; finally, *Geopsittacus occidentalis* and *Loriculus philippensis* were more preferred in variant 2 than in variant 1.

Scoring procedure confirmed agreement among the respondents ($W = 0.246$, $n = 316$, $p<0.001$), as well as high positive correlation between mean preferences exhibited by men and women ($r^2 = 91.7\%$; $p<0.0001$). Mann-Whitney tests revealed significant ($p<0.05$, Bonferoni adjusted) effect of gender on preference in two species out of 39 examined ones. Both *Agapornis fischeri* and *Psittaculirostris edwardsii* were more preferred by women than men. Mean scores of individual species closely correlated with corresponding mean ranks obtained by ranking procedure (variant 1): $r^2 = 81.9\%$ ($p<0.0001$).

Complete set. The scores obtained for the complete set of 367 pictures also revealed sufficient congruence among the respondents (PC1 explains 17.3% of total variation). The correlation of species means with mean ranks obtained for the corresponding 40 species set, containing the identical pictures (variant 2), was high: $r^2 = 84.5\%$ ($p<0.0001$).

Amazons. Congruence among the respondents was less pronounced, but still statistically significant ($W = 0.157$, $n = 65$, $p<0.001$). Preferences were affected by gender (Hotelling test: $T2 = 197.80$, n males = 30, n females = 35, $F_{33,31} = 2.95$, $p<0.0016$): men preferred *A. guildingii,* while women *A. viridigenalis* (Bonferoni adjusted t-tests at $\alpha = 0.05$). Nevertheless, preference ranks of individual species provided by men and women were correlated ($r^2 = 21.8\%$; $p = 0.0053$). Mean transformed ranks of amazons species were not correlated with mean scores of corresponding species obtained for the complete set ($r^2 = 6.6\%$; $p = 0.1425$).

Macaws. Congruence among the respondents was high (standardized; $W = 0.287$, $n = 72$, $p<0.001$) and no effect of gender on human preferences was found by multivariate Hotelling test ($T2 = 14.60$, n males = 32, n females = 41, $F_{16,56} = 0.72$, $p = 0.7622$). Mean transformed ranks of particular species of macaws were correlated with mean scores of corresponding species obtained for the complete set ($r^2 = 56.9\%$; $p = 0.0005$).

Traits associated with human preference

The complete set was large enough to assess the effects of particular colors on human preferences. For this purpose, we performed GLM in which preference scores were taken as dependent variable and presence of red, orange, yellow, green, blue, pink-purple, white and black colors as well as body size and shape as explanatory variables. This model ($r^2 = 29.5\%$) revealed that what is more preferred are parrots characterized by large body size ($\beta = -0.214$; $F_{1,358} = 19.3$, $p<0.0001$) and long tail ($\beta = -0.370$; $F_{1,358} = 65.7$, $p<0.0001$), and those having blue ($\beta = -0.163$; $F_{1,358} = 12.8$, $p = 0.0004$), orange ($\beta = -0.147$; $F_{1,358} = 10.5$, $p = 0.0013$), and yellow ($\beta = -0.145$; $F_{1,358} = 10.3$, $p = 0.0014$) colors. On the contrary, green parrots tended to be less preferred ($\beta = 0.097$; $F_{1,358} = 4.0$, $p = 0.0474$).

Correlates of worldwide zoo-population size

Reduced set. We found significant positive correlation between the number of individuals kept in zoos worldwide and human preference ranks (Variant 1: $r^2 = 38.2\%$, $p<0.0001$; Variant 2: $r^2 = 14.3\%$, $p = 0.0162$; Variant 3: $r^2 = 4.1\%$, $p = 0.2118$; pooled variants 1–3: $r^2 = 19.9\%$, $p = 0.0039$, see Fig. 2 and Fig. 3), as well as with mean scores (Variant 1: $r^2 = 37.2\%$, $p<0.0001$) among 40 parrot species. When we applied partial correlation to remove the effect of foreknowledge (i.e., proportion of respondents who marked the particular species as known), the relationship between mean scores and zoo population size remained significant ($r^2 = 13.7\%$, $p = 0.021$).

In order to also examine the effects of other factors on zoo population size, we performed GLMs. The initial full model included preference ranks (computed from pooled variants), range size, body size, body shape, and IUCN listing as explanatory variables, and it revealed significant effects of the former two factors only. Final model explained 43.8% of variation in zoo population size: preference rank ($\beta = 0.422$; $F_{1,37} = 11.4$, $p = 0.0017$) and range size ($\beta = 0.476$; $F_{1,37} = 14.5$, $p = 0.0005$).

Complete set. When all 367 species were included, the correlation between mean scores of human preference and the number of individuals kept in zoos worldwide decreased to $r = 0.304$ ($r^2 = 9.2\%$, $p<0.0001$, Fig. 4). Nevertheless, 16 of the 18 (=5%) most preferred parrot species were kept in numbers exceeding 50 individuals. Zoo populations exceeding this value were recorded in 98 out of 367 extant species only.

Next, additional explanatory variables were included and GLM performed. No effect of taxonomic uniqueness ($F_{1,348} = 2.8$, $p = 0.0978$) and IUCN listing ($F_{1,348} = 2.1$, $p = 0.1435$) was found, so these variables were excluded. The reduced model ($r^2 = 44.9\%$) included mean scores of human preferences ($\beta = -0.264$; $F_{1,350} = 28.8$, $p<0.0001$), range size ($\beta = 0.415$; $F_{1,350} = 94.2$, $p<0.0001$), body size ($\beta = -0.352$; $F_{1,350} = 42.7$, $p<0.0001$), and body shape ($\beta = 0.146$; $F_{1,350} = 6.7$, $p = 0.0099$). The effect of clade, treated as a random factor, was also significant ($F_{9,350} = 4.7$, $p<0.0001$).

Amazons and macaws. In amazons, the number of individuals kept in zoos worldwide was correlated with preference ranks of individual species ($n = 34$; men: $r^2 = 13.6\%$, $p = 0.0321$; women: $r^2 = 21.1\%$, $p = 0.0063$; genders pooled: $r^2 = 28.1\%$, $p = 0.0013$; Fig. 5). In macaws, this correlation was positive as well ($n = 16$; $r^2 = 31.6\%$, $p = 0.0235$; Fig. 6).

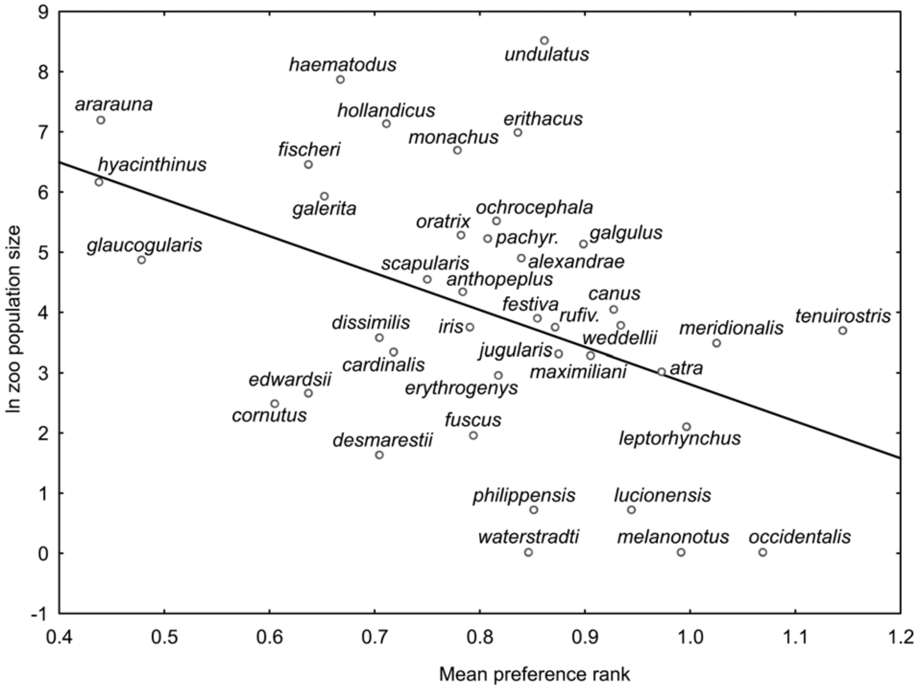

Figure 2. Preference ranks of the reduced parrot picture set. The figure shows the relationship between mean preference rank of parrots (variants of pictures pooled) and its worldwide zoo population size in the reduced set of 40 species ($R^2 = 19.9\%$). The higher the rank, the lower the human preference of the species is.
doi:10.1371/journal.pone.0012568.g002

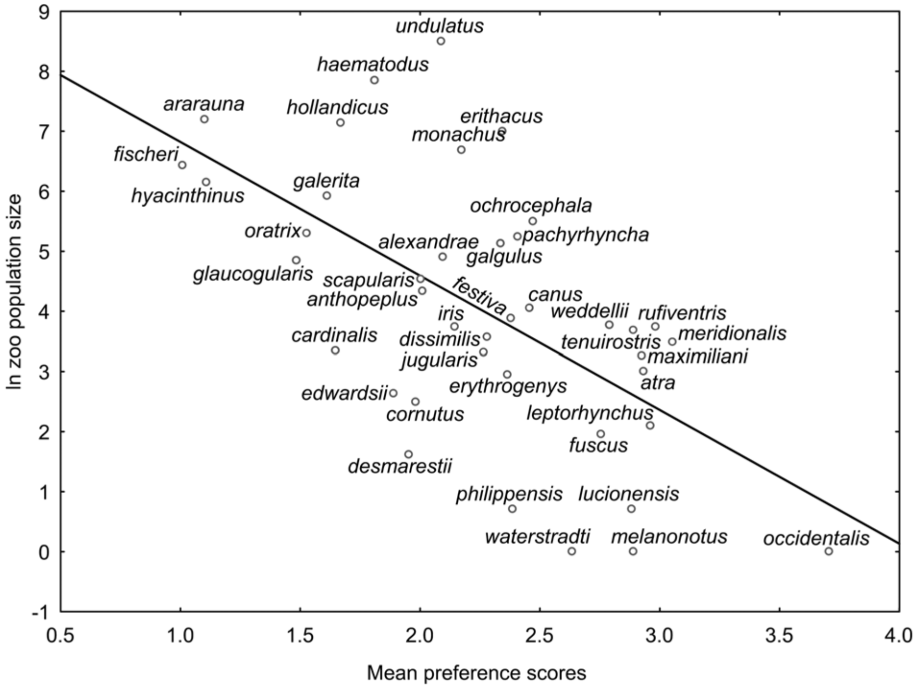

Figure 3. Preference scores of the reduced parrot picture set. The figure shows the relationship between mean preference scores of parrots (picture variant 1) and its worldwide zoo population size in the reduced set of 40 species ($R^2 = 37.2\%$). The scale of scoring ranged from 0 to 6. The higher the mean score, the lower the human preference of the species is.
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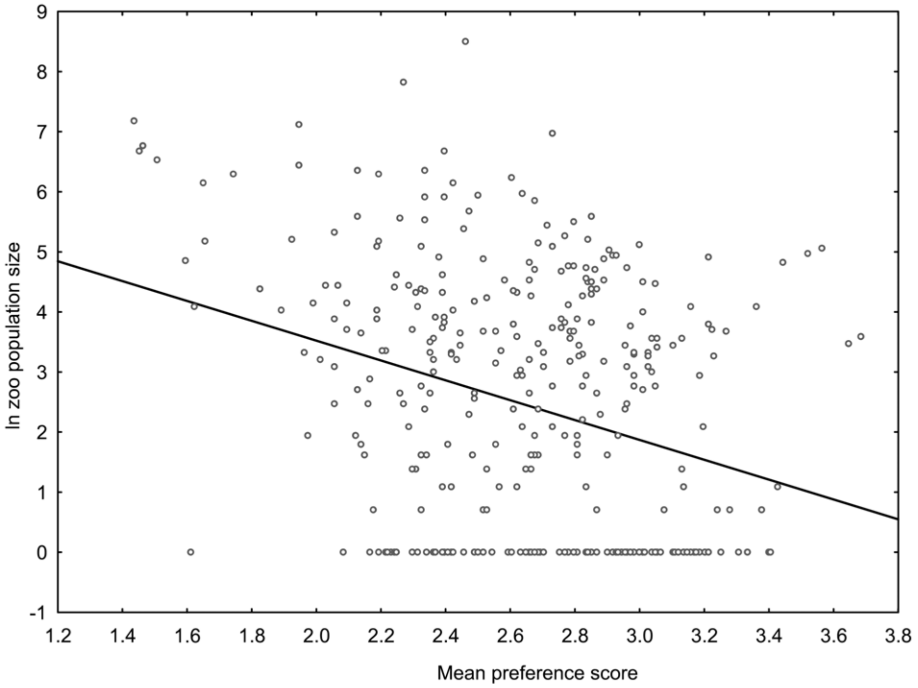

Figure 4. The complete set of 367 parrot pictures. The figure shows the relationship between mean preference scores of parrots (picture variant 2) and its worldwide zoo population size in the complete set of 367 species ($R^2 = 9.2\%$). The scale of scoring ranged from 1 to 5. The higher the mean score, the lower the human preference of the species is.
doi:10.1371/journal.pone.0012568.g004

Discussion

We found a fairly good agreement among the respondents in aesthetic preferences towards pictures of parrot species. In this respect, there were no substantial differences between the sets of pictures representing the whole diversity of parrots (complete and reduced set) and those covering just a small clade, such as macaws or amazons. Nevertheless, the respondents' agreement was the

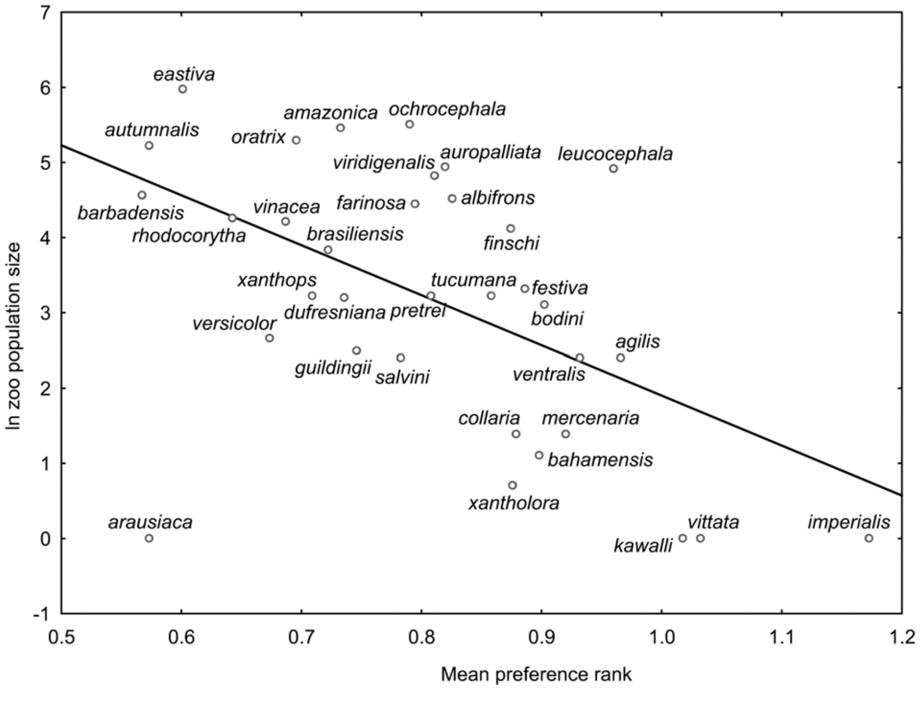

Figure 5. The amazons. This figure shows the relationship between mean preference rank of amazons (shape adjusted pictures) and its worldwide zoo population size (34 species/subspecies; $R^2 = 28.1\%$). The higher the rank, the lower the human preference of the species is.
doi:10.1371/journal.pone.0012568.g005

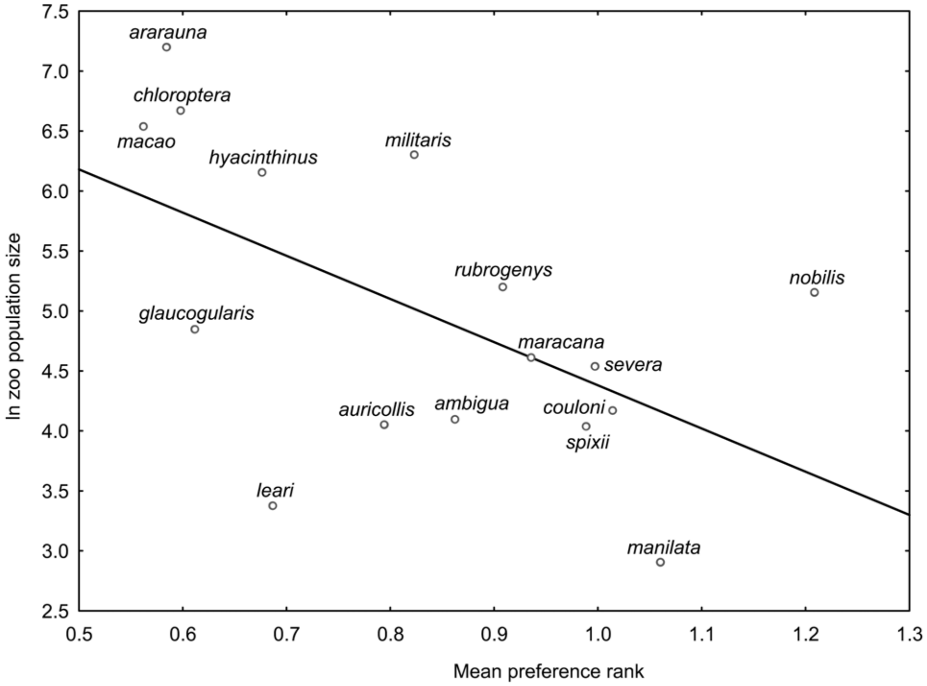

Figure 6. The macaws. This figure shows the relationship between mean preference rank of macaws (shape adjusted pictures) and its worldwide zoo population size (16 species/subspecies; $R^2 = 31.6\%$). The higher the rank, the lower the human preference of the species is. Mean preference rank of the extinct *Anodorhynchus glaucus* is 0.81.
doi:10.1371/journal.pone.0012568.g006

lowest in the case of amazons who are highly homogenous in their morphology, coloration, and pattern, and the respondents repeatedly expressed complaints about similarity of evaluated pictures within this set.

We were not surprised much by the agreement among the respondents evaluating relatively small sets of pictures by ranking method. In our previous papers, we used the same method for evaluation of human preferences within various vertebrate taxa [37,47], including some birds [48], and we found comparable results. In contrast, we expected that the respondents might be confused by extremely extensive sets, but the respondents fairly agreed, even in evaluation of the complete set, consisting of as many as 367 parrot species. Moreover, the resulting mean scores fit well with the ranks obtained by ranking procedure within a reduced set of 40 pictures. This is even more surprising as two methods of evaluation are compared: ranking of real simultaneously presented pictures and scoring of virtual pictures successively shown on screen. But the direct comparison between these evaluation methods, which we carried out in the variant 1 of the reduced set, confirmed that these methods produce nearly equivalent results.

Gender differences in evaluation of parrot beauty were small enough to be omitted in the study analysing the relationship between animal beauty and representation of particular species in zoos worldwide. Zoo curators and visitors belong to both genders, and, thus, decision making is not done exclusively by either one. In this context, pooling the data seems to be adequate, in spite of significant comparisons between the genders. Gender differences in species ranking are, of course, worthy of further examination.

High congruence in evaluation of pictures does not necessarily mean that these pictures reliably represent particular parrot species. We compared human preferences towards 40 parrot species of the reduced set, as assessed using three variants of pictures. Although there was a basic agreement in ranking the species, it was apparently lower than those in the above discussed comparisons, concerning the identical pictures. Thus, reliability of pictures may represent a possible methodological pitfall that potentially decreases precision of human preference estimates. We tried to avoid this problem either by combining the results obtained for different variants of pictures (reduced set) or by repainting the colors and patterns into the same shape (silhouette) of the parrot. The latter approach is, however, applicable exclusively in the case of morphologically homogenous groups as macaws and amazons.

The superstars of our beauty competition tended to be large, colorful and long-tailed parrots, while small and dull (green) parrots received no attention. Visual inspection of the most prominent losers (e.g., *Psittrichas fulgidus, Nestor notabilis, N. meridionalis, Cacatua tenuirostris, Enicognathus leptorhynchus*) suggests that they usually possess an exaggerated, hawk-like beak (curved and sharp), which might be perceived by humans as weaponry. The effect of body size on human preferences may be surprising, considering that the respondents evaluated size-standardized pictures, providing no direct information about the absolute body size of the parrots. Thus, either are large parrot species statistically more beautiful per se, or are the human respondents able to estimate the real body size of the depicted parrots. Allometric component of body shape (already contributing to the first principal component, treated here as a multivariate body size) could play a role in both of these scenarios. Nevertheless, we can not exclude the effect of the respondents' previous knowledge of some depicted species, enabling to predict the body size of similar parrots.

Relationship between human preferences and the size of worldwide zoo population was positive and significant within all four examined sets of parrot species. We previously reported similar relationships within some other taxa of vertebrates as boid snakes [37], basal mammals (monotrems, marsupials, Afrotheria and Xenarthra), Laurasiatheria (comprising mainly of ungulates, carnivors and insectivors), terrestrial birds, and pheasants [48]. This suggests that selective keeping of beautiful species in zoos is a more widespread phenomenon, not exclusive to the parrots.

Correlation between beauty of the species and its representation in zoos does not provide any information concerning the direction of the putative causal relationship responsible for the observed statistical association. Thus, we cannot exclude the alternative hypothesis that the species highly represented in zoos worldwide have better chance to be preferred by the respondents because of their higher rate of prior experience with commonly exhibited species. We argue, however, that typical respondents never met the vast majority of vertebrate species including parrots. When complete species lists of any taxonomic level are evaluated, previous knowledge is too rare to be responsible for the observed correlations. This problem is worthy of further experimental examination.

One can argue that our respondents belong to just a single culture and that perception of beauty may fundamentally differ in people of different cultures and experiences. Nevertheless, our previous study revealed a surprisingly close correspondence between rankings of snake species by people from such different cultures as are those that are in Europe and Papua New Guinea [47]. Our unpublished data also suggest high cross-cultural correspondence in ranking of other vertebrate taxa including parrots (e.g. correlation coefficient between Europe and east of Lesser Sunda Archipelago was $r^2 = 0.38$; Frynta, unpublished results).

Proportion of variation in zoo population size attributable to human preferences varied among the studied sets; the highest values were found within macaws ($r^2 = 31.6\%$) and amazons ($r^2 = 28.1\%$), while the most relaxed ones were within reduced ($r^2 = 19.9\%$) and especially the complete ($r^2 = 9.2\%$) sets. Relatively low percentage, revealed by the analysis of the complete set, may be explained either by lower precision of human preference estimates (only one non-standardized variant of pictures; possible confusion due to large set of evaluated species), or by masking effect of the vast majority of parrot species which are both not especially attractive to humans and poorly but erratically represented in zoo collections. The former explanation suggests that we probably underestimated rather than overestimated the size of the effect, while the latter one emphasizes that a subset of species (e.g., the most beautiful or most represented in zoos) is affected much more than the remaining ones.

Inclusion of additional variables into the model, partially controlled for the effect of phylogeny, revealed that, besides human preferences, body size and range size also contribute to the worldwide zoo population sizes of individual parrot species. The substantial positive effect of animal body size on its representation in zoo collections is an almost universal rule [30]. Such relationships were previously reported in various animal taxa [37,48]. Body size is an apparent trait for zoo visitors and curators making decisions about which species would be kept and bred. In practice, unlike in our experiments, it is an integral component of parrot attractiveness that cannot be easily separated. Because we adjusted parrot pictures to the same size, our respondents had no direct information on body size of the evaluated species (as discussed above, allometric relationship between body segments may provide some indirect information) and we succeeded in keeping the effect of body size apart.

The larger the geographic range of distribution, the higher the zoo population size of the parrot species is. Widespread parrot species are easier to obtain and import, yet the slope of allometric relationship between zoo population size and distribution range is much smaller than one (0.344; 95%CI = 0.264–0.424). That means species with small distribution range are still relatively overrepresented. This may be interpreted as evidence that zoos tend to keep and breed rare species in their collections preferentially.

In contrast to the above factors, neither IUCN listing nor taxonomic uniqueness, i.e., the variables best reflecting conservation value of the species, had effect on zoo population size. This finding is alarming because zoos seem to pay no systematic attention to species with urgent conservation needs. This conclusion is of course based on the analysis of aggregate data and thus does not imply absence of beneficial rescue programmes managed by zoos. Alternatively, these data may be interpreted, e.g., as an evidence of undesired effect of legal barriers preventing zoos from obtaining species worthy of conservation efforts.

The absence of selective keeping of endangered species by zoos may be attributed to a dual function of zoos and does not necessarily mean the absence of conservation efforts and consequences. The primary function of these institutions is educational and cultural. Successful exposition of not only rare, but also common species improves public views towards animals and may as the so-called flagship species indirectly support conservation efforts of other (similar and/or related) species in need. In spite of this, endangered species may play the same role for visitors as the common ones, while filling the conservation role at the same time. This is in agreement with the 'Ark' concept [49] supported by the WAZA (World Association of Zoos and Aquariums) strategy [50]. Because zoos are currently the best and the most expensive breeding institutions, their focus on endangered species could be highly beneficial for an ex situ conservation. Regional Parrot TAGs (Taxon Advisory Groups) already support these priorities in their suggestions for the establishment of parrot studbooks [51].

The finding that perceived beauty of a parrot species enhances its likelihood to be kept in zoos may have serious consequences for conservation biology. It further corroborates the hypothesis that the fate of the species may be considerably affected by its core attractiveness to humans. Thus, contemporary conservation biology would benefit from focusing on animal beauty and human evolutionary psychology. Moreover, it is a demonstration that the animal morphological traits affecting human behavior towards these animals may affect success of not only individuals, but also species (when facing species selection caused by human pressure).

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Author Contributions

Conceived and designed the experiments: DF HB. Performed the experiments: SL SB. Analyzed the data: DF SL SB HB. Wrote the paper: DF SL HB.

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