Charles University in Prague, Faculty of Science
Department of Zoology

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Ecology and Ethology Group

Mgr. Silvie Lišková

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

Ph.D. Thesis

Supervisor: doc. RNDr. Daniel Frynta, Ph.D.

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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).

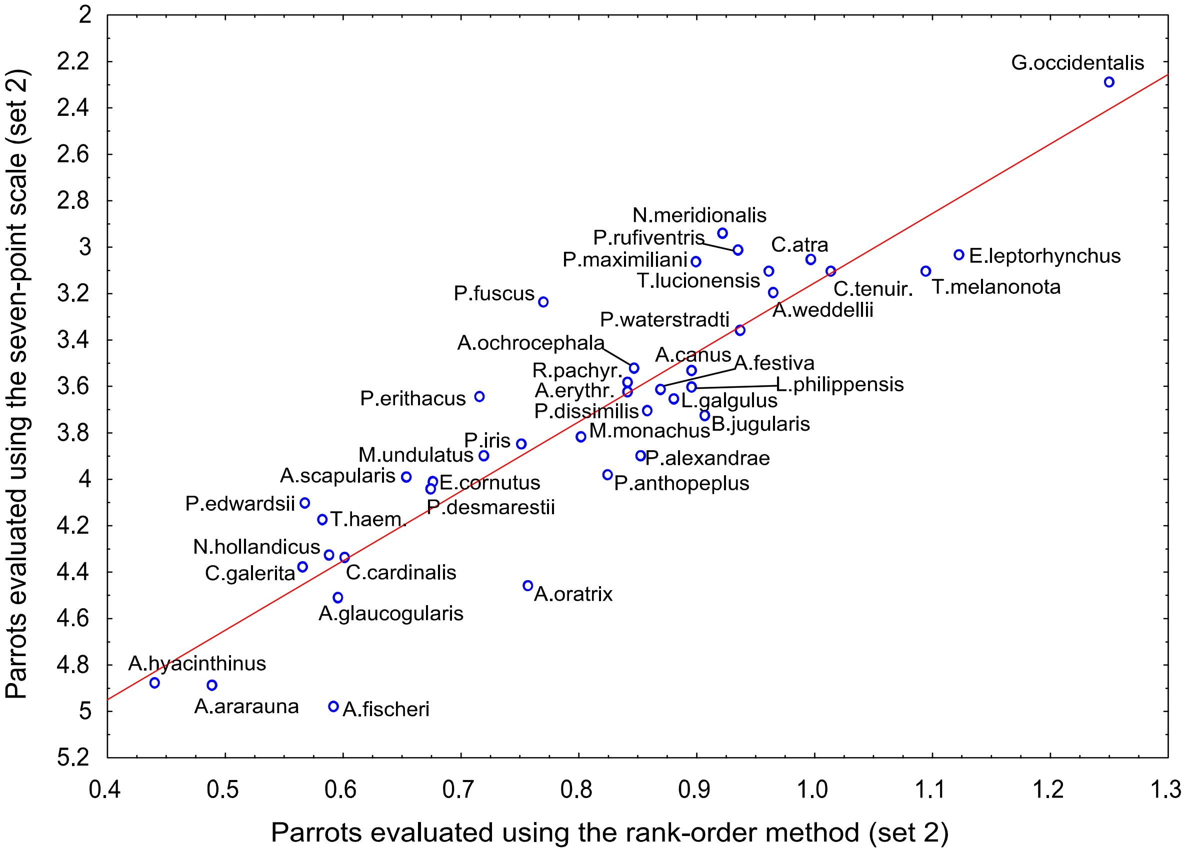

Figure 1b. Correlation of the results obtained from the order-rank and the Likert seven-point scale methods of evaluation of human preferences. A set of 40 painted pictures of parrots was evaluated using the two methods by different respondents. For a detailed description of both of the methods and the 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.

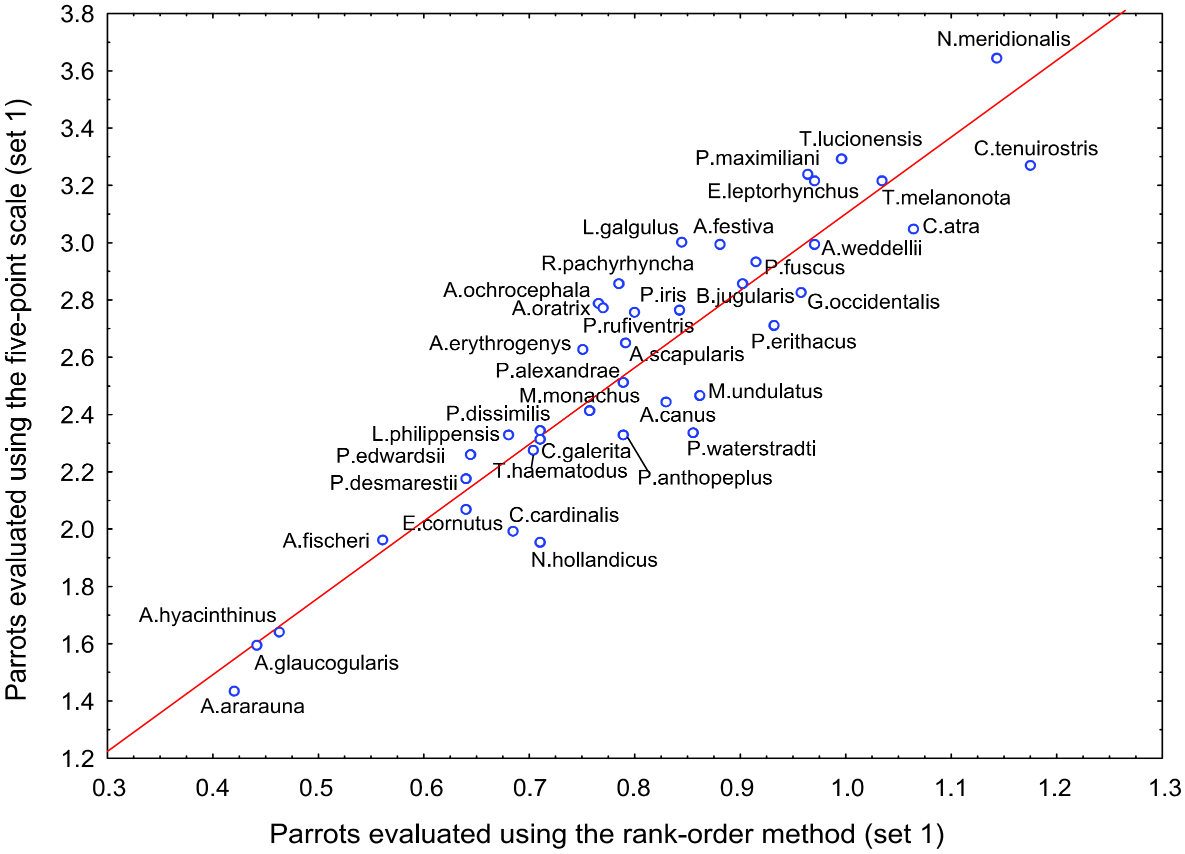

Figure 1b. Correlation of the results obtained from the order-rank and the Likert five-point scale methods of evaluation of human preferences. The order-ranked set consisted of painted pictures of 40 selected parrot species, while the set ranked on a five-point scale contained all extant 367 species. 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]

1 Department of Zoology, Faculty of Sciences, Charles University in Prague, Prague, Czech Republic, **2** Faculty of Biosciences, Department of General Zoology, University of Duisburg-Essen, Essen, Germany

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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Competing Interests: The authors have declared that no competing interests exist.

* E-mail: frynta@centrum.cz

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

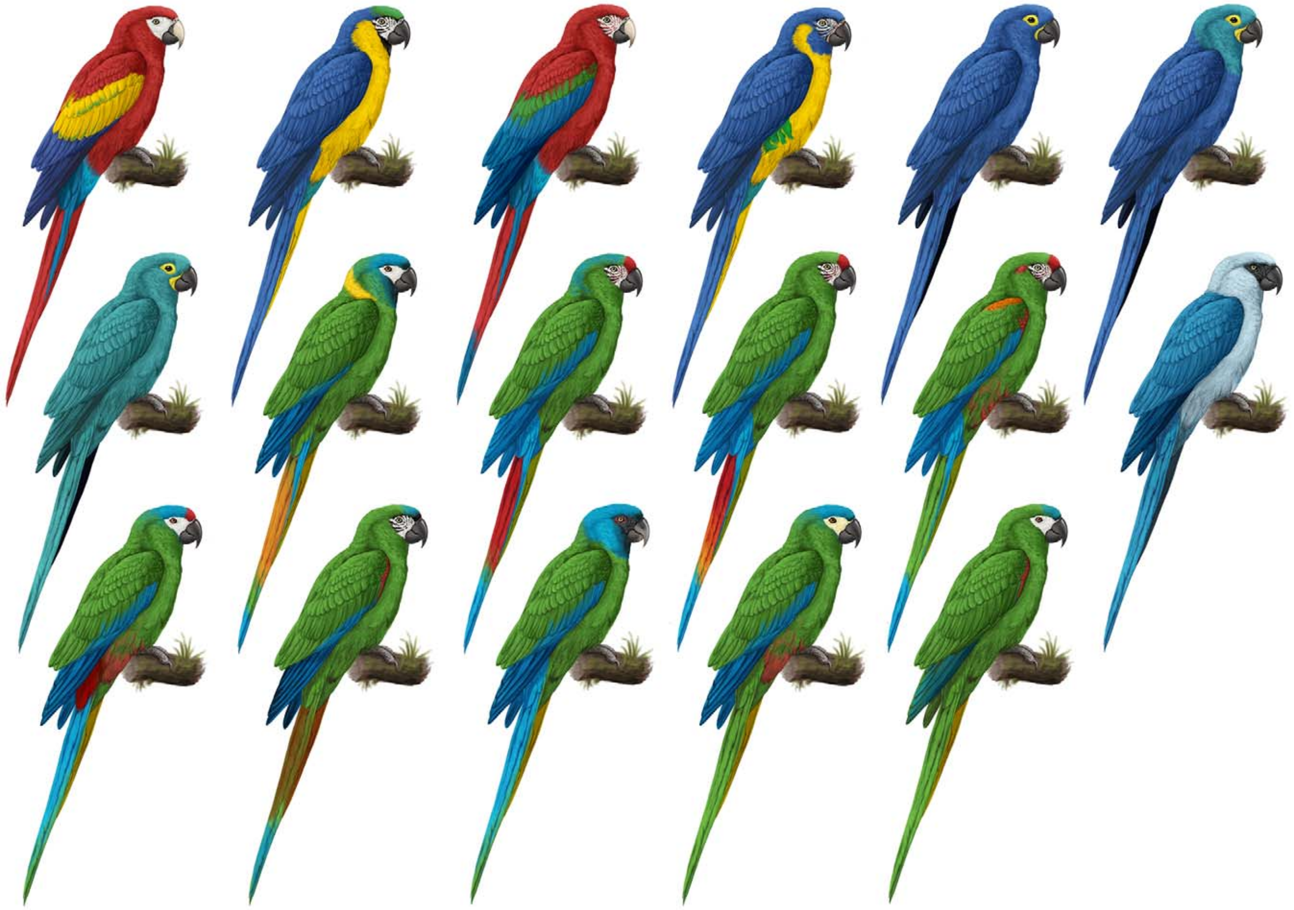

Figure 1. The standardized pictures of 17 macaw species. They are arranged in rows according to perceived attractiveness from the most preferred (top left) to the least preferred (bottom right) species by human respondents.
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and dividing by its standard 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).

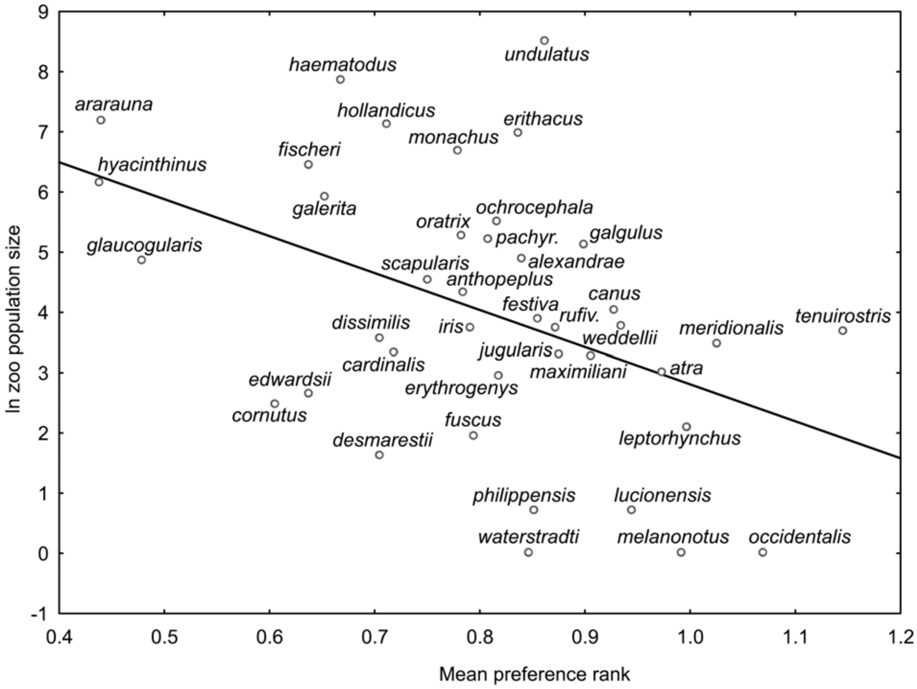

Figure 2. Preference ranks of the reduced parrot picture set. The figure shows the relationship between mean preference rank of parrots (variants of pictures pooled) and its worldwide zoo population size in the reduced set of 40 species ($R^2 = 19.9\%$). The higher the rank, the lower the human preference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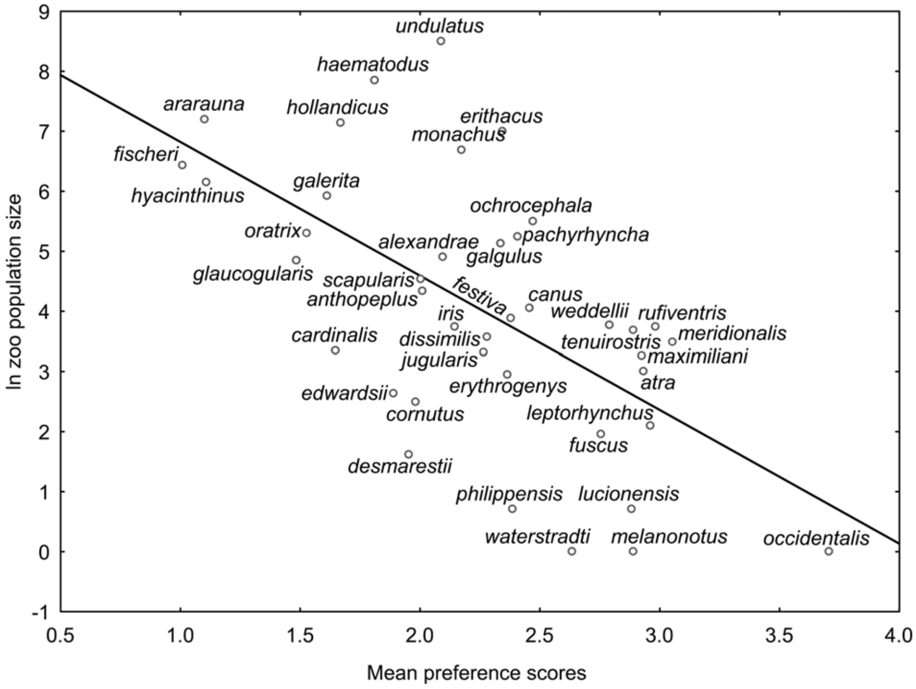

Figure 3. Preference scores of the reduced parrot picture set. The figure shows the relationship between mean preference scores of parrots (picture variant 1) and its worldwide zoo population size in the reduced set of 40 species ($R^2 = 37.2\%$). The scale of scoring ranged from 0 to 6. The higher the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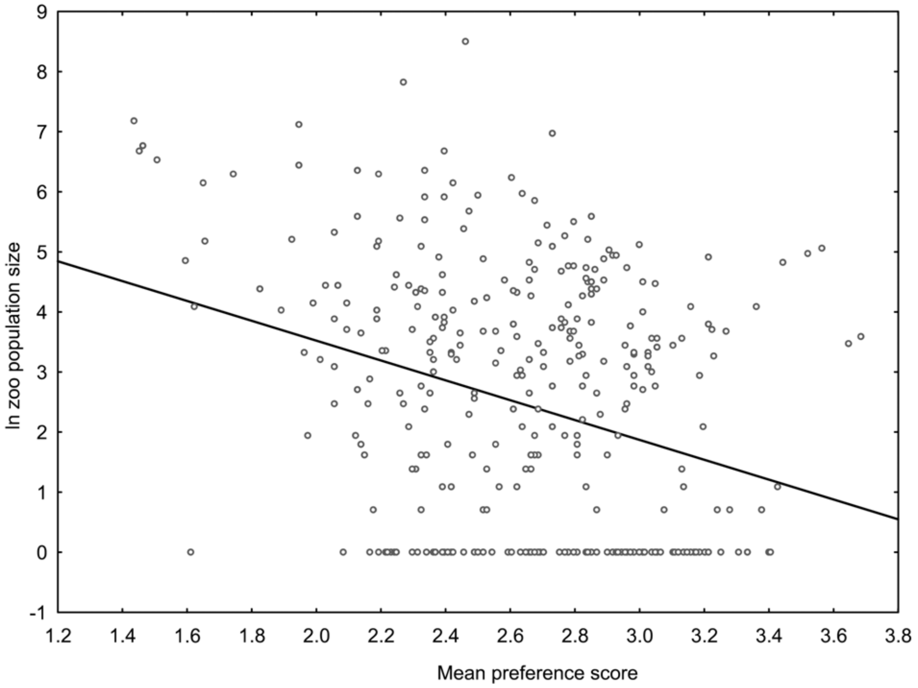

Figure 4. The complete set of 367 parrot pictures. The figure shows the relationship between mean preference scores of parrots (picture variant 2) and its worldwide zoo population size in the complete set of 367 species ($R^2 = 9.2\%$). The scale of scoring ranged from 1 to 5. The higher the mean score,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

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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

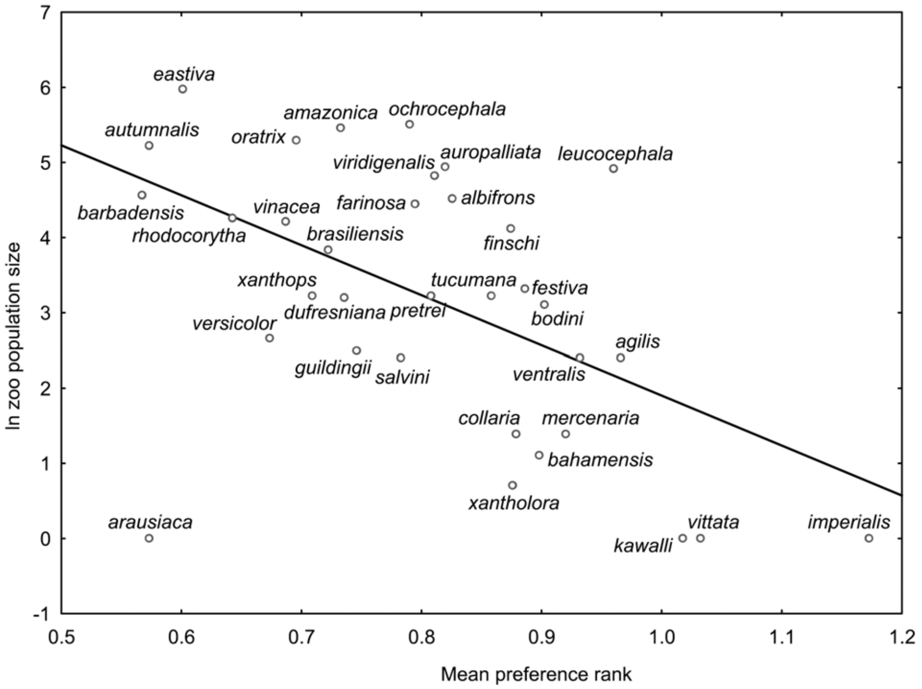

Figure 5. The amazons. This figure shows the relationship between mean preference rank of amazons (shape adjusted pictures) and its worldwide zoo population size (34 species/subspecies; $R^2 = 28.1\%$). The higher the rank, the lower the human preference of the species is.

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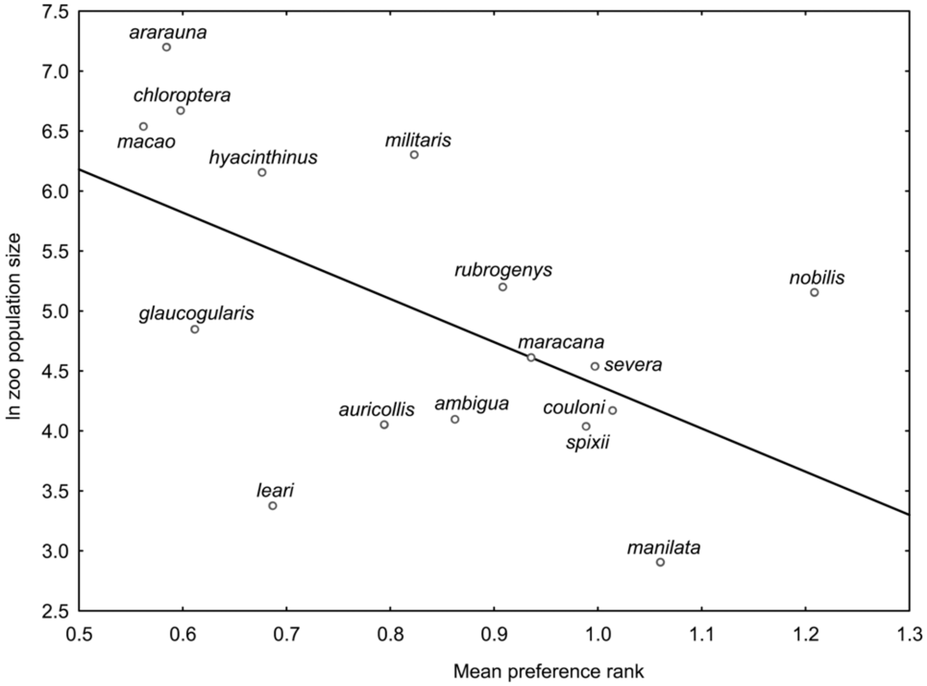

Figure 6. The macaws. This figure shows the relationship between mean preference rank of macaws (shape adjusted pictures) and its worldwide zoo population size (16 species/subspecies; $R^2 = 31.6\%$). The higher the rank, the lower the human preference of the species is. Mean preference rank of the extinct *Anodorhynchus glaucus* is 0.81.
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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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Appendix 3

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What Determines Bird Beauty in Human Eyes?

Silvie Lišková and Daniel Frynta
Department of Zoology, Charles University, Prague, Czech Republic

Address for correspondence:
Daniel Frynta,
Department of Zoology,
Faculty of Science,
Charles University,
Viničná 7, CZ-12844
Prague 2, Czech Republic.
E-mail: frynta@centrum.cz

ABSTRACT Some authors have argued that human preferences for "beautiful" birds may skew the selection of species used to promote conservation programs. This evokes questions about the importance of color, shape, and other appearance traits of bird in affecting human preferences for birds. The aim of this study was to assess the traits affecting human preferences towards all non-passerine and five passerine bird families (n = 102), and to see whether such preferences correspond within a family or are species-specific. Using an Internet survey, we asked 200 human respondents to evaluate pictures of bird species, with two randomly chosen from each family, according to their attractiveness. The respondents were mainly from the Czech and Slovak Republics, but 67 came from other countries (the majority of which were English-speaking). An additional 100 respondents, exclusively from the Czech and Slovak Republics, evaluated the same pictures converted to silhouettes, to test the effect of shape versus color. We included various factors such as morphometric traits (i.e., measurements of body segments and the area the bird silhouette filled in the picture), body weight of the species, and colors, lightness, and saturation of the pictures in the statistical analyses, to help explain any variation in human preferences. We found that human preferences were significantly affected by bird morphology; however, the colors blue and yellow, as well as the overall lightness, were significant as well. The preferences for species belonging to the same family were positively correlated, possibly due to similarity in the body shape of related species. We suggest that finding the traits that determine human preferences toward birds may help conservationists promote a conservation program based on the selection of the correct, scientifically determined, flagship species.

Keywords: attractiveness, avian taxa, coloration, ethnozoology, morphotypes

The appearance of birds and other animals plays an important role in sexual and natural selection, as it serves as a signal to potential sexual partners or predators (Maynard Smith and Harper 2003), and as such many scientists have studied this for decades. Many authors have focused on the specific role of particular color types, that is, mainly carotenoid-based yellow-red (e.g., Hill 1992; Olson and Owens

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1998; Fitze, Tschirren and Richner 2003), melanin-based black-brown (e.g., Rohwer 1975; McGraw 2003; Griffith, Parker and Olson 2006), and structural colors (e.g., Andersson, Ornborg and Andersson 1998; Pearn, Bennett and Cuthill 2001; Delhey et al. 2003). They have also paid attention to the symmetry of shapes (the textbook example is the tail of a barn swallow, see Møller 1994). Both pattern and general appearance of the perceived subject are taken into account when they are seen by a bird (Dolenská et al. 2009), and it has been demonstrated that birds are capable of recognizing and categorizing the shapes of their potential predators (Lorenz 1939; Tinbergen 1939, 1948; Tvardíková and Fuchs 2010). It is therefore evident that various structures of an animal and their coloration may evoke significant responses from the animal's predators and/or conspecifics.

Human ancestors have evolved closely with birds; thus, birds provide relevant stimuli not only to their respective species, but also to mankind and other primates (Macedonia and Polak 1989). Recently, attention has moved from studies of the effects of visual signals on animal receivers to the effects on humans, as well as the accompanying consequences on the conservation of endangered species (Metrick and Weitzman 1996; Gunnthorsdottir 2001; Seddon, Soorae and Launay 2005; Frynta et al. 2009, 2010). An extensive body of literature is devoted to the research of various animal characteristics that affect human attitudes toward species, including willingness-to-pay (WTP) for the conservation of different taxa and species. Birds are repeatedly reported as one of the most appealing animal taxa (Czech, Krausman and Borkhataria 1998; Seddon, Soorae and Launay 2005), next to mammals and large reptiles (such as turtles; Simon, Leff and Doerksen 1995; Leader-Williams et al. 2007; Price and Fa 2007), and as such receive much more attention from policy-makers, conservationists, zoo curators, and individual people as opposed to small, unattractive animals (e.g., invertebrates; Kellert 1993). The preferred characteristics, often considered in the studies of WTP, include large body size (Coursey 1998; Ward et al. 1998), resemblance to humans (Burghardt and Herzog 1980), cultural importance (Kellert 1985), averageness (Halberstadt and Rhodes 2003), overall attractiveness (Gunnthorsdottir 2001; Martín-López, Montes and Benayas 2007), and color (van Hook 1997; Stokes 2007).

It was demonstrated that humans prefer the colors yellow and blue in pictures of parrots, while green (in the case of tree-dwelling parrots, green is present in most of the species and could be considered cryptic) was received negatively. When humans considered their preferences towards parrots, the shape of the birds also mattered, as long-tailed species were more preferred. The most popular/attractive parrots were kept in zoos worldwide in significantly higher numbers, compared with the less attractive, yet endangered, ones (Frynta et al. 2010). And because modern zoos, in addition to in-situ conservation of species, may play an important role in species conservation through possible (or realized) ex-situ breeding programs (Soulé et al. 1986; Balmford, Mace and Leader-Williams 1996; Lees and Wilcken 2009), this in turn can be interpreted as less conservation effort given to "ugly species" (as perceived by humans).

In our study, we aimed to analyze more closely human preferences towards representatives of all bird families (using pictures of birds, for the purpose of data collection), covering a wide variety of morphotypes (diverse morphological species variation), which contrasts with the already analyzed species-rich, but morphologically less diverse, family of parrots. We focused on the following issues: (1) statistical modeling of the contribution of size, shape, and color factors in the prediction of human preferences for birds; (2) further separation of the roles of bird colors/patterns and shape in human preferences. We assessed this by comparing preferences for colorless and patternless silhouettes with those of fully colored pictures. If there is congruence, the body shape itself either affects the preferences or is sufficient in allowing the respondents to recognize the bird; (3) whether human preferences for species are less variable within than between bird families. If there was only a little morphological variance within a bird family, as is typically the case due to phylogenetic properties, human respondents would show more or less similar preferences for different species within families, instead of preferences that differ between species of different families. Thus, human preferences would correspond within two species chosen randomly within a family.

Prior to our analyses, we compared the preferences of both sexes and Czech versus non-Czech residents, to exclude the possibility that preferences are determined by the gender and culture of the respondents.

Methods

Selection of Species

We examined the aesthetic attractiveness of the bird species by presenting pictures of them to people. For the purpose of data collection, we selected two species at random from each of all extant non-passerine bird families (*n* = 97; as recognized by BirdLife International 2009). We also included five families of passerine birds out of 96 recognized extant families. The selection included New Zealand wrens (*Acanthisittidae*), pittas (*Pittidae*), cotingas (*Cotingidae*), scrub-birds (*Atrichornithidae*), and wagtails, pipits, and longclaws (*Motacillidae*), each selected randomly from distant phylogenetic groups (basal passerines, Old World suboscines, New World suboscines, families sister to oscines and oscines; Barker et al. 2004; Chesser and Have 2007). The remaining passerine families were excluded from the study because of their close morphologic and phylogenetic similarity and disproportional representation among extant avian families. Moreover, the inclusion of the complete set of passerines would have increased the number of pictures in the set to over 360 species, which could have led to a possible habituation (or fatigue) of the scoring respondents.

Where possible, we avoided selecting two species from a single genus by removing the members of already selected genera from the list of species designated for random selection. In the cases of monotypic families (including just one species; *n* = 14 for non-passerine birds), we selected only one species. For the within-family correlation analyses, we inserted the first-selected species within all families into a group named “A,” while we named the second-selected species group “B.” Each group consisted of 88 species, as we excluded monotypic families from the correlation analyses.

Testing Attractiveness

We adopted pictures of the190 selected species from the nine volumes of *Handbook of the Birds of the World* (del Hoyo et al. 1992–2004). In order to avoid possible effects of body position, size, and background quality on people’s rating of the pictures, we adjusted them so each had a white background and we resized them so that the pictured birds were of a similar relative size. Because the image plates from the books used were painted to face right in some species and left in others, we turned the left-facing bird pictures horizontally to unify the whole set. Each picture was individually rotated to fit a 2:3 ratio rectangle either horizontally (e.g., tropicbirds, hoopoes, pigeons, and most of the waders; *n* = 94 species) or vertically (e.g., owls, woodpeckers, flamingos, and storks; *n* = 96 species), always paying attention to the position of the bird so that it still looked realistic for the given species.

To score the attractiveness of each bird species, we adopted the already established method we used in our previous study (Frynta et al. 2010). This assessment strategy of scoring pictures on the Internet uses only a limited scoring scale (see below), but it benefits from the ability to present pictures to the respondent consecutively and in large numbers.

The full set of 190 selected bird species was evaluated by 200 respondents: 133 being from the Czech Republic and the Slovak Republic (83 females, 50 males) while 67 came from other countries, of which the majority were English-speaking (31 USA, 9 UK and Ireland, 6 Australia and New Zealand; 2 Argentina, 1 Belgium, 1 Canada, 2 Finland, 3 France, 3 Germany, 1 Israel, 2 Italy, 1 Poland, 1 Russian, 4 Sweden; 53 of which were females, 14 males). The respondents answered willingly to a promotional thread posted on Internet social network websites, art websites, bird-related forums, etc. The Czech and Slovak respondents were given the instructions in the Czech language, while all other participants received the information in English. Each respondent was asked to evaluate each of the 190 bird species according to their beauty (see below). The pictures were presented on a computer screen in a random order. One scoring session consisted of 6 blocks of 32 pictures (30 in the case of the last block). At the beginning of the session, the first block of 32 species appeared as groups of thumbnails on six consecutive screens (six thumbnails on each of the first five screens; two on the last screen), to provide the respondent with basic information about the variation in appearance of the birds. After the respondent viewed all 32 thumbnails, he/she was asked to score the beauty of the birds on larger pictures (360 × 540 or 540 × 360 pixels), appearing one after another on the screen, on a 5-point scale (1 = "the most beautiful bird", 5 = "least beautiful, or ugliest"; as instructed on the website). The respondents themselves determined the timing of the presentation of the pictures on the screen—a picture was replaced by another one when the respondent successfully entered a score. The process was repeated until the last species from the block was scored. Then, the respondent could decide whether to take a break and return to the application to finish the scoring later, or to continue scoring right away. Some respondents scored all 190 bird pictures (in 6 blocks) in one session, which usually took about 30 to 60 minutes. Some respondents stretched the scoring of different blocks over a few weeks.

To evaluate the attractiveness of the actual body shape of the birds, we repeated the above process with 102 images of bird silhouettes. We used the same pictures as in the previous experiment (88 species from set A and 14 monotypic species), but they were blackened so that each picture consisted only of the white background and the bird silhouette. An additional 100 respondents (Czech and Slovak only) evaluated this set. This survey session consisted of three blocks of 34 pictures each.

All respondents agreed to participate in the project voluntarily. Each participant provided informed consent and additional information about country of residence, gender, and age. The experiments were performed in accordance with European law (approval no. 2009/2) and were approved by The Institutional Review Board of Charles University, Faculty of Science.

Explanatory Variables

We adopted the standard body masses of each species from Dunning (2007). We also determined the proportional measurements of body segments (body length measured from the neck-ending to the cloaca position; the length of legs, tail and neck; beak diameter; beak perimeter from the tip to the base of the forehead; eye diameter), together with the surface area each bird filled on the white background, using ImageJ 1.40g (Rasband 1997–2008). We then

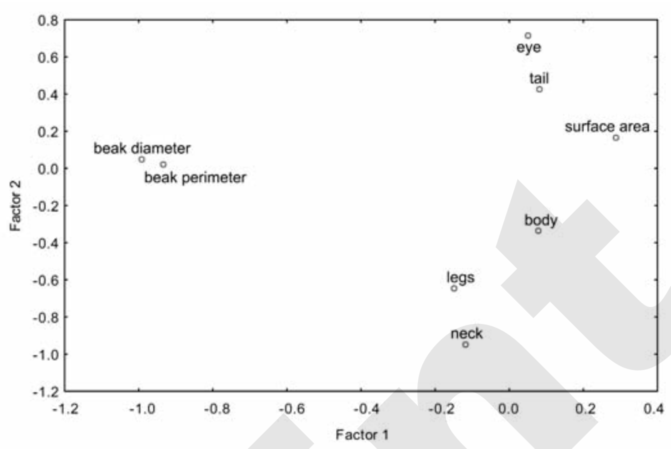

Figure 1. Plot of loadings of varimax normalized maximum likelihood factors, computed from morphometric traits of the bird pictures.

extracted maximum likelihood factors from these log-transformed traits (varimax normalized). The first extracted factor, accounting for 24.8% of variation, was interpreted as relative length of the beak, while the second one (26.9%) corresponded to relative size of the neck and eye (short neck and big eye correspond to high values of the factor scores; for loadings see Figure 1).

We used the following procedure to characterize the colors present in each picture. The pixel values of the pictures were transformed from the red-green-blue (RGB) colorspace to the so-called hue-lightness-saturation (HSL) colorspace. Hue values are similar to angles on a color wheel, in which certain angles correspond with certain colors. The extraction procedure followed Newsam (2005, page 102). In order to avoid dual counting of some pixels (due to the hue angle overlap) and to improve correspondence between color definition and human perception, we adjusted the angle definitions of Newsam (2005) as follows: red (< 350°; 18°), orange/brown (< 18°; 45°), yellow (< 45°; 63°), green (< 63°; 170°), blue (< 170°; 270°), purple (< 270°; 315°), and pink (< 315°; 350°). The color value that was extracted from the picture represented the number of pixels of each color present in the picture (including transparent pixels weighted by their transparency) divided by the sum of all non-transparent pixels (the area of the bird "silhouette"). The transparency (A) covered the interval 0–1, 0 being fully transparent, 1 being a fully visible pixel; the sum of A could be imagined as the number of all pixels the bird covered, compared with the transparent background. The partial transparency of pixels was present only in a minority of pixels at the soft outline of the bird.

The values for saturation (S) and lightness (L), covered the interval 0–1. Because humans perceive pixels with extreme values of lightness and saturation as black/white and gray (Newsam 2005), respectively, we defined three additional "colors": black (L < 0.27), white (L > 0.8), and gray (S < 0.27). Color diversity was then counted as the number of colors (incl. black, white, and gray) present in the picture. The color was considered present when there was equal or more than 3% of the given color in the picture. Some pictures contained "stray" pixels of one or more of the defined colors (mostly purple and pink) because the color-extraction software created for this purpose counted every single pixel. Thus, if there were less than 3% of all pixels of the color present, we excluded these colors from the color diversity factor count as these pixels were not clearly visible and distinguishable in the bird pictures as actual colors.

Additional variables describing the visual quality of each picture that we used to explain human preferences were mean values of S and L, weighted by A, and standard deviation of S and L, again weighted by A.

In order to verify that the details of color value definition had no substantial effect on the results, we computed color representation according to the original definition of Newsam (2005), and we altered the black ($L < 0.2$) and gray ($S < 0.2$) values. This alteration of color definitions had a minor effect on the results. Thus, we present only those results obtained for the adjusted color definition described above. Also, the orange/brown color was not included in the statistical models, to avoid depletion of the degrees of freedom.

Statistical Analyses

In order to quantify and test congruence in species ranking provided by the respondents, we adopted Kendall's Coefficient of Concordance. The variables showing lognormal distribution (body masses and body measurements) were transformed by natural logarithm prior to the analyses. The portion of colored pixels in tested pictures was square-root arcsin transformed. 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. We performed most calculations in R (R Development Core Team 2010), Statistica 6.0. (Statsoft, Tulsa, OK, USA), and SPSS 16.0 (Chicago, IL, USA).

Results

There was a significant level of agreement amongst respondents in their preferences for avian species. Kendall Ws were 0.181 ($n = 190$, $\chi^2 = 4551$, $df = 132$, $p < 0.001$) for Czech and Slovak respondents and 0.213 ($n = 190$, $\chi^2 = 2668$, $df = 66$, $p < 0.001$) for the respondents of other nationalities. Multivariate analysis of variance revealed no effects of nationality (Wilks = 0.4466, $F_{(102, 95)} = 1.15$, $p = 0.240$), gender (Wilks = 0.5162, $F_{(102, 95)} = 0.87$, $p = 0.750$) or their interaction (Wilks = 0.5606, $F_{(102, 95)} = 0.73$, $p = 0.941$) on the scoring of the studied bird species. Consequently, the mean scores of the Czech and Slovak respondents closely correlated with those of other nationalities ($r^2 = 0.839$). These results allowed us to pool together the respondents for further analyses. The bird families most preferred and least preferred by the respondents are shown in Table 1.

We analyzed the effects of morphometric traits (factors 1 and 2, see the methods section), colors and their diversity, lightness (Lmean, LSD), saturation (Smean, SSD), and body weight on the mean preference scores of the 190 studied species (full-color pictures). The full model was, step-by-step, reduced using an AIC criterion. The final model ($r^2 = 0.442$, $F_{(7,182)} = 22.38$, $p < 0.001$; the difference between full and reduced models: $F = 0.59$, $p = 0.822$; for coefficients see Table 2) included the following factors: factor 2 ($F_{(1,182)} = 93.72$, $p < 0.001$), black ($F_{(1,182)} = 10.89$, $p = 0.001$), yellow ($F_{(1,182)} = 14.08$, $p < 0.001$), blue ($F_{(1,182)} = 13.79$, $p < 0.001$), purple ($F_{(1,182)} = 5.58$, $p = 0.019$), LSD ($F_{(1,182)} = 12.37$, $p < 0.001$), and body mass ($F_{(1,182)} = 6.25$, $p = 0.013$). Thus, nearly one half of the variance in the preference scores of the bird species was successfully explained by the analyzed factors, mostly by the relative size of the neck and eye (factor 2). Alternatively, we introduced the bird family as a random factor into the reduced model and computed marginal model using the nlme R package (an additional package within the R statistical software that allowed us to account for correlations between species belonging to the same family), in order to remove the effect of statistical dependence between species

Table 1. The most and least attractive avian families, as evaluated by the respondents ($n = 200$).

Family Name	Mean Attractiveness Score
The Most Attractive Families	
Falcons and caracaras (Falconidae)	1.72
Rollers (Coraciidae)	1.75
Bee-eaters (Meropidae)	1.80
Treeswifts (Hemiprocnidae)	1.84
Owls (Strigidae)	1.85
The Least Attractive Families	
Guineafowl (Numididae)	3.84
New World vultures (Cathartidae)	3.65
Magpie goose (Anseranatidae)	3.58
Cassowaries (Casuariidae)	3.52
Guans and curassows (Cracidae)	3.52

Mean attractiveness score is based on the scores of two randomly selected species from the given family, depicted in full color. Attractiveness scores: 1 = the most beautiful bird, 5 = the least beautiful bird.

Table 2. Human preferences towards 190 bird species depicted in full color. Coefficients and their significance for the reduced model explaining human preference scores of bird species by their morphometric and coloration traits.

	Coefficients Estimate	*SE*	*t* value	*p*	Minimum	Maximum	Effect Size
(Intercept)	2.643	0.176	14.995	< 0.001			
Factor 2	–0.190	0.041	–4.642	< 0.001	–1.763	2.058	–0.727
Black	0.341	0.117	2.918	0.004	0.030	1.219	0.405
Yellow	–0.631	0.233	–2.710	0.007	0.000	0.710	–0.448
Blue	–1.088	0.308	–3.539	0.001	0.000	0.824	–0.896
Purple	–3.112	1.394	–2.232	0.027	0.000	0.227	–0.706
SD lightness	–1.685	0.507	–3.325	0.001	0.091	0.375	–0.479
Body mass	0.052	0.021	2.500	0.013	1.335	11.617	0.532

The effect sizes are defined as the change in the predicted value due to the increase of the predictor from its observed minimum to maximum value. Residual standard error = 0.3807, $df = 182$, $r^2 = 0.442$.

representing the same family. Although an ANOVA revealed a highly significant difference between this model and the standard one (log-likelihood ratio 25.41, $p < 0.001$), the alternative model provided almost the same results; only the effect of the color purple dropped below the level of formal significance ($F_{(1,182)} = 3.75$, $p = 0.060$).

Mean preference scores of the bird silhouettes (further referred to as silhouette score) closely correlated with those of the full-color pictures of the same species ($n = 102$ species of the subset A plus monotypic families, $r^2 = 0.513$; Figure 2). Thus, we included the silhouette score into the set of the predictors and repeated the above GLM procedure analyzing the preference score of the full-color pictures. The final model ($r^2 = 0.765$, $F_{(7,94)} = 47.93$, $p < 0.001$; the difference between full and reduced models: $F = 0.44$, $p = 0.936$; for coefficients see Table 3)

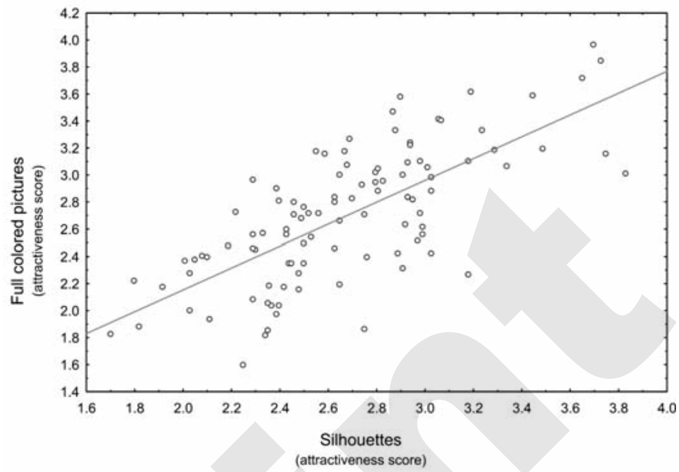

Figure 2. Relationship between the mean attractiveness scores of the full-color bird pictures and that of their silhouettes ($r^2 = 0.513$). Only one species (set A) of each family was included.

Table 3. Human preferences towards 102 bird species depicted in full color and their predictability by the silhouette score. Coefficients and their significance for the reduced model explaining human preference scores of bird species by attractiveness scores of their silhouettes as well as by their morphometric and coloration traits.

	Coefficients Estimate	*SE*	*t* value	*p*	Minimum	Maximum	Effect Size
(Intercept)	1.178	0.214	5.512	< 0.001			
Silhouette score	0.756	0.057	13.187	< 0.001	1.700	3.830	1.610
Factor 2	–0.195	0.026	–7.519	< 0.001	–1.763	2.048	–0.742
Grey	–0.243	0.115	–2.112	0.037	0.165	1.212	–0.254
Red	–0.415	0.158	–2.631	0.010	0.000	0.942	–0.391
Yellow	–0.521	0.231	–2.252	0.027	0.000	0.498	–0.259
Blue	–1.786	0.323	–5.530	< 0.001	0.000	0.369	–0.658
SD lightness	–0.785	0.437	–1.797	0.076	0.091	0.375	–0.223

The effect sizes are defined as the change in the predicted value due to the increase of the predictor from its observed minimum to maximum value. Residual standard error = 0.2403, $df = 94$, $r^2 = 0.765$.

included the following factors: silhouette score ($F_{(1,94)} = 220.26$, $p < 0.001$), factor 2 ($F_{(1,94)} = 71.23$, $p < 0.001$), gray ($F_{(1,94)} = 0.61$, $p = 0.437$), red ($F_{(1,94)} = 4.68$, $p = 0.033$), yellow ($F_{(1,94)} = 6.63$, $p = 0.012$), blue ($F_{(1,94)} = 28.88$, $p < 0.001$), and LSD ($F_{(1,94)} = 3.23$, $p = 0.076$). Thus, the introduction of the silhouette score (reflecting the evaluation of the body shape) considerably increased the explanatory power of the model. Nevertheless, the dominant effect of factor 2 and the contribution of the colors blue and yellow remained unchanged.

Comparison of the mean preference scores of the bird species (full-color pictures) belonging to the same family (sets A and B) revealed that these values were correlated ($n = 88$, $r^2 = 0.541$, Figure 3) and that this correlation was higher than that of most predictors except for morphometric traits ($r^2 = 0.794$ and 0.713 for factors 1 and 2, respectively), body mass ($r^2 = 0.770$), and green color ($r^2 = 0.690$; see Table 4). The results show that the similarity of

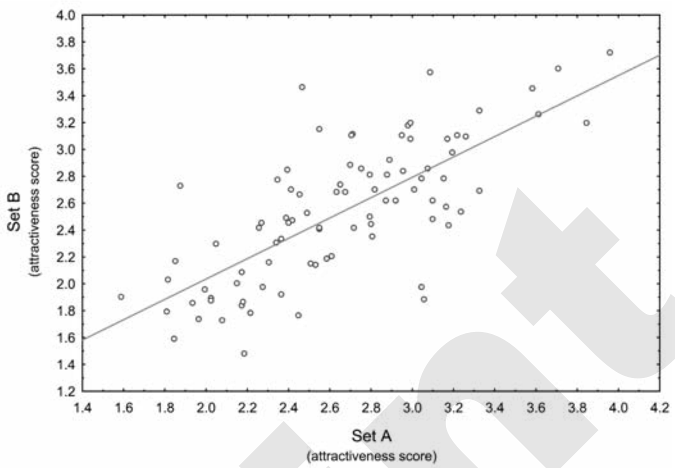

Figure 3. Relationship between the mean attractiveness scores of two randomly selected species from each family (sets A and B; $r^2 = 0.541$).

Table 4. Trait correlations (expressed as r^2) between two randomly selected species of each bird family (sets A and B).

A vs. B	r^2
Attractiveness	0.541
Body mass	0.770
Color diversity	0.090
Mean saturation	0.157
Mean lightness	0.246
Sd saturation	0.125
Sd lightness	0.134
White	0.211
Black	0.257
Gray	0.044
Red	0.052
Orange	0.115
Yellow	0.118
Green	**0.690**
Blue	0.435
Purple	0.306
Pink	0.205
Factor 1	**0.794**
Factor 2	**0.713**

All correlations were significant at $\alpha = 0.05$. The traits with correlation coefficients (r) higher than 0.707 (i.e., explaining more than 50% of variance) are marked in bold.

human preferences for the species belonging to the same family may be explained by morphological rather than color traits.

We attempted to explain the preference score differences between the species of the same family by corresponding differences in explanatory variables. The full model was not significant

($F_{(17,70)} = 1.07$, $p = 0.400$), however, the reduced one (including factor 1, white, gray, Smean and body mass) was ($F_{(5,82)} = 2.91$, $p = 0.018$). The only significantly contributing factor was the mean saturation, Smean ($F_{(1,82)} = 6.53$, $p = 0.012$). These results suggest that related species are morphologically similar, thus the explanation for their differences in human preferences rely on the otherwise less-influencing coloration traits.

Discussion

Colors play an important role in human life; thus, one would expect them to have a major effect on people's preferences for birds. Surprisingly, in our study, a morphological trait (factor 2) was the best predictor of human scoring of bird species based on preference. The shorter the neck and the bigger the eyes, the more attractive the species was to the respondents. Because juvenile animals, including juvenile humans, are characterized by relatively large eyes and short extremities (Alley 1983), the effect of factor 2 may be interpreted as a manifestation of human preference for baby schema (Lorenz 1943) in the appearance of humans and other animals (Gould 1979; Eibl-Eibesfeldt 1989; Glocker et al. 2009), including pets (Archer and Monton 2011).

The importance of shape in human preferences for bird species may also be deduced from the fact that scoring of the colorless and patternless silhouettes correlated well with that of the full-color pictures. We cannot exclude, however, that humans are somehow able to imagine the respective bird colors and patterns from their characteristic silhouette, especially when related species (e.g., belonging to a single family) sharing almost the same silhouette tend to possess similar coloration and pattern. Nevertheless, the coloration and pattern of related species sometimes differ. The birds in our set were randomly selected from existing species worldwide and even a specialist bird-watcher would be unable to memorize all the avian species and the details of their coloration. This further favors the above hypothesis, that shape strongly affects bird attractiveness.

Coloration traits were also found to have a significant effect on preferences, especially the proportion of the colors blue and yellow, as well as variation in lightness. Previously, using a comparable design, we demonstrated that blue and yellow also significantly increases human preferences for parrot species (Frynta et al. 2010). Psychologists have devoted much effort to analyze the influence of colors on human emotions and behavior (for reviews, see Ball 1965; Bellizzi, Crowley and Hasty 1983). Special attention has been paid to this role in color preferences, resulting in the success of advertising campaigns to change shopping behavior (e.g., Bellizzi and Hite 1992). These studies are consistent with our results that the color blue is associated with attractiveness (Crowley 1993), as well as the general importance of lightness and saturation to human preferences (Gorn et al. 1997). Less well interpretable is the preference for the color yellow, which is sometimes reported as rather unattractive to humans (Kaya and Epps 2004). The color red is usually reported as an arousing and distracting signal (Wolfson and Case 2000; Hill and Barton 2005; Ioan et al. 2007), which may affect human evaluation of animals with warning coloration (Marešová, Landová and Frynta 2009). However, in our study we found no specific effect of this color. It should be mentioned here that we paid no specific attention to coloration pattern due to its great variation and the difficulty in coding it into a small number of reliable traits applicable across all studied bird families. Partial aspects of the pattern are, however, inherently reflected by some of the evaluated coloration traits as, for example, color diversity, lightness, and saturation.

Body mass and morphometric traits (factors 1 and 2) were highly correlated when species belonging to the same family were compared (sets A and B). This suggests that a considerable part of the variation in these traits is associated with higher taxonomic levels. This can be explained by their association to life-history (life cycle-related traits, such as age at maturity, fecundity, and life span) variation, 80–90% of which is nested into order and/or family levels (Bennett and Owens 2002). In contrast, coloration traits (and possibly patterns) were less associated with the family level in our data set. Thus, conservative morphology (remaining nearly unchanged for dozens of millions of years of evolution) may lead to selective attractiveness of entire bird clades (families). However, color variation may provide a chance to find an attractive species even within a neglected clade.

Phylogenetic dependence of morphological characteristics may raise the question of whether our analyses dealing with species data have to be phylogenetically adjusted (i.e., the procedure of performing a removal of the possible effects of statistical dependence of species data due to shared evolutionary ancestry; e.g., by independent contrasts; Felsenstein 1985) or not. We decided to avoid the procedure in this study because of the following specific reasons: (1) human respondents are not primarily affected by phylogenies, but rather by superficial similarities resulting in a cognitive categorization of animals (cf. Berlin 1992); (2) we selected species according to families, thus, we avoided clusters of closely related species; (3) we included the taxonomic level with the highest level of variation in morphology and appearance; and (4) the avian phylogenies above the family level are still unstable (i.e., new phylogenetic hypotheses, poorly compatible with the previous ones, are published by different taxonomists every year) and not clearly associated with external body characteristics (Ericson et al. 2006; Pereira and Baker 2006; Livezey and Zusi 2007; Mayr 2007; Brown et al. 2008).

We substituted real birds with their pictures to examine their attractiveness to humans, though the validity of this substitution might be questioned. Our previous study on parrots confirmed that preference ranks of the same species that are presented using pictures from various sources are not identical, but do still sufficiently correlate (Frynta et al. 2010). Recently, we compared human preferences towards living coral snakes and their photographs and we found close correspondence of the results (Landová et al. 2012). According to our knowledge, a similar study carried out on bird taxa has not been done. Nevertheless, since the preferences scored on bird pictures correlate with the sizes of worldwide zoo populations of the given parrot species, it is likely that preferences of pictures do reflect those of living birds (Frynta et al. 2010).

We found no differences between the preference scores for the avian species of the respondents from Central Europe (Czech and Slovak) and the other countries (70% from English-speaking countries). This may be attributed to a similarity in cultures derived from Europe and thus belonging to a single, Euro-American culture (circum mediterranea; Murdock 1967). One can argue that the perception of beauty may differ only in people of fundamentally different cultures and experiences. Nevertheless, our previous study revealed a surprisingly close correspondence between rankings of aesthetic preferences for snake species by people from very different cultures such as those in Europe and Papua New Guinea (Marešová, Krása and Frynta 2009; Frynta et al. 2011). Our unpublished data also suggest high cross-cultural correspondence in the ranking of other vertebrate taxa including parrots (e.g., correlation coefficient between Europe and east of Lesser Sunda Archipelago was 0.62; Frynta, unpublished results).

The absence of significant gender differences in our study is not surprising; in similar studies concerning animal attractiveness, such differences are usually subtle (Herzog 2007; Marešová and Frynta 2008; Frynta et al. 2010).

Precise knowledge of the factors enhancing the attractiveness of birds and other animals to humans may be of great importance for conservation practices which need public support. The selection of proper flagship species based on scientific evidence could help attract human attention and support of conservation programs more efficiently. In this respect, the evidence from psychological studies of advertisements may be really inspiring and useful in developing further research.

In conclusion, considering the factors investigated in our study, human preferences for different bird species seem to be primarily affected by bird morphology However, coloration, especially blue, yellow, and lightness variation may also be important. The understanding of human preferences towards animal species is still limited and, for conservation reasons, more attention should be devoted to this topic.

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Human Preferences for Colorful Birds: Vivid Colors or Pattern?

Silvie Lišková, Eva Landová, Daniel Frynta*

Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ-12844 Praha 2, Czech Republic

*Corresponding author; e-mail: frynta@centrum.cz; phone: +420-221951846, +420-737772867; E-mail to coauthors: silka@atlas.cz, evalandova@seznam.cz

Abstract

In our previous study, we found that the shape of a bird plays a major role in the determination of human preferences, with colors lagging far behind. Thus, we asked: What about pattern? In the present study, we focused on a small passerine family, the Pittidae, with vivid coloration but uniform shape and asked whether the preferences of human respondents towards uniformly shaped, colorful birds are determined by pattern rather than color.

We asked 100 human respondents to rank 43 colored pictures of all extant species and color-differing subspecies/sexes of pittas. Another 100 respondents ranked the same set of pictures set to grayscale, thus lacking chromatic information about the birds' appearance. Using PCA analysis, we extracted the first two multiple principal component axes from the preference ranks to include them in further analyses. Surprisingly, the first axis (PC1) extracted from the preferences of the grayscale set highly correlated with the PC2 axis of the colored set, and vice versa - the PC1 axis of the colored set highly correlated with the PC2 axis of the grayscale set. Such close mutual correlation of the color and grayscale axes suggests that principal cues determining the ranking of the color pictures are also present in the grayscale pictures that possess only achromatic components.

To find the traits determining human preferences, we performed GLM analysis in which we tried to explain the mean preference ranks and PC axes by the following explanatory variables: the overall lightness and saturation (both means and SD), edges (pattern) and the portion of each of the basic color hues (blue, green, yellow, and red).

The results showed that the mean preference ranks/PC1 axis of the grayscale set is explained mostly by the birds' pattern, while the colored set ranking is mostly determined by the overall lightness (darker pictures are preferred). In short, people tend to rank grayscale pictures according to pattern, while they rank color pictures according to overall lightness. The more complex pattern the bird possess (e.g., a wavelets-decorated belly), the more preferred it is. The only colors to slightly affect human preferences towards vividly colored pittas were blue and green.

Keywords: Attractiveness; coloration; conservation; avian taxa; ethnozoology; evolutionary psychology

1. Introduction

A large number of birds posses various conspicuous ornaments, e.g., contrasting or colorful spots and/or feathers (e.g., long tail feathers of some pheasants, quasals or whydahs, crests of cacatuas and turacos, or colorful patterns of many parrots, toucans and pittas; del Hoyo et al. 2003). These traits have evolved as the means of visual communication with their conspecifics, predators, and competitors, making their bearers the winners of the sexual and/or natural selection process (Bennett and Owens 2002; Andersson 1994). Irrespective of the primary function of these traits in the microevolutionary ways to help the individuals to survive and to reproduce, a secondary function rises with the modern age strongly affected by pressure from mankind. Humans perceive certain traits as “beautiful” or “ugly” and treat their bearers accordingly. The “beautiful” animals are selectively kept by zoological gardens worldwide (Frynta et al. 2009; Frynta et al. 2013), and these also receive more conservation-oriented attention by both public and federal funding (Metrick and Weitzman 1996). It is thus important to ask which appearance traits are perceived and judged by humans as “beautiful”.

Colors have long been known to connect with human emotions and feelings, such as sadness or happiness (Gao et al. 2007), and this may in turn affect human preferences for certain colored animal traits. Saturated basic color hues of blue, green, and yellow are usually associated with positive feelings. The blue color is reported to evoke the feeling of calmness, restfulness, peace, security, and comfort; green is linked with peace, comfort, hope, and happiness; and yellow is perceived as joyful, lively, energetic and cheerful (Ball 1965; Kaya and Epps 2004; Crozier 1997). The color red, being more ambiguous, is sometimes perceived positively with emotions like love, happiness, and energy (Crozier 1997; Kaya and Epps 2004), but simultaneously evokes anger and hatred (Mahnke 1996;

Kaya and Epps 2004). Red is also often reported to cause excitement and arousal (Wilson, G. D. 1966; Wolfson and Case 2000; Elliot and Maier 2007), enhance human performance in contests (Hill and Barton 2005), and function as a distracter (Ioan et al. 2007) lessening a person's concentration and performance (Elliot et al. 2007). From achromatic colors, only white is perceived positively, and this is true for people of both Western and Eastern traditions, despite the known fact that white is associated with death in China (Kaya and Epps 2004; Saito 1996). Black and grey colors were perceived negatively as depressive hues (Kaya and Epps 2004), associated with sadness, hatred, mourning, and sorrow (Ball 1965; Mahnke 1996). These attributes of black (low lightness) and gray (low contrast) also cause a notable shift from positive to negative perception when mixed with otherwise positive hues, lowering peoples' preferences for dark and dull colors, such as brown being less attractive compared to orange (Manav 2007). Low lightness is also reported to cause people to feel less relaxed, and hues with low contrast elicit lower excitement (Gorn et al. 1997).

According to the principle of linguistic relativity (linguistic determinism, Whorf and Carroll 1956), human cognitive perception and categorization of colors is linked with the color terms existing in the languages of various cultures. This stimulated cross-cultural comparisons of color naming and perception (Berlin and Kay 1969). Recently, Kay et al. (2010) performed a detailed study of 110 genetically diverse languages, which led them to recognize a certain universal pattern in the emergence of color terms in human languages. The first colors that are usually named, and thus distinguished, are black and white. This partition means that people recognize "light" and "dark" colors of any hue. The importance of black and white colors' recognition in this partition may be influenced by the fact that objects are recognizable, even during a night (dark) environment, with illumination too low to stimulate hue sensation. The next rule for color terms partition as described by Kay et al. (2010) is the distinction of a warm and cool hue spectrum, with red, yellow, and its intermediates coming under the "warm", and with green, blue, and its intermediates coming under the "cold" category. This distinction is long-recognized by color specialists in the fields of both art and science, and it is also very interesting to note that the intermediate hue of yellow-green, which links together these dual spectra, affects human emotions negatively, evoking associations with sickness and disgust (Kaya and Epps 2004). The third rule of forming color terms highlights the importance of the color red. As noted above, the emotional meaning of red hues is controversial, causing arousal and quickening heartbeat, which may point to a special importance of this color for human recognition. Altogether, the terms for the colors black, white, yellow, green, blue, and red, which are considered the basic hues, appear primarily, being followed by the terms for grey, brown, orange, pink, purple and other possible intermediate and mixed colors (Kay et al 2010).

The vivid colors of birds are meant to be seen by their conspecifics, which posses tetrachromatic vision, an ancestral evolutionary trait in terrestrial vertebrates (Bowmaker 2008; Hart et al. 2008). But are humans, as members of the mammalian clade, able to see and appreciate the avian colors in full? During the mammalian ancestry of small and nocturnal animals, their color vision was reduced to a dichromatic state (Zhao et al. 2009, Heesy and Hall 2010). Dichromatic vision is consistent with the warm-cool spectra discrimination, recognizing the short-wave spectrum on one side and long-wave spectrum on the other side (Jacobs 2009). Humans and some other monkeys and apes (independently in Old World primates and New World howler monkeys) regained true trichromatic vision, but the third gene for opsin with sensitivity in long wavelengths (red) has evolved only recently when compared to the evolutionary history of mammals (see Martin and Ross 2005 and references herein). In this light, we may ask about the importance of achromatic colors for human preferences as compared to blue, green, and yellow hues on one side (evolutionarily ancestral) and red on the other side (evolutionarily recent). If the origin of human emotions and preferences reach far into the long ancestry of small nocturnal mammals, achromatic colors (consisting of variance in lightness and contrast and forming the base of patterns and shapes) should play a major role in assessing human aesthetic preferences. These would be followed by the ancestrally seen hues of blue, green and yellow. On the other side, red is known as an exciting color causing arousal, important in primate communication (Setchell et al. 2006) and food gathering (Surridge, et al. 2003). Thus, the position of this color in human aesthetics forms a very interesting question.

In our previous studies, we showed that morphology and selected colors affected human preferences towards birds. In parrots, humans preferred long tails along with blue and yellow colors, while green color (present on most of the parrots in majority) affected preferences negatively (Frynta et al. 2010). The study of all non-passerine bird families that followed confirmed the significance of blue and yellow colors, with red and purple colors also having a minor effect. More importantly, it revealed that the bird shape, or silhouette, was the strongest predictor of human preferences. However, this study did not include “pattern” as a predictor in the analyses, as the light-contrast differences were only represented by the standard deviation (SD) of lightness. It therefore raised a question about the importance of pattern to human preferences towards birds, as compared to colors and shape.

In this paper, we examined the effects of colors and pattern on human aesthetic preferences of birds. For this purpose, we selected pittas: a monophyletic group of colorful Old World tropical passerine birds (Moyle et al. 2006) sharing almost the same shape (silhouette), but highly diversified when concerning color and pattern.

Human aesthetic preferences are linked to the evolution of the visual system. As such, the phylogenetic position of humans who belong to the mammalian group of primates should be considered when studying human preferences. The evolutionary theory, as mentioned above, assumes that the ancestor of all mammals was a small, nocturnal animal (Kemp 2005). For nocturnal mammals living in the dark, the ability to distinguish objects in achromatic contrast and pattern is of the utmost importance. On the basis of this theory, we can hypothesize that the importance of achromatic vision may be superior to color vision in recent mammals, including primates and humans. The results of human cognitive categorization and color naming as studied by Kay et al (2010) is in agreement with this. We tested this hypothesis by analyzing the effects of lightness and achromatic pattern on human aesthetic preferences for colorful birds. Simultaneously, we analyzed the effect of basic colors such as red, yellow, green, and blue, asking whether there is some pattern that would confirm the duality of red and yellow (warm colors) on one side and green and blue (cold colors) on the other side. We also investigated the position of the red color, which seems to be salient in the context of evolution of human vision and human color naming and which causes bipolar emotional feelings and arousal.

In short, we tested the effects of (1) lightness and pattern, (2) warm-cool colors continuum and (3) red color on human aesthetic preferences for pittas. This testing was performed by showing pictures of pittas to human respondents in both full color and grayscale.

2. Material and Methods

2.1 Selection of species

For the purpose of this study, we selected the morphologically uniform family of Old World passerine birds – the pittas (Pittidae). This group is characterized by flamboyant colors and contrasting patterns that vary considerably among species. Few species are also sexually dichromatic. We examined the aesthetic attractiveness of these birds by presenting a set of 43 pictures to human respondents. The set of pictures included all 32 extant species of pittas (BirdLife International 2011) and two distinctly colored subspecies (*Pitta guajana irena, P. sordida rosenbergii*). In nine distinctly sexually dichromatic species, we included pictures of both sexes (*P. baudii, P. caerulea, P. cyanea, P. elliotii, P. guajana, P. gurneyi, P. nipalensis, P. schneideri, P. soror*). The colored pictures were adopted from the 8th volume of the *Handbook of The Birds of The World* (del Hoyo et al. 2003). In order to avoid possible effects of body position, size, and background on rating, the pictures were adjusted with white backgrounds and resized so that the pictured birds were of a similar relative size.

2.2 Testing of human preferences

The assessment of human preferences of the depicted birds followed the ranking method used in Marešová and Frynta 2008; Marešová et al. 2009a,b; Frynta et al. 2009, 2010, 2011 and Lišková and Frynta 2013. The respondents were Czech citizens, mostly 19-29 years old. Each person was exposed to one set, i.e. 43 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 bird, 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 43, 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 100 respondents (50 males and 50 females). To evaluate separately the attractiveness of the pattern of the birds, we repeated the above process with the same set of images set to grayscale. This set was evaluated by another set of 100 Czech respondents (50 males and 50 females).

All respondents agreed to participate in the project voluntarily. Each subject provided an informed consent and additional information about gender and age. The experiment was performed in accord with the Czech and European law and was approved by the institutional ethical committee (No. 2009/2)

2.3 Picture processing

We used a similar procedure in our previous study (Lišková and Frynta 2013) to characterize the colors present in each picture. Pixel values of the pictures were transformed from the red-green-blue (RGB) colorspace to the so-called hue-lightness-saturation (HSL) colorspace. Hue values are similar to angles on a color wheel, in which certain angles correspond to certain colors. The extraction procedure followed Newsam (2005). In order to avoid dual counting of some pixels (due to the hue angle overlap) and to improve correspondence between color definition and human perception, we adjusted the angle definitions of Newsam (2005) as follows: red <350°; 18°), orange/brown <18°; 45°), yellow <45°; 63°), green <63°; 170°), blue <170°; 270°), and violet-rose <270°; 350°). However, only the basic colors as defined by Kay et al. (2010) were included in further analyzes, excluding the orange and violet-rose colors. Moreover, the orange hue as depicted on the actual pictures was mixed with such values of saturation and lightness that it was perceived as "brown" in most of the pictures, which further substantiated the exclusion of the hue; and the violet-rose hue was too rare (very underrepresented) to be analyzed reliably.

We analyzed the portion (in percent) of each such defined color as depicted on the bird (Figure 1a, b). Although all pixels on the picture, including the background (the area around the object of interest), have their own value for hue, the background pixels were intentionally excluded from the color proportions value analysis using their transparency. This was done using the following method: The color value that was extracted from the picture responded to the number of pixels of each color present in the picture (including transparent pixels weighted by their transparency) divided by the sum of all non-transparent pixels (the area of the bird "silhouette"). The transparency (A) covered the interval 0-1, 0 being fully transparent, 1 fully visible pixel; the sum of A could be imagined as the number of all pixels the bird covered, compared to the transparent background. The partial transparency of pixels was present only in a minority of pixels at the soft outline of the bird.

The values for saturation (S) and lightness (L) covered the interval 0-1. Because human respondents perceive pixels with extreme values of lightness and saturation as black/white and gray (Newsam 2005), respectively, we defined three additional "colors": black ($L < 0.20$), white ($L > 0.80$), and gray ($S < 0.27$). Additional variables describing visual quality of each picture that we used to explain human preferences were mean values of S and L, weighted by A, and standard deviation of S and L, again weighted by A.

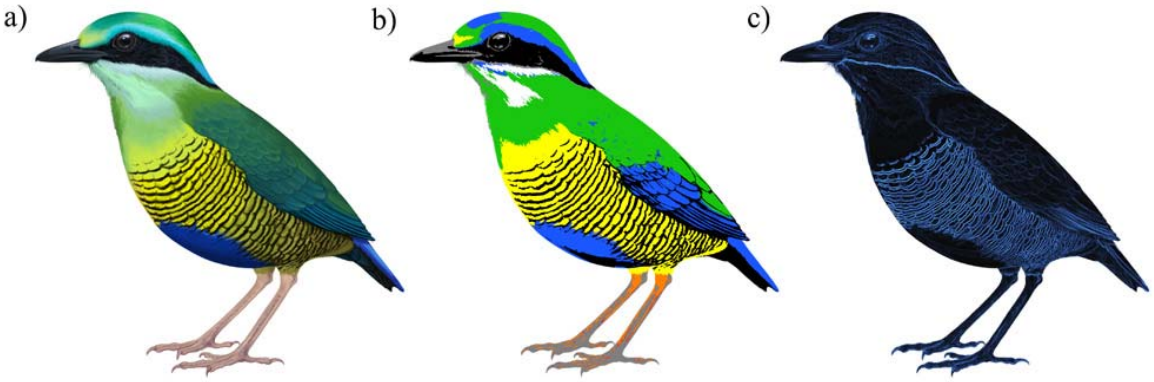

Figure 1. **Colors and edges extractions from the full colored pictures were done using a special software.** a) The full-colored, original example of a pitta picture (*Pitta elliotii*); b) This picture shows the pitta transformed into fewer pre-defined colors, which were extracted as percentages of total pixels of the given color; c) The last picture shows the edges detection, interpretable as the complexity of the pattern.

The complexity of various patterns as wavelets and spots on the birds' belly and wings was defined as the portion of contrasting patches on each picture, measured through edge detection which was processed using the math function of Sobel operator (Sobel 1978). Each contrasting patch of pixels was detected as an edge and "drawn" on the picture as a light outline – the higher the count of such contrasting patches, the more light outlines there were generated on the picture (Figure 1c). The final value of the pattern variable, further referred to as "edges" in the text, corresponded to the overall lightness of the generated picture – the lighter the outcome picture, the more complex pattern the bird possessed. In the present picture set, the minimum and maximum values for edges reached from around 0.19 to 0.53.

2.4 Statistical analyses

In order to quantify and test congruence in species ranking provided by different respondents, we adopted Kendall's Coefficient of Concordance as implemented in SPSS v.16.0 (SPSS Inc 2007). The contribution of the combinations of the color/greyscale and sex to the variability in ranking species of pittas was examined and visualised in Redundancy Analysis (RDA) as implemented in CANOCO (ter Braak and Smilauer 2002).The portion of colored pixels in the tested pictures was square-root arcsin transformed prior to the analyses. Principal Component Analysis (PCA) was performed to visualize the multivariate structure of the data sets and to extract uncorrelated axes for further analyses. MANOVA and General Linear Models (LMs) were applied to test the effects of independent explanatory variables. Full LMs were further reduced according to Akaike criterion until log-likelihood tests revealed significant comparison between the full and reduced models. We performed most calculations in R (R Development Core Team 2010) and Statistica 6.0. (Statsoft 2001).

3. Results

Multivariate analysis of variance (MANOVA) revealed effects of coloration versus grayscale (Wilks = 0.4482, $F_{42,\ 155} = 4.53$, $P < 0.0001$) and gender (Wilks = 0.6940, $F_{42,\ 155} = 1.63$, $P = 0.0175$), but not their interaction (Wilks = 0.7231, $F_{42,\ 155} = 1.41$, $P = 0.941$), on the ranking of the studied bird species. See the contribution of particular species to these differences as visualized by RDA plot in Figure 2. When t-tests were performed for each species and set, the gender differences were statistically significant only in six cases. *P. angolensis*, *P. arcuata,* and *P. reichenowi* were more preferred by male respondents and *P. caerulea* (male) and *P. erythrogaster* by female respondents in the colored picture set, while *P. angolensis* and *P. arcuata* were more preferred by males and *P. gurneyi* (male) by females in the grayscale picture set. Because the gender differences were small and involved only six out of 43 examined species of pittas, we decided to pool the genders in further analyses concerning the means or multivariate axes (PCA) computed from the preference ranks. Both of these methods extract the agreement among respondents and thus further blend the minor effects of gender. The agreement between the respondents was assessed by Kendall's W. It appeared significant ($n = 100$; $df = 42$; $P < 0.001$) in both colored and grayscale picture sets (Kendall's W = 0.139 and 0.206, respectively).

We performed LMs analyzing the factors contributing to the preferences of pitta pictures as evaluated by our respondents. For the colored picture set, we introduced the following explanatory variables to explain the mean preference ranks: lightness and saturation (both means and SD), edges, and basic color hues (blue, green, yellow, and red). The initial full-model ($r^2 = 0.7589$) revealed a significant contribution of lightness (both mean and SD), edges, blue, green, and yellow. The final reduced model ($r^2 = 0.7496$; see Table 1a and Fig. 3) confirmed the effect of mean lightness ($F = 21.98$; $p < 0.0001$), edges ($F = 25.54$; $p < 0.0001$), blue ($F = 19.90$; $p = 0.0001$), green ($F = 27.22$; $p < 0.0001$), and yellow ($F = 7.42$; $p = 0.0099$), but SD saturation ($F = 5.74$; $p = 0.0219$) was also significant.

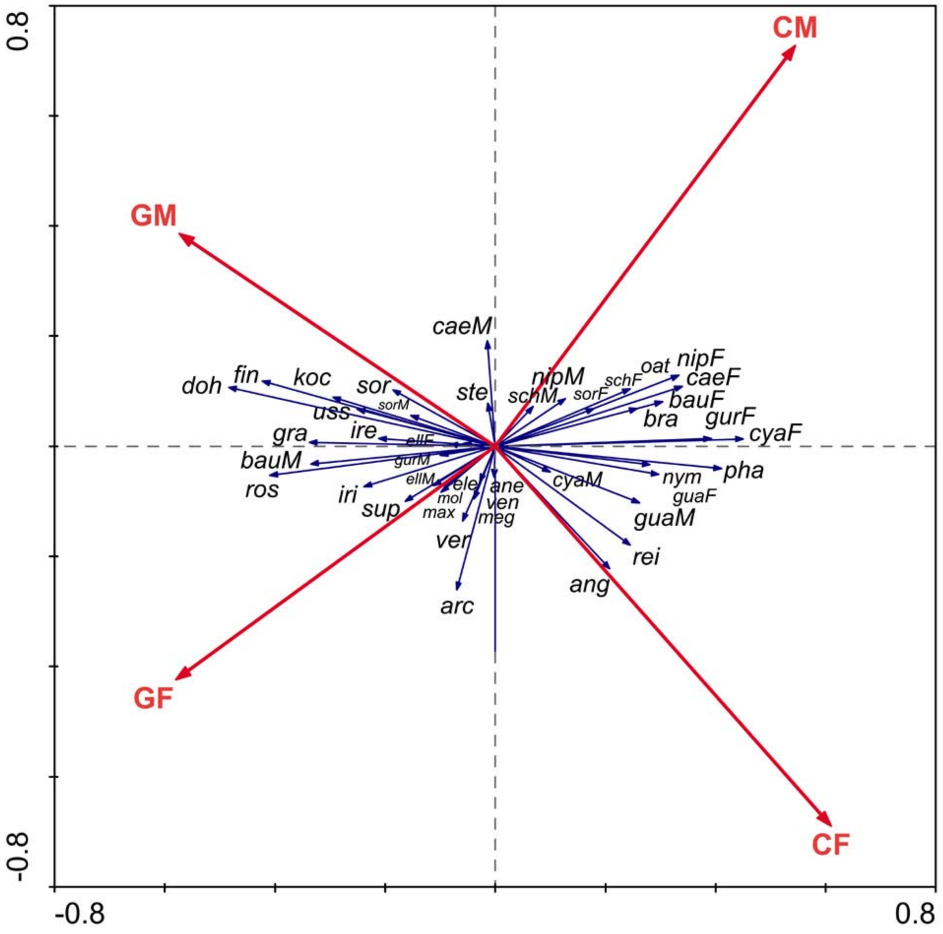

Figure 2. The projection of groups of respondents and species of pittas into the first two RDA axes. Eigenvalues of RDA1 and RDA2 axes are 0.067 and 0.011, respectively. **CM** - men evaluating colored pictures; **CF** - women evaluating colored pictures; **GM** - men evaluating grayscale pictures; **GF** - women evaluating grayscale pictures. Species names are abbreviated as follows: **ane**: *Pitta anerythra*, **ang** - *P. angolensis*, **arc** - *P. arcuata*, **bauM** - *P. baudii* male, **bauF** - *P. baudii* female, **bra** - *P. brachyura*, **caeM** - *P. caerulea* male, **caeF** - *P. caerulea* female, **cyaM** - *P. cyanea* male, **cyaF** - *P. cyanea* female, **doh** - *P. dohertyi*, **ele** - *P. elegans*, **ellM** - *P. elliotii* male, **ellF** - *P. elliotii* female, **fin** - *P. erythrogaster finschii*, **gra** - *P. granatina*, **guaM** - *P. guajana* male, **guaF** - *P. guajana* female, **ire** - *P. guajana irena*, **gurM** - *P. gurneyi* male, **gurF** - *P. gurneyi* female, **iri** - *P. iris*, **koc** - *P. kochi*, **max** - *P. maxima*, **meg** - *P. megarhyncha*, **mol** - *P. moluccensis*, **nipM** - *P. nipalensis* male, **nipF** - *P. nipalensis* female, **nym** - *P. nympha*, **oat** - *P. oatesi*, **pha** - *P. phayrei*, **rei** - *P. reichenowi*, **schM** - *P. schneideri* male, **schF** - *P. schneideri* female, **sor** - *P. sordida*, **ros** - *P. sordida rosenbergii*, **sorM** - *P. soror* male, **sorF** - *P. soror* female, **ste** - *P. steerii*, **sup** - *P. superba*, **uss** - *P. ussheri*, **ven** - *P. venusta*, **ver** - *P. versicolor*.

When evaluating the mean preference ranks of the grayscale pictures, those explanatory variables involving coloration (saturation, blue, green, yellow, red) were not applicable and thus we performed LMs including only mean and SD lightness and edges. Both full- and reduced models ($r^2 = 0.5486$ and 0.5351, respectively; see Table 1b and Fig. 3) revealed the effects of edges (the reduced model: $F = 39.79$; $p < 0.0001$) and mean lightness (the reduced model: $F = 6.25$; $P = 0.0166$).

Because the respondents' discrimination may reflect more than one axis (set of characters), we extracted multiple principal component axes from the preference rankings. The first three principal axes explained 28.4%, 13.7%, and 7.7%, respectively, of the total variance of the colored picture set. The corresponding values for the grayscale picture set were 31.0%, 16.0%, and 8.4%. We further analyzed these components and found that the first and second components of both sets are mutually closely correlated (PC1 color vs PC2 grayscale: $r^2 = 0.6428$, $p < 0.0001$; PC2 color vs PC1 grayscale: $r^2 = 0.8256$, $p < 0.0001$) and thus probably reflect a similar set of traits used by the respondents as a guide for ranking.

In order to identify these putative traits, we analyzed the first two principal axes by LMs in a similar way to the mean values of preference ranks as described above. First, we analyzed PCs derived from the grayscale picture set that represents a simpler model. PC1 of the grayscale set ($r^2 = 0.6801$, Table 1c) was explained by edges ($F = 72.5$; $P < 0.0001$) and mean lightness ($F = 8.45$; $P = 0.0060$). PC2 of the grayscale set ($r^2 = 0.7501$, Table 1d) was explained by mean lightness ($F = 83.06$; $P < 0.0001$), SD lightness ($F = 29.02$; $P < 0.0001$), and edges ($F = 5.01$; $P = 0.0309$). Next, we analyzed PC1 derived from the color set and included PC2 derived from the grayscale set as a predictor instead of the edges and lightness, which already contributed to this variable. The resulting LM ($r^2 = 0.8655$; see Table 1e) revealed that besides the fundamental contribution of PC2 grayscale ($F = 167.77$; $P < 0.0001$), highly significant and positive effects of blue ($F = 26.16$; $P < 0.0001$) and green ($F = 17.23$; $P < 0.0001$) colors on human preferences of colored pictures were also present.

Table 1. Anova tables and coefficients of General Linear Models (LMs).

a) Response: Mean preference ranks of the colored set

	Anova		Coefficients:			
	F	p	Estimate	Std. Error	t	p
(Intercept)			0.430	0.171	2.509	**0.0167**
Mean L	21.98	**<0.0001**	0.754	0.256	2.942	**0.0057**
Edges	25.54	**<0.0001**	-0.176	0.050	-3.548	**0.0011**
Std S	5.74	**0.0219**	-0.694	0.389	-1.783	0.0831
Blue	19.90	**0.0001**	-0.480	0.078	-6.155	**<0.0001**
Green	27.22	**<0.0001**	-0.175	0.065	-2.703	**0.0104**
Yellow	7.42	**0.0099**	-0.315	0.115	-2.725	**0.0099**

b) Response: Mean preference ranks of the grayscaled set

	Anova		Coefficients:			
	F	p	Estimate	Std. Error	t	p
(Intercept)			0.330	0.152	2.178	**0.0354**
Edges	39.79	**<0.0001**	-0.394	0.069	-5.725	**<0.0001**
Mean L	6.25	**0.0166**	-0.669	0.267	-2.500	**0.0166**

c) Response: PC1 extracted from the grayscaled set preference ranks

	Anova		Coefficients:			
	F	p	Estimate	Std. Error	t	p
(Intercept)			1.019	0.999	1.020	0.3141
Edges	72.51	**<0.0001**	2.406	0.359	6.695	**<0.0001**
Mean L	8.46	**0.0060**	3.557	1.301	2.735	**0.0093**
Std L	1.95	0.1706	4.086	2.927	1.396	0.1706

d) Response: PC2 extracted from the greyscaled set preference ranks

	Anova		Coefficients:			
	F	p	Estimate	Std. Error	t	p
(Intercept)			-3.450	0.883	-3.906	**0.0004**
Mean L	83.06	**<0.0001**	11.635	1.149	10.124	**<0.0001**
Std L	29.02	**<0.0001**	-10.677	2.587	-4.127	**0.0002**
Edges	5.01	**0.0309**	-0.711	0.318	-2.239	**0.0309**

e) Response: PC1 extracted from the colored set preference ranks

	Anova		Coefficients:			
	F	**p**	**Estimate**	**Std. Error**	**t**	**p**
(Intercept)			-1.718	0.493	-3.485	**0.0013**
PC2 greyscale	167.78	**<0.0001**	-0.387	0.098	-3.947	**0.0004**
Std S	3.82	0.0586	5.991	1.949	3.074	**0.0041**
Mean S	3.26	0.0794	-2.202	0.942	-2.336	**0.0253**
Blue	26.19	**<0.0001**	2.638	0.402	6.569	**<0.0001**
Green	17.23	**0.0002**	1.280	0.348	3.675	**0.0008**
Yellow	3.02	0.0907	1.042	0.475	2.196	**0.0348**
Red	3.86	0.0576	0.991	0.505	1.963	0.0576

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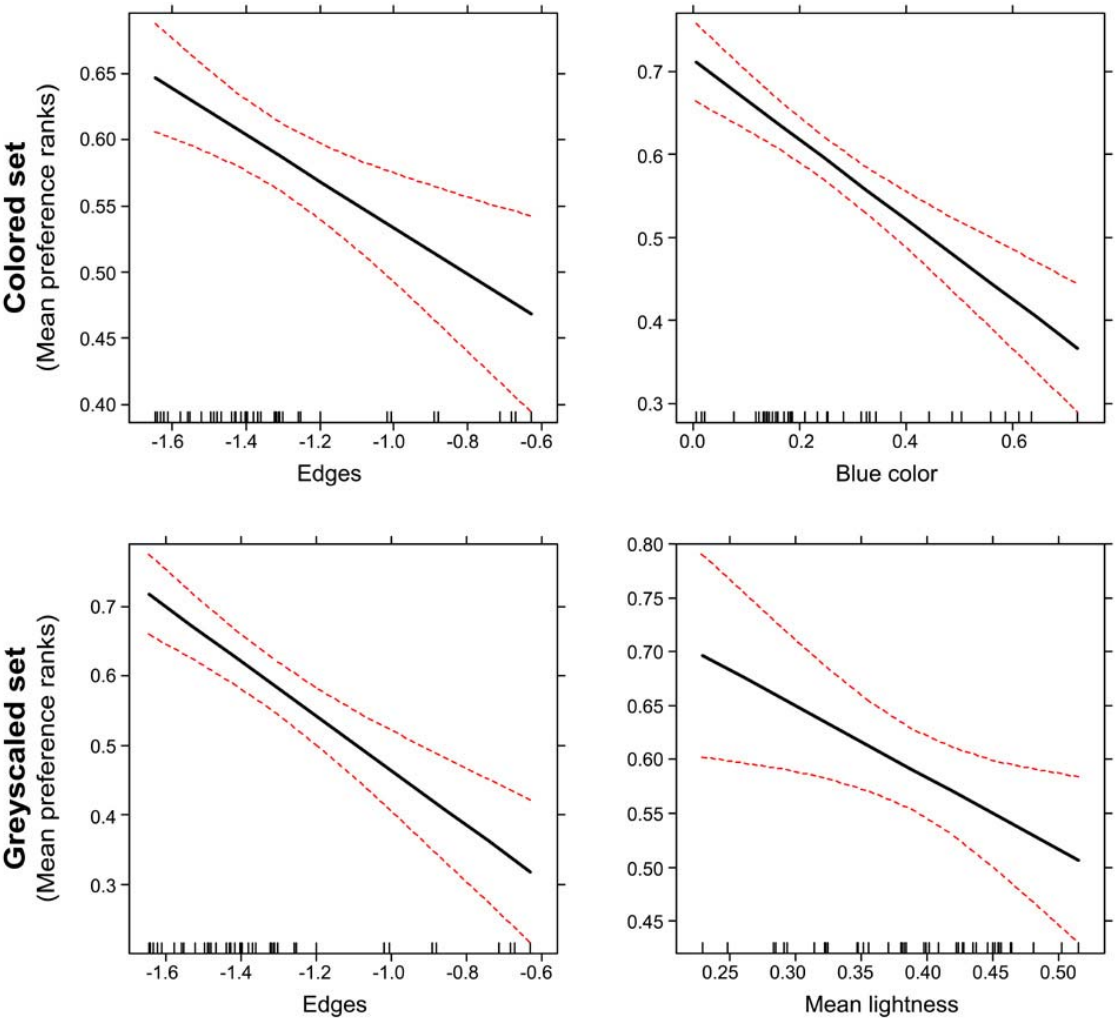

Figure 3. Effect sizes as revealed by General Linear Models (LMs). The figures show the change in the dependent variables attributable to the change of the partial explanatory variables as predicted by the models.

4. Discussion

We analyzed the effects of colors and achromatic components (mean and SD of lightness, pattern) on human preferences towards colorful birds of the family Pittidae. Surprisingly, the respondents ranked the birds' aesthetics similarly in both the full colored and grayscale picture sets. More detailed analysis of the preference ranks revealed that in both cases, pattern and lightness components affected human preferences more than the analyzed color hues. Blue and green hues were the only colors that had minor, yet significant, effects on human aesthetic ranking of the colored birds picture set.

One would expect that the respondents are able to rank color pictures more easily and reliably than the grayscale ones. During the testing procedure, the respondents showed higher willingness to rank the colored pictures as these apparently presented a more appealing and motivating challenge. However, our results show that the Kendall coefficient of agreement was a bit higher among the respondents ranking the grayscale than among those ranking the colored set. This finding may be explained by the distracting effect of colors on the respondents. It was shown on both monkeys (Saito et al. 2005) and humans (Morgan et al. 1992; Saito et al. 2006) that dichromats solved tasks involving detection of objects camouflaged in red pattern with a better success than trichromats.

In our study, the mean ranks of pictures resulting from the grayscale set were slightly, but significantly, correlated with those obtained from the color test ($r^2 = 0.1024$; $P = 0.0365$). Nevertheless, multivariate analyses clearly revealed that the same two main axes are behind the ranking of both sets. We extracted the first two main principal components (PC, multivariate orthogonal axes) from the ranking results of both color and grayscale sets. The colored set PC1 closely correlated with the grayscale set PC2 and vice versa (grayscale PC1 correlated with color PC2). Such close mutual correlation of the color and grayscale axes suggests that principal cues determining ranking of the color pictures are also present in the grayscale pictures possessing only achromatic components. Thus, these principal cues cannot be composed of chromatic colors. The fundamental role of achromatic components was further supported by the GLM analyses of the PC axes. These axes may be interpreted mainly as the pattern complexity for grayscale PC1/color PC2 and overall lightness for grayscale PC2/color PC1. The presence of the chromatic component in the color pictures, however, affects the priority of the axes adopted for aesthetic ranking. It induces a switch from primary use of the pattern axis to the lightness one. In short, people tend to rank grayscale pictures according to pattern, while they rank color pictures according to overall lightness.

In this regard, it is useful to review the role of chromatic and achromatic (shape and pattern) information in solving various human cognitive tasks. In the study of Mullen and Beaudot (2002), color vision performed worse than luminance vision in a shape discrimination task. Shape has also been found to play a primary role in object recognition (electrophysiologically measured) when human respondents were instructed to pay attention to various objects or colors on a computer screen (Proverbio et al. 2004). They were able to discriminate colors faster if these were associated with canonical shapes (e.g., a yellow chicken was recognized faster than a yellow piglet), but not vise versa; canonical colors did not help the respondents to recognize shapes faster. However, when naming objects is the task, canonic chroma helps to name the objects faster (Therriault et al. 2009), and in some cases, chroma helps humans to recognize objects faster and to remember them better (Wichmann et al. 2002; Spence et al. 2006). Whenever the shape of an object is unavailable for some reason, chromatic information helps in the object recognition (Yip and Sinha 2002, Steeves et al. 2004; Liebe et al. 2009), especially when the respondents already posses “color knowledge” of particular objects stored in long-term memory (Mapelli and Behrmann 1997). In ultra-rapid recognition tasks, however, both humans and monkeys are able to categorize an animal or food object on flashing pictures regardless of the presence of chromatic information (Delorme et al. 2000). Moreover, humans are able to categorize the objects even if presented in a grayscale at a very low luminance contrast (Macé et al. 2005). Similar 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). Thus, shape and grayscale pattern provide primary information for human perception, while color contributes to cognitive interpretation and memory processing of an already recognized object (picture).

The ranking procedure in our experiment instructed the respondents to arrange the pictures according to a gradient of aesthetic preferences. The objective of the testing was not categorization of the objects and the respondents were not instructed to intentionally do so, however, it has been previously shown that in a similar experiment using the same testing method, the respondents still categorized the ranked subjects (snakes; Marešová et al. 2009b; Landová et al. 2011). This resembles the task recognized as unsupervised human categorization by some authors (Pothos and Chater 2002; Pothos and Close 2008). Although the respondents were mainly students of biology, the majority of them did not recognize that the tested birds belonged to the family Pittidae and none of the respondents were able to distinguish the particular species. This may be why the role of chroma was not so prominent in the ranking of aesthetics of birds, as the respondents did not try to intentionally categorize the species, nor needed to recognize them using long-term memory references.

Our results showed that human respondents rank the attractiveness of colorful birds mainly on the basis of lightness and pattern. This finding is in agreement with the model of color categorization and naming of Kay et al (2010) which finds “black” and "white" colors as the first to appear in lingual color terms construction. In other words, the separation of black and white can be understood as the separation of dark and light colors (as perceived in luminance and partially also chromatic contrast), which may in fact correspond to the distinction along the axis of overall perceived lightness.

In this study, the only chromatic colors to affect human preferences towards the birds depicted in color were blue and green. This implies the relevance of the division of chromatic spectrum into warm and cool colors, with warm colors having no effect on human aesthetic preferences towards pittas. Blue and green hues are often reported to positively affect emotional feelings of humans who associate both of the hues together with peace and calmness (Ball 1965; Kaya and Epps 2004). Blue birds were repeatedly placed on top positions within various contexts (in various bird groups, tested independently): blue-and-white flycatcher, indigo-banded kingfisher, hyacinth macaw, and Indian roller (Frynta et al. 2009, Frynta et al. 2010, Lišková and Frynta 2013). 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 over 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.

We found no effect of the color red on human aesthetic preferences of pittas. This may be explained by a relatively short history of the color's recognition in primates. The cones sensitive to red light have evolved in a common ancestor of Old World monkeys and apes, i.e., relatively recently when compared to those sensitive to green and blue light. It is recently a matter of discussion whether trichromatic primates have any advantage over the dichromatic ones. Traditional views supported by many papers say that trichromatic primates are quicker in foraging for red ripe fruits (e.g., Surridge 2003; Osorio and Vorobyev 1996) or young leaves (Lucas, et al. 1998; Dominy and Lucas 2001). However, a recent study of Hiramatsu et al. (2008) found no advantage of trichromats in the recognition of food in black-handed spider monkeys. They show that luminance contrast was the main determinant of the variation of foraging efficiency. Moreover, the uneven distribution of L, M, and S cone sensitivities in primates (as opposed to even distribution, optimal for maximal color discrimination, found in non-mammalian tri- or tetrachromats such as birds or bees; Osorio and Vorobyev 2005, Kremers 2005) may also point out to the importance of luminance contrast discrimination, because separate L and M cones have the potential to corrupt luminance signals (Osorio et al. 1998).

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 (Watt et al. 2003, 2006), and thus, its importance may lie especially in its ability to catch attention.

Although there is immense evidence in the importance of colors in many aspects of human lives, such as emotional affection, easier object categorization, arousal, or selective attention, we found only little effect of colors on human aesthetic preferences of birds. The only colors that had minor effects were blue and green. The main factors affecting human preferences were the pattern and overall lightness. This finding emphasizes the key role of the luminance contrast discrimination, the importance of which is shared ancestrally within dichromatic primates.

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A

Animal Beauty, Cross-Cultural Perceptions

Daniel Frynta, Eva Landová and Silvie Lišková
Department of Zoology, Charles University of Prague Faculty of Science, Praha 2, Czech Republic

Synonyms

Aesthetic preferences; Aesthetic ranking of animals; Animal attractiveness; Biophilia theory

Definition

The concept of animal ► beauty explicates human ► cognitive abilities (cross-culturally in agreement) to subjectively perceive, evaluate, and categorize animals. The perception is determined by objective animal qualities such as size, shape, color, pattern, similarity to humans or familiar objects, and behavior. The perception of animal beauty projects into the ► qualities of human life, such as ► recreation activities (birdwatching, fishing, hunting, attending zoos and wildlife reserves), ► happiness, friendship, and ► pet keeping, as well as animal welfare and ► conservation.

Description

Living animals evoke higher attention in humans than inanimate objects (New, Cosmides, & Tooby, 2007), because they might have represented predatory threat or suitable prey for our ancestors. Thus, humans have evolved universal ► cognitive abilities to perceive, rank, and categorize animals, which allowed them quick and adequate reactions to these animals. People possessing very distant cultures and different levels of scientific knowledge are able to name and categorize animal species in a very similar way (Berlin, 1992), using universal principles. People also inherently tend to affiliate with other species (e.g., the "biophilia" theory, Wilson, 1984) and employ ► aesthetic judgments in their attitude to animals (Thornhill, 1993). These subjective abilities of priority attention devoted to animals, employing aesthetic judgments towards them and their categorization together with biophilia, allowed us to measure the animal beauty reliably by asking ► human respondents.

The ► biodiversity of animals (even when counting just vertebrates) is too vast for humans to know or imagine (Frynta et al., 2009); people of ► illiterate hunter-gatherer societies are able to name only about 600 genera of animals (up to 773 species, Berlin, 1992). People of the industrial world encounter as much animals, with maybe some more, thanks to their access to media such as books and the Internet. It is therefore needed to select a partial set of species for the purpose of

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animal beauty measurement. *The respondents are able to* evaluate both living animals and their pictured representatives; both methods of presentation usually provide similar results (Landová, Marešová, Šimková, Cikánová, & Frynta, 2011). In most cultures, the respondents tend to discuss the pictured animals in a way that indicates that they viewed the animals as living creatures rather than just colorful images (Frynta et al., 2011).

It is important to note that regardless of the existing interindividual differences which may be caused by ▶ personality, individual ▶ experience, mistakes, gender, or other factors not controlled for, the respondents' agreement in the ranking of beauty is still highly significant. There is general agreement in beauty of many studied animal groups: parrots (Frynta, Lišková, Bültmann, & Burda, 2010), various bird families (Frynta et al., 2009; Lišková & Frynta, in press), mammals, and reptiles (Frynta et al., 2009), especially snakes (Frynta et al., 2011; Landová et al., 2011; Marešová & Frynta, 2008; Marešová, Krása, & Frynta, 2009; Marešová, Landová, & Frynta, 2009).

There might be agreement in the subjective beauty evaluation because it is linked to objective features of the evaluated animals. Which animal characteristics are perceived as beautiful? It was Au1 hypothesized by Morris (1967) that it is the presence of anthropomorphic features that makes the animal attractive, for example, flat face, no/small tail, facial expression ability, or tool use. One such textbook example is the baby schema presented as early as in 1943 by Konrad Lorenz, which says that humans prefer animal characteristics that resemble children: large eyes, bulging cranium, or retreating chins (Lorenz, 1943, 1950/1971). It has been shown that Mickey Mouse, the well-known and favorite Disney character, evolved through years accordingly to this scheme to meet the preferences of human beholders (Gould, 1979). Portmann (1979) postulated that the brain size of an animal, in the meaning of animal intelligence, might also affect the perceived attractiveness positively, which links the animal attractiveness to similarity with humans as well.

Animals also possess physical characteristics that are preferred by humans. The most prominent one is the body size. The larger the animal, the stronger is the sensory stimulation of human subject (sensory bias), which affects the attractiveness judgment, usually, but not necessarily, in a positive way. This can explain the phenomenon of "charismatic megafauna" (e.g., popularity of large mammals such as elephants, rhinos, and gorillas; Entwistle & Dunstone, 2000). Czech respondents ranked giant pandas, large cats, bears and giraffes as the most beautiful mammals (Frynta, Šimková, Lišková, & Landová, 2012). Nevertheless, smaller animals may sometimes be preferred because of other prominent characteristics like "fluffy hair" and big eyes, which form the quality of "cuteness," as perceived by humans. Pikas, bush babies, red pandas, and wombats placed among such preferred but small- to medium-sized mammals. Body size can also be linked by a specific meaning to the observer. For example, children of various age groups preferred differently sized animals: very young children preferred big mammals, which Morris (1967) interpreted as their need to bond with a parent (a guardian), while older children preferred smaller mammals to get themselves into the role of a parent (Figs. 1 and 2).

Another important collection of animal features considered by humans when ranking animal attractiveness is shape, pattern, and color. The mutual connections of these characteristics which together form human preferences have been demonstrated on birds. The beauty of birds is mainly determined by their body shape: short neck, long legs and tail, and large eyes are perceived as attractive. This was demonstrated by an experiment in which human respondents evaluated only black silhouettes of birds, freed of the information about pattern and color, and the resulting evaluation was comparable to that of fully colored and patterned pictures of birds (Lišková & Frynta, in press). In the absence of body shape variation, pattern becomes dominant over colors in the determination of human preferences, as seen on morphologically similar example of pittas, the exotic Old World colorful songbirds (Frynta & Lišková, 2012). Coloration only enhances the respondents' decision, which heeds coloration just partially and mainly focuses on overall coloration. Among all colors, only one seems to consistently and positively affect human preferences, and that is the blue color. Blue birds were repeatedly placed on top positions within various contexts (in various bird groups, tested independently): blue-and-white flycatcher, indigo-banded kingfisher, hyacinth macaw, and Indian roller (Frynta et al., 2009; Frynta et al., 2010; Lišková & Frynta, in press) (Fig. 3).

The evaluation of beauty is complex due to the fact that animals possess various characteristics of appearance, as noted above; however, the complexity might rise even more due to the various aesthetic criteria across human cultures. It has been reported that the aesthetics of commercial products often significantly vary between cultures (Limon, Kahle, & Orth, 2009; Pearce, Harvey, & Jamieson, 2010). A contrary hypothesis of ► evolutionary psychology states that our ancestors have developed an adaptive sense of "animal attractiveness" and preference to animal species that became part of human mind before geographic and cultural diversification of our kind (Barkow, Cosmides, & Tooby, 1992). Various stimuli may contribute both to aesthetic differences and agreement in human evaluation of beauty. Thus, experiments were performed to assess the possible aesthetic ► cross-cultural differences using animal pictures as a substitute of real animals, as evolutionarily relevant stimuli for humans. Non-surprisingly, the agreement in preferences of English-speaking people evaluating the beauty of bird families using an Internet survey based on the ► Likert scale (1 pointing to the most beautiful bird; Lišková & Frynta, in press) was consistent with such evaluation of central ► European people from the Czech Republic and Slovakia. It was of great interest to compare the European aesthetic preferences with those of a more distant culture, both culturally and geographically, and thus, villagers from Papua New Guinea were asked to evaluate the beauty of boid snakes (Frynta et al., 2011): Papuans have entirely different cultural background compared to Europeans, and moreover, they live in much closer contact with wild animals, especially snakes. In the Australian zoogeographical area, most local snake species belong to the family Elapidae and are highly poisonous (O'Shea, 1996). Therefore, it was expected that the aesthetic apprehension of the tested boid snakes would significantly differ between people from Europe and Papua (Marešová, Krása, & Frynta, 2009). Interestingly enough, regardless of the different attitude towards snakes, the Papuans' aesthetic preferences tightly correlated with the Europeans', with only six species (out of 32) differing slightly. Moreover, the disparity in ranking was not explicable by personal experience and/or the role of the particular species in the local culture, as four of the tested species with New Guinean distribution did not contribute to the ethnic differences (Fig. 4).

The considerable cross-cultural agreement in preferences towards snake species was further supported when people from another three continents were included in the comparison: the villagers from Bolivia (South America), Philippines (Southeastern Asia), Rajasthan and Delhi in India (South Asia), and Malawi (sub-Saharan Africa), and Morocco (North Africa). The agreement of these cultures and Papuans appeared even closer than those between Papuans and Europeans, although the ► experience with the presented species differed in each of the societies – the local snake faunas of each region differ, the human societies encounter the fauna with different frequency, and also the attitude of people towards ► media such as television differs greatly.

Discussion

The above-mentioned cross-cultural agreement applies not only to the evaluation of snakes but also to other animals such as lizards, turtles, birds, and mammals, as tested in Eastern Indonesia and Europe (unpublished results). These findings may be explained either by the hypothesis that human preferences are determined by primordial sensory mechanisms shared by all people (and possibly our primate relatives) or by processing rules specific to animal objects that evolved in a response to selection pressures affecting human ancestors in the past. Nevertheless, cross-cultural congruence in the evaluation of animal beauty is a phenomenon of extreme importance. This may be an example of the so-called universals, the traits that are shared by all human beings across every population and culture (Brown, 2004). Within various realms – cultural, social, lingual, behavioral, etc. – these include, for example, myths and legends, ethnocentrism, dancing, color naming rules, wariness around, or fear of snakes. In ethology, this phenomenon has been known as species-specific typical behavior for a long time. Species-specific typical behavior is somehow predetermined either genetically or ontogenetically, and it is present in most (usually all) individuals of the given species, when reacting to a specific stimulus or situation (Bolhuis & Verhulst, 2009). The finding that all people prefer the same animals is not so trivial; in fact, imagine a similar situation with other human universals, for example, the ► dancing. All people around the world and across all cultures like dancing, but every society performs a dance specific to their culture. If these societies were given a choice and would be taught and presented to all other existing dances, would they all prefer just samba?

The phenomenon of wildly shared preference for certain animal types within a given group of species might lead to selective protection/neglecting of some species in global ► conservation network, and thus contribute to the species composition of future biota. In present situation, endangered species of many taxa compete with one another for financial and political support provided within conservation projects, and the winners are the attractive animals: the numbers of individuals of animal species kept in zoos worldwide is highly correlated with human preferences, as reported in various groups of reptiles, birds, and mammals (Frynta et al., 2009; Frynta et al., 2010; Marešová & Frynta, 2008). Human aesthetic preferences seem to be a new ecological factor, which influences animal lives, ► diversity, and survival, in this modern, human-changed world. Last but not least, the proximity of beautiful animals per se positively affects ► human well-being, happiness, friendship, contentment, and other factors that enlighten the ► quality of human life.

Cross-References

- ► Aesthetic Value
- ► Affective Connection to Nature
- ► Beauty
- ► Consumer Society
- ► Cross-Cultural Validation
- ► Gene-Environment Interaction
- ► Human Research Ethics
- ► Illiteracy
- ► Media Literacy
- ► Parent–Child Relationships(s)
- ► Subjective Well-Being (SWB)

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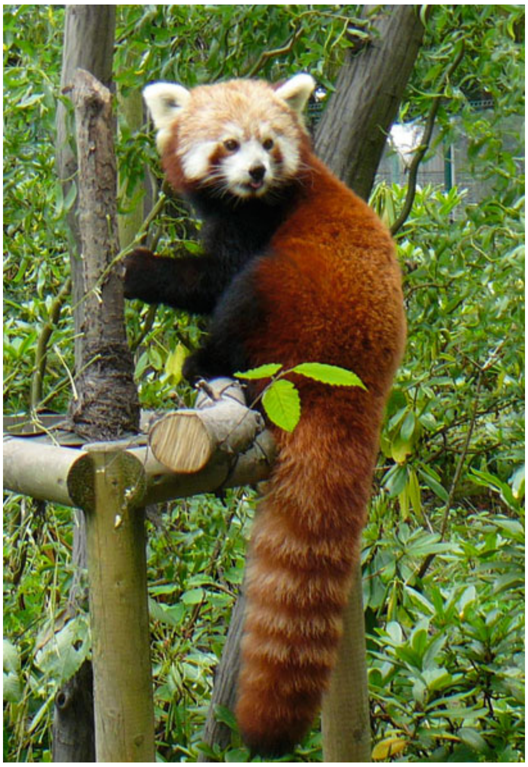
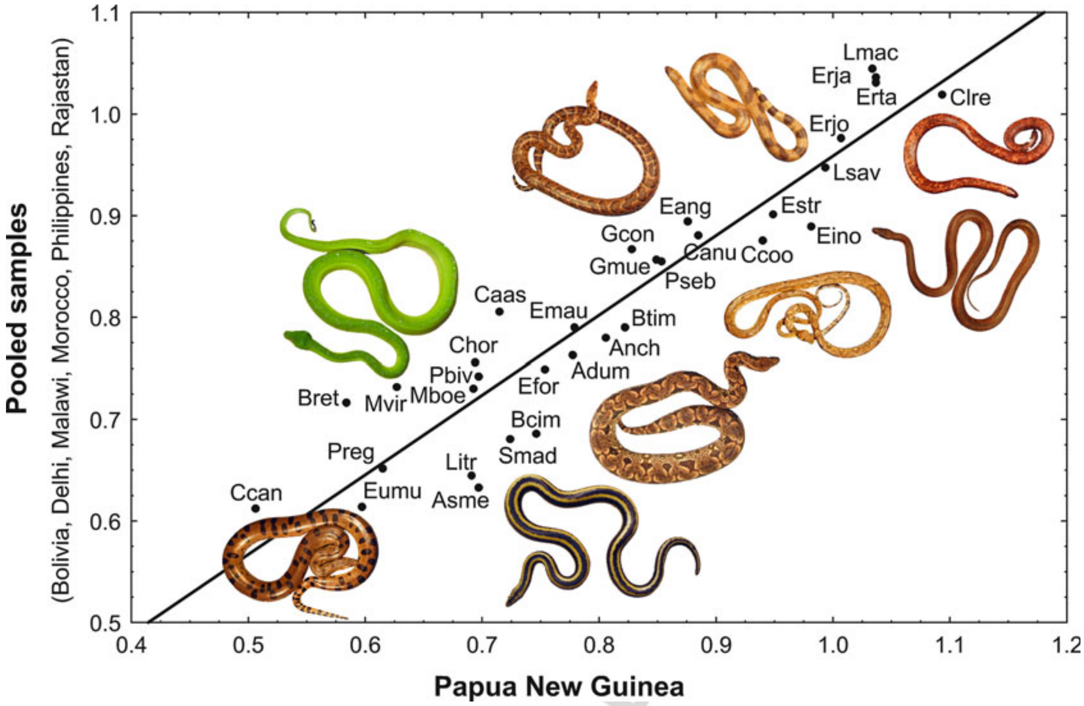


Animal Beauty, Cross-Cultural Perceptions, Fig. 1 An example of the most preferred species within particular higher taxa according to Czech respondents. Red panda (*Ailurus fulgens*), Laurasiatheria, Ailuridae

Animal Beauty, Cross-Cultural Perceptions, Fig. 2 Forty-three pictures of pittas from the family Pittidae were evaluated by Czech respondents according to preferences, both in full color and gray scale. In both sets of pictures, the male blue pitta (*Pitta cyanea*; depicted) placed within the top five. The scattered, spotty pattern showed to be a significant factor determining human preferences. The blue color is another factor that is preferred by human respondents on birds, which has proven significant in other bird sets of pictures: blue-and-white flycatcher (passerines), indigo-banded kingfisher (nonpasserine terrestrial birds), blue-and-yellow macaw (parrots).The common wombat (*Vombatus ursinus*) represents the most preferred species within a group of basal mammals. The preferred features of mammals are fluffy ears, dense fur, and short nose, all resembling fuzzy bear cubs

Animal Beauty, Cross-Cultural Perceptions, Fig. 3 The family Falconidae, represented by the orange-breasted falcon (*Falco deiroleucus*) in the set of 97 nonpasserine and 5 passerine bird families, placed as the most preferred one. The key feature determining human preferences towards bird families rich in morphological variability was the shape of the bird, as shown on a set of black bird silhouettes correlating closely with the full-colored bird pictures



Animal Beauty, Cross-Cultural Perceptions, Fig. 4 Relationship between mean measures of perceived beauty of the pooled data (Bolivia, Delhi, Malawi, Morocco, Philippines, and Rajasthan) and corresponding values obtained in Papua New Guinea. Please note that the higher value, the less preferred the species is. Species abbreviations are as follows: Adum, *Acrantophis dumerili*; Anch, *Antaresia childreni*; Asme, *Aspidites melanocephalus*; Bcim, *Boa constrictor imperator*; Canu, *Corallus annulatus*; Ccan, *C. caninus*; Ccoo, *C. cookii*; Chor, *C. hortulanus*; Clre, *Calabaria reinhardtii*; Caas, *Candoia aspera*; Eang, *Epicrates angulifer*; Efor, *E. fordi*; Eino, *E. inornatus*; Emau, *E. maurus*; Estr, *E. striatus*; Erja, *Eryx jaculus*; Erjo, *Eryx johnii*; Erta, *Eryx tataricus*; Eumu, *Eunectes murinus*; Gcon, *Gongylophis conicus*; Gmue, *G. muelleri*; Lsav, *Liasis savuensis*; Lmac, *L. mackloti*; Litr, *Lichanura trivirgata*; Mboe, *Morelia boeleni*; Mvir, *M. viridis*; Pret, *Python reticulatus*; Pbiv, *P. molurus bivittatus*; Preg, *P. regius*; Pseb, *P. sebae*; Ptim, *P. timoriensis*; Smad, *Sanzinia madagascariensis* (Adapted from Frynta et al., 2011)

Are Animals in Zoos Rather Conspicuous than Endangered?

D. Frynta, J. Marešová, E. Landová, S. Lišková,
O. Šimková, I. Tichá, M. Zelenková and R. Fuchs
Ecology and Ethology Group, Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic;
e-mail: frynta@centrum.cz

Abstract

The chapter challenges the assumption that humans generally treat all animal species equally according to their need of conservation. We have reviewed recent studies suggesting that humans show strong preferences toward particular animal species/taxa and are willing to protect them more than others. Such understanding of human preferences is an important part of conservation strategies.

The main body of the chapter is based on original data analyses performed separately for main reptile, bird and mammalian taxa. The representation of animal taxa in zoos and the sizes of zoo populations are reviewed. Human preferences to particular species and/or families were examined directly by presenting their pictures to the respondents. The results showed that factors affecting human aesthetic preferences toward particular species differ among higher taxonomic groups. We concluded that animal attractiveness (both body size and beauty itself) influences human effort devoted to ex situ breeding projects more than inclusion in Red book lists. Special attention has to be paid to less preferred, but endangered species. Fortunately, the highly preferred species are present in almost every family and also among threatened species. Thus, the zoos can replace preferred but common species by endangered one that meets both, conservation as well as visitor’s aesthetic criteria.

Introduction

Captive breeding has enabled survival of numerous species facing extinction. The stories of such species as California condor (*Gymnogyps californianus*), Hawaiian goose (*Branta sandvicensis*), black-footed ferret (*Mustela nigripes*), Guam rail (*Gallirallus owstoni*), Lord Howe Island woodhen (*Gallirallus sylvestris*), golden lion tamarin (*Leonthopithecus rosalia*), European bison (*Bos bonasus*), addax (*Addax naomaculatus*), scimitar-horned oryx (*Oryx dammah*), Arabian oryx (*Oryx leocoryx*), southern white rhino (*Ceratotherium simum simum*) or Przewalski’s horse (*Equus przewalskii*) are well-known textbook examples (cf. Frankham et al. 2002, Frankham 2008). Many of these species were saved owing to few individuals unintentionally kept in various zoos, private farms and circuses. At the time of the crisis, these animals became founders of rescue breeding programs. Nowadays the proportion of potentially endangered species is rapidly increasing and in fact no species is actually safe from possible disaster (Wilson et al. 2002). Thus the maintenance of captive populations is a form of survival insurance.

Some reintroduction programs were fairly successful (e.g., Denton et al. 1997, Brighsmith et al. 2005, White et al.2005, Bertolero et al. 2007, Brown et al. 2007, but see Price and Fa 2007). Nevertheless, the value of zoo populations as a source for future reintroduction may be questioned (e.g., Jule et al. 2008). Captive populations are affected by unintended behavioral (McDougall et al. 2006), morphological (O’Regan and Kitchener 2005, Connolly and Cree 2008) and genetic adaptations (Frankham 2008) to captivity. Most damaging are usually the loose of genetic variation and inbreeding (for review see Frankham et al. 2002). However, these problems as well as those associated with obtaining enough individuals for successful reintroduction event may be avoided by keeping source populations in sufficient numbers (i.e., hundreds or thousands specimens).

It is, however, not self-evident that any endangered species will be kept in sufficient numbers. Zoos are luxury hotels in the world full of animal refugees. Consequently, there is an excess of species in need and accommodation capacity is strictly limited (Soulé 1986, Wilson 1992, Tudge 1995). Moreover, new zoo exhibits tend to be larger and support markedly fewer individuals than the older ones (Baker 2007) as legal standards of welfare and veterinary care become more and more strict. As a result of these requirements the costs of keeping animals tend to gradually rise. This further escalates competition among animal species for ex situ breeding programs and increases the role of human decision making (Cohn 1992). The winners may be the species that satisfy human aesthetic and emotional requirements, rather than those most vulnerable. Moreover, fashon may further enhance risky fluctuations in captive populations of endangered species in a similar manner as reported in breeds of domestic dogs (Herzog et al. 2004).

Thorough analysis of reintroduction projects (Seddon et al. 2005) demonstrated apparent taxonomic bias, e.g., some attractive vertebrate taxa as mammals (especially artiodactyls and carnivores) and birds (anseriforms, falconiforms, gruiforms and galliforms) are overrepresented. As a result, species composition of future biota is more and more affected by an artificial species selection.

Animals have been an integral component of the human environment and culture from the very beginning of our species. Even illiterate hunter-gatherers were able to name and categorize animal species in a very similar way as contemporary scientists (Berlin 1992). Evolutionary psychologists suggest that our mind is evolutionarily prepared to respond to animal stimuli (Barkow et al. 1992). There is an innate predisposition to easily learn fear of snakes and spiders (Davey et al. 1998), and on the other hand, people experience positive emotions toward other taxa. It is not accidental that large herbivores, domestic animals and birds frequently occurred in paintings since the Pleistocene (Lewis-Williams 2002, Guthrie 2005) up to the Modern Age (Baenninger 1988, Barkow et al. 1992). Both positive and negative emotions raise human interest in the particular species. It should be emphasized that the vast majority of species are inevitably neglected by us. Anthropologists and ethnobiologists demonstrated in tribal societies that the number of generic names, each representing an independent concept of an animal, usually does not exceed 500 units (for a review see Berlin 1992). Thus our mental capacity devoted to animals is scant in view of the worldwide diversity of the vertebrate genera. Consequently, the endangered species compete with one another for our attention that may help them by providing financial and political support for conservation projects.

As a rule, distribution of any conservation effort and willingness to support varies greatly from species to species. Funding decisions by FWS (Federal Wildlife Service) are not related to a species recovery priority rank (Simon et al. 1995). The U.S. federal government's protection and spending decisions concerning individual species are based more on "visceral" characteristics of the species (i.e. physical size and the degree to which the species is considered to be a "higher form of life") than on "scientific" ones (i.e. degree of endangerment and "taxonomic uniqueness") (Metrick & Weitzman 1996). Incredibly, a 10% increase in body length is associated with an 8.6% rise in funding. Sometimes, human willingness to protect a species may even negatively correlate with the degree of endangerment. Metrick and Weitzman (1998) reported this phenomenon in public comments on the changes in the Red List. There is more public support for saving species perceived as attractive, larger in size (Gunnthorsdottir 2001) and resembling humans (Samples et al. 1986).

Animal taxa differ also in its social construction and political power (expressed as, e.g., number of NGOs supporting particular animals). Birds receive the highest public support among vertebrates; however, mammals and fish also belong to "advantaged" taxa. In contrast, amphibians and reptiles (except turtles and tortoises) receive almost no support (Czech et al. 1998, see also Kellert 1985).

Humans are able to differentiate between attractive and unattractive animals, e.g., cat or tiger faces from early childhod (Quinn et al. 2008). Interestingly, nearly all species reported by respondents as most preferred are mammals (Morris 1967). Although, human-animal relationships in zoos are more complex phenomenon (Hosey 2008), popularity of zoo animals may be successfully explained by simple traits as body size (Ward et al. 1998). Plethora additional hypotheses were proposed (e.g., Morris 1967) to explain differential attractiveness of animal species for humans: most studied were the effects of juvenile body proportions (Gould 1979, Pittenger 1990), form close to average appearance (Halberstadt and Rhodes 2003) and conspicuous coloration (e.g., Van Hook 1997, Stokes 2007).

Although perceived attractiveness of animal species is easy to quantify and its potential consequences for conservation practice are fundamental, little attention has been paid to these issues so far. Moreover, existing studies usually suffer from comparisons among unrelated groups of animals and small number of compared species. Quantitative studies carried out on a finer taxonomic scale are therefore needed.

Recently we studied the influence of factors putatively enhancing sensory stimulation of human observers (i.e., zoo visitors and/or keepers) on ex situ conservation efforts. We analyzed worldwide zoo populations of boas and pythons; we have found strong positive effects of perceived attractiveness on the zoo population size of the species worldwide (Marešová and Frynta 2008).

Although we are aware of that local culture may affect human preferences toward animal species, an elementary cross-cultural agreement could be reasonably expected. This assumption derived from evolutionary psychological theory (Barkow et al. 1992) should, however, be subjected to further testing. Our preliminary data reveal surprisingly close correspondence between rankings of snake species by people from such different cultures as are those in Europe and Papua New Guinea (Marešová, Krása and Frynta, in press).

In this chapter we examine population sizes of animals in zoos worldwide. We focus on three classes of terrestrial vertebrates (Amniota): reptiles, birds and mammals, and analyze factors affecting representation of these animals in zoos. Besides taxonomic bias (uneven representation of particular taxa) and representation of endangered species, we paid special attention to body size and perceived attractiveness of zoo animals.

Data Sources and Testing Procedures

To avoid problems with uncertain nomenclature and taxonomy, we used the following species lists which are nowadays widely accepted by vertebrate zoologists: Wilson and Reeder (2005, available on http://nmnhgoph.si.edu/msw/) for mammals, Masi (1996, available on http://www.scricciolo.com/classificazione/sibley's_index.htm) and The BirdLife Checklist (The BirdLife Taxonomic Working Group (BTWG), 2008; based mainly on Sibley and Monroe (1990, 1993); available on http://www.birdlife.org/datazone/species/taxonomy.html) for birds and The TIGR Reptile Database for reptiles (Uetz et al. 2008; available on http://www.reptile-database.org). The extinct and domestic animals (dog, cat, cow, horse, goat, sheep, camels, lamas, pig, laboratory mouse, rat, guinea pig, hen, turkey, goose and duck) were excluded, although some of them may be viewed as endangered (Taberlet et al. 2008). The IUCN status of all species was obtained from the official IUCN website (IUCN 2008; http://www.iucnredlist.org). The above species lists do not match one another exactly and also their agreement with taxonomies used by zoos is limited. To avoid mistakes we resolved these disparities ad hoc, and therefore the total numbers of species in particular taxa may a bit deviate from that found in the original databases.

The population size of each species in worldwide zoo collections was obtained from The International Species Information System database (ISIS, http:// www.isis.org, downloaded on 1 January 2008). It seems to be the only relevant public source covering approximately 730 zoos and aquaria all over the world.

It may be argued that the database does not include all keepers as some local zoos as well as private breeders are not comprised. However, we consider the institutions participating in ISIS to be the most important since they support a much larger number of animals, at least in the case of some larger species, compared with that kept by the other breeders. Last but not least, breeding programs of these credible institutions are well coordinated and attract the attention of the general public and the media, thus helping the selected species gain additional support. The number of individuals kept in zoos provides therefore a good estimate of the conservation efforts.

To assess human preferences towards animal species, we asked our respondents (mostly students from various faculties of the Charles University in Prague) to sort particular sets of pictures and rank the animals according to the perceived aesthetic attractiveness (beauty) following method of Marešova and Frynta (2008).

We carried out these analyses at two different levels: (1) Species, by comparing particular species within a family (pythons and boas – Boidae, pheasants – Phasianidae, antelopes and allies – Bovidae) or an order (turtles – Testudines); (2) higher taxa, by comparing families or sufamilies, each represented by a randomly selected species (see under Effects of perceived attractiveness and body size on higher taxonomic scale; Table 3).

For statistical analyses we used STATISTICA 6.0, StatSoft Inc. (2001). Prior the statistical analyses, the data were normalized when necessary; population and body sizes were log-transformed, while relative ranks of pictures were square-root arcsin transformed. Either GLM models or Multiple Linear Regression were applied. The agreement in ranking the pictures was visualized by Principal Component Analysis (PCA). The percentage of explained variability by the first principle component (PC1) was used to quantify the congruence among the respondents.

Representation of Vertebrate Classes in Zoos

It has been previously demonstrated that the vertebrate species kept in zoos are unequally distributed among higher taxa. Mammals and birds are obviously overrepresented while amphibians and fishes tend to be underrepresented (e.g., Price and Fa 2007, Leader-Williams 2007). Nevertheless, the differential representation of vertebrate taxa in the worldwide zoo population is worth further analyses. This is an obligatory step towards understanding the underlying processes that control the efficiency of ex situ conservation.

Even a first glance at the data (Table 1) is eloquent. The numbers of species kept in zoos are surprisingly high. As many as 1154 reptile, 2337 bird, and 990 mammalian species, representing 13.4%, 24.3%, and 18.5% of non-extinct species of these groups, respectively are listed among the zoo population.

The total numbers of individuals kept in zoos are about the same for birds and mammals (200 and 152 thousand, respectively), while the corresponding figure is nearly three times lower for reptiles (67 thousands). When the number of individuals kept in zoos was scaled to the total number of living species of the given class, the difference was even more evident. In zoos, there are just 7.80 reptiles, but 20.74 birds and even 28.45 mammals per total number of living species. Only a small portion of this difference may be attributed to the fact that reptiles (as well as amphibians and fishes) are more frequently kept in small zoos and private collections which are not covered by the ISIS database. As mammals and birds are in general more active, possess higher metabolism (Schmidt-Nielsen 1984), need larger spaces and more keeper’s care than reptiles and other cold-blooded vertebrates, their clear overrepresentation in zoos is in a strong contradiction to the elevated costs of keeping them (see also Balmford 2000). Obviously, this phenomenon reflects some kind of human preference in favor of these warm-blooded animals.

Table 1. Representation of reptiles, birds and mammals in zoos.

Class:	Reptiles	Birds	Mammals
number of living species	8602	9627	5353
number of individuals in zoos	67073	199686	152314
number of species kept in zoos	1154	2337	990
number of species with zoo population size over 50	247	634	416
number of species with zoo population size over 500	28	80	79
number of zoo individuals per living species	7.8	20.7	28.5
% zoo species out of all living species	13.4	24.3	18.5
% species with zoo population size over 50 out of all living species	2.9	6.6	7.8
% species with zoo population size over 500 out of all living species	0.3	0.8	1.5
% zoo species with population size over 50 out of all zoo species	21.4	27.1	42.0
% zoo species with population size over 500 out of all zoo species	2.4	3.4	8.0
number of individuals in zoos/ n of species kept in zoos	58.1	85.5	153.9

mean size of zoo population computed from log-transformed data	12.6	14.5	30.3
median	12	13	34.5
lower quartile	3	3	6
upper quartile	39	57	141
H‘ (Index of diversity, Shannon and Wiener 1963)	5.543	6.152	5.671
J‘ (Index of equitability, Sheldon 1969)	0.786	0.793	0.822
H‘/H‘max (real biodiversity in zoos/maximal possible biodiversity)	0.612	0.671	0.660

We understand the network of zoos (cf. Field and Dickie 2007) as a specific habitat supporting specific synusy of the animals that may be studied by the methods adopted from the ecology of communities. We applied the standard indices of species diversity (H’; Shannon 1963; natural logarithms were used for the computations) and equitability (J’; Pielou 1966, Sheldon 1969). The former index increases with increasing number of species as well as with increasing equitability of their representation in the synusy (worldwide zoo network in our case). The latter one (ranging from 0 to 1) quantifies only the equitability component of diversity and is thus independent on the number of species. It is the ratio between the observed H’ and maximum theoretical value of H’ computed for the observed number of species in a given sample. As the equitability assessed by J’ omits the species which are not present in zoos by at least one individual, we computed an additional modified index of equitability (I) as the ratio between H’ and the maximum theoretical H’ computed for the total number of species in the taxon (class).

In general, the values of all the three indices were fairly similar among the studied classes of vertebrates. From this it follows that zoos are not extremely selective with respect to the vertebrate classes. There are, however, some remarkable differences. Birds as a specious group with the highest number of zoo species have a higher index of diversity (H’=6.15) than less specious mammals (5.67) and reptiles (5.54). Surprisingly, our modified index of equitability also suggests that zoos support higher species diversity in the case of birds (I=0.671) and mammals (0.660), than in reptiles (0.612). In contrast, the standard index of equitability was somewhat higher in mammals (J’=0.822) than in birds (0.793) and reptiles (0.786). Thus, the biodiversity of warm bloodied vertebrates is better represented in zoos than that of reptiles, but the main reasons clearly differ between birds and mammals. These are high number of bird species kept in zoos, while fairly equal size of captive populations in the case of mammals.

Size of Captive Populations

The worldwide zoo populations of most vertebrate species are extremely small (Table 1). Zoos keep on average 58, 85 and 154 individuals per one reptile, bird and mammalian species occurred in zoos, respectively. These figures are, however, much higher than those typical for zoo species of these taxa. It is due to log-normal distribution of zoo population sizes. When this statistical distribution is taken into account, the respective means decrease to 12.6, 14.5 and 30.3. One half of the reptile, bird and mammalian species have the worldwide zoo population smaller than median values 12, 13, and 34.5, respectively. Populations of such sizes are obviously not sustainable and stochastic demographic and genetic processes lead to their extinction or genetic degradation within a few generations nearly inevitably (Frankham et al. 2002) even in such improbable case that all kept animals take part in reproduction. It is really doubtful whether perpetuation of such small populations in captivity may play any beneficial role in ex situ conservation except attracting the public and providing an opportunity for zoo staff training and accumulation of skills in how to keep and breed a given species (for the role of zoos in conservation education see Sterling et al. 2007).

On the other hand, some successful rescue breeding projects started with only handful captive specimens. Sometimes, small number of founders was enough even for reestablishment of free-ranging population (e.g., Taylor et al. 2005). This is in accord with population genetic theory suggesting a few (>10) unrelated individuals of diploid species contain vast majority of the overall genetic variation of the large source population. Therefore, from purely genetic perspective even narrow bottlenecks followed by a rapid restoration of the population size are not as risky as prolonged maintenance of low or moderate population size (Frankham et al. 2002). Thus presence of just a few unrelated individuals in zoos may occasionally save the species if captive population is immediately expanded when necessary, e.g., after unexpected crisis of the wild populations (but see Hale and Briskie 2007 for negative effects of bottlenecking). The prerequisite that the founding animals have to be unrelated says in another words either obtained from nature or from another large captive population. This, however, requires blurring boundaries between captive and wild populations (Dickie et al. 2007).

Fundamental theory of population ecology suggests that removal of handful individuals have usually no deleterious effect on wild populations. In steady-state or increasing populations, the removed individuals are easily replaced by those born and/or survived due to relaxation of density dependent factors. Even in most declining populations, loose of few individuals does not matter. In spite of this, it is increasingly difficult to source animals from wild (Dickie et al. 2007). Administrative obstacles, usually resulting from misinterpretation and/or bureaucratic abuse of conservation legislation (Holst and Dickie 2007) prevent zoos to exchange the blood and captive populations of small size become inbred or extinct.

Population size is without any doubt the most important factor of population viability (Raup 1991, Wilson 1992, Frankham et al. 2002). Small populations are prone to rapid extinction especially due to stochastic demographic factors (Lande 1999) and negative effects of accumulation of deleterious mutations via genetic drift and/or inbreeding (Kimura 1983, Lande 1999, Rodrígez-Clarc1999, Frankham et al. 2002). Both these processes decrease sharply with increasing population size and thus large populations are much safer than the smaller ones. As the theory of population viability is complex and many parameters necessary for its estimates are usually not easily available for particular species, we adopted straightforward arbitrary criteria based solely on the size of the zoo population worldwide. Our approach was based on empirical experience that the minimum population size necessary for short-time captive maintenance of animal species/breed under controlled conditions is about 50 (Soulé 1980), and populations over about 500 individuals are not affected by inbreeding depression (Reed et al. 2007). Nevertheless, we keep in mind that the theory suggests rather continuous increase of the risks as well as its dependence on population history, generation time, and many other parameters (for review see Frankham et al. 2002). Moreover, estimates of minimum viable population are much larger: amphibian and reptiles 5,409, birds 3,742 and mammals 3,876 individuals (Traill et al. 2007).

We focused on the species whose zoo populations exceeded these arbitrary criteria and found 247 (28) reptiles, 634 (80) birds, and 416 (79) mammals with zoo populations over 50 and 500 (given in parentheses) individuals. Although one might perceive these values as small and invaluable, we consider the support of 2.9% (0.3%) of reptile, 6.6% (0.8%) of bird and 7.8% (1.5%) of mammalian species relevant enough to justify funding of the zoos.

Relative Representation of Endangered Species

Not all vertebrate species are currently at risk of extinction; therefore the beneficial role of captive breeding in conservation of global species diversity may be enhanced by selective keeping of endangered species. We analyze here the representation of the species listed by IUCN in the categories "nearly threatened" or higher. Among the studied vertebrate classes, there are 481 reptiles (5.6% of extant species), 1869 birds (19.4%), and 1145 mammals (21.4%) of these categories (further referred as IUCN species). Thus, reptiles seem to be nearly four times less endangered than birds or mammals. Otherwise, they may be just less frequently listed in IUCN categories as members of the group attracting less human attention.

Zoos keep 167 IUCN species of reptiles, 364 IUCN species of birds and 250 IUCN species of mammals (Table 2). Interestingly enough, the IUCN species are nearly three times more represented among the zoo species of reptiles (34.7%) than among those absent in zoos (12.7%; χ^2=198.7, df=1, P<0.0001). The corresponding difference was much smaller for mammals (25.3 versus 20.6%, χ^2=10.4, df=1, P<0.0012). For birds we found an inverse relationship with the IUCN species being underrepresented in zoos: 15.6 versus 20.6% (χ^2=29.1, df=1, P<0.0001).

Besides the presence or absence of the IUCN species in zoos, there is an even more important issue: the population size of these species supported by the global network of zoos. Fortunately, mean zoo populations of the IUCN species are as a rule somewhat larger than those of less endangered. This difference was higher in reptiles (27.5 versus 11.1 individuals; t-test: t=6.51, df=1152, P<0.0001) than in birds (23.7 versus 13.3; t=5.50, df=2334, P<0.0001) and mammals (48.0 versus 28.4; t=4.07, P=0.0001; see Table 2).

More illustrative are plots comparing distribution of population sizes among the IUCN and non-IUCN species (Fig. 1-3). In addition to overrepresentation of the IUCN taxa, it is clearly visible that within each analyzed class, a handful percent of the species with the largest population sizes in zoos are apparently overrepresented as their data points deviates from the strait line characterizing the remaining species.

Table 2. Representation of endangered species in zoo collections.

Class:	Reptiles	Birds	Mammals
number of living IUCN species (degree of "nearly threatened" or more)	481	1869	1148
number of IUCN species kept in zoos	167	364	250
IUCN species with zoo population size over 50	70	141	130
IUCN species with zoo population size over 500	6	20	23
mean size of zoo population of IUCN species*	11.1	23.7	26.4
number of living non-IUCN species	8121	7758	4205
number of non-IUCN species kept in zoos	988	1973	740
non-IUCN species with zoo population size over 50	177	492	286
non-IUCN species with zoo population size over 500	22	60	56
mean size of zoo population of non-IUCN species*	27.5	13.3	48

*Computed from log transformed data.

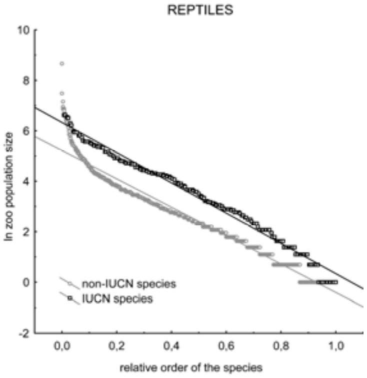


Figure 1. Size distribution of worldwide zoo populations of reptiles: a comparison of endangered species (IUCN category NT-nearly threatened or higher) with the remaining ones (non-IUCN). ln population size = log transformed number of individuals of a given species kept in zoos worldwide. Population sizes are sorted in descending order on the x axis. Order of each species was scaled to the total number of IUCN or non-IUCN species.

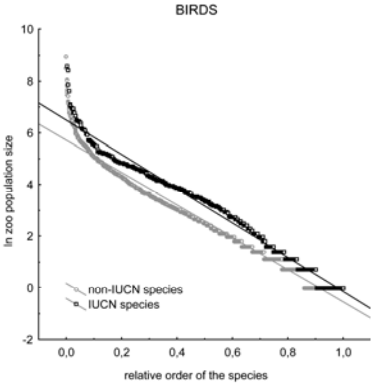


Figure 2. Size distribution of zoo populations of birds: a comparison of endangered species (IUCN category NT-nearly threatened or higher) with the remaining ones (non-IUCN). ln population size = log transformed number of individuals of a given species kept in zoos worldwide. Population sizes are sorted in descending order on the x axis. Order of each species was scaled to the total number of IUCN or non-IUCN species.

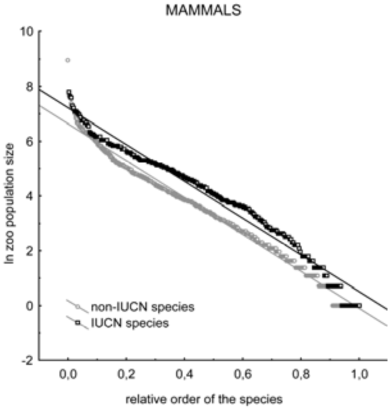


Figure 3. Size distribution of zoo populations of mammals: a comparison of endangered species (IUCN category NT-nearly threatened or higher) with the remaining ones (non-IUCN). ln population size = log transformed number of individuals of a given species kept in zoos worldwide. Population sizes are sorted in descending order on the x axis. Order of each species was scaled to the total number of IUCN or non-IUCN species.

That is why we paid special attention to the species whose zoo populations are large enough to secure short-term survival in captivity.

Effects of Perceived Attractiveness and Body Size among Related Species

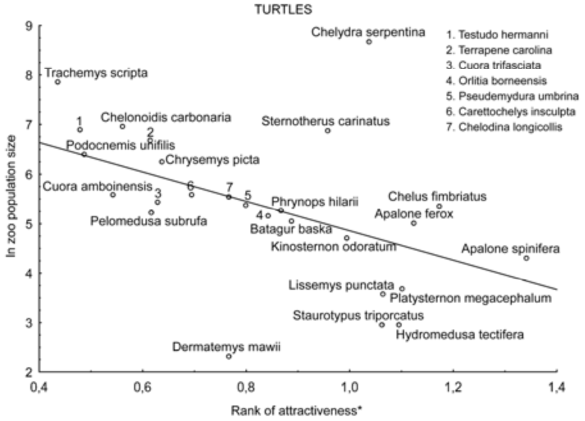
Pythons and Boas

Recently, we studied human preferences towards a representative sample of 56 species of pythons and boas of the family Boidae. Colorful and patterned species such as the rainbow boa (*Epicrates cenchria cenchria*), ball python (*Python regius*), Burmese python (*Python molurus bivittatus*), red blood python (*P. brongesmai*), Emerald tree boa (*Corallus caninus*) were most preferred, while brownish Hispaniola boa (*Epicrates gracilis*)*,* Puerto Rican boa (*E.inornatus*)*,* olive python (*Liasis olivaceus*)*,* Indian sand boa (*Eryx johni*)*,* ringed tree boa (*Corallus annulatus*) were least preferred. We clearly demonstrated that the sizes of the worldwide zoo populations of individual boid species are closely correlated with both body size and human preferences (β=0.39 and -0.39; Marešová and Frynta 2008). The question was whether such a close dependence of the zoo population on factors reflecting sensory and/or emotional stimulation of the visitors/keepers is universal or is confined to the specific taxa such as snakes evoking arousal in most human beings. To answer this question we also performed similar experiments also in turtles as well as in one bird and one mammalian group.

Turtles

Captive breeding programs are really fundamental for survival of several species of turtles and tortoises (Testudines) which are heavily exploited or even extinct in the wild. Thus zoos may play an important role in conservation of these animals. Currently, ISIS reports in zoos 31,078 individuals belonging to 221 species (of about 298 extant species of chelonians). Since zoo visitors perceive turtles as a very homogenous group, we had to include the species representing all turtle subfamilies to increase both taxonomic and morphological variation. In this analysis we selected the most abundant zoo species and the subfamilies exceeding 20 extant species that were represented by two most abundant species kept in zoos. There was a fairly good agreement among the 25 respondents; PC1 explained 57% of the total variation in species ranks.

Next, we excluded three obligatory marine species that are difficult to keep in zoos and carried out the GLM analysis. The size of the zoo population was significantly predicted by human aesthetic preferences ($F_{(1,23)}$=6.3, P=0.0197), but not by body size ($F_{(1,23)}$=3.8, P=0.0647) or IUCN listing ($F_{(1,23)}$=1.7, P=0.2081). The correlation between human aesthetic preference and size of zoo populations (Figure 4) was only moderate (r=-0.492), but highly significant (P<0.0107).



*Please note that the higher value of mean rank, the less attractive animal.

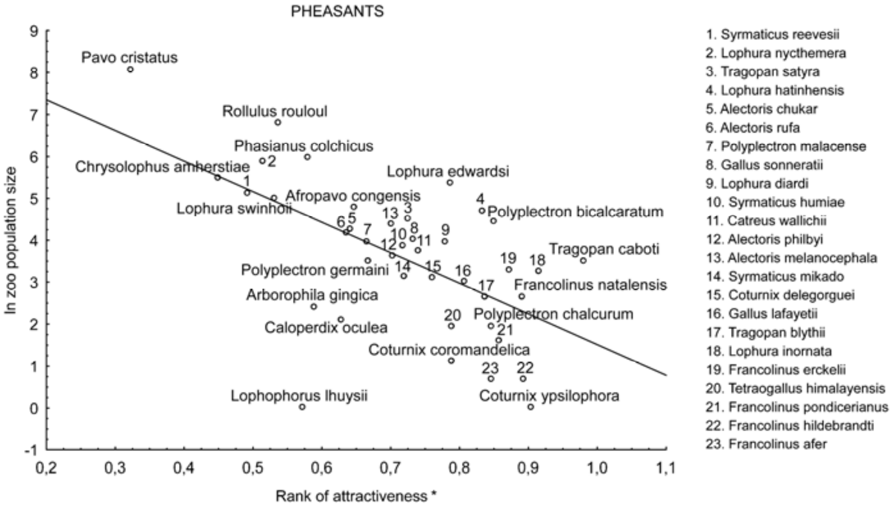
Figure 4. Relationship between size of zoo populations and human preferences in turtles (Testudines). Rank of attractiveness = mean square-root arcsin transformed rank. ln zoo population size = log transformed number of individuals of a given species kept in zoos worldwide. R2 = 24.2%, P = 0.0107, y = 7.83 * x -2.97.

The most deviating point from this relationship represents the common snapping turtle (*Chelydra serpentina*). Although the zoo population of this species is the largest, it was not preferred by our respondents. Nevertheless, this discrepancy may be easily explained by emotional arousal induced by the dangerous species.

Pheasants

Pheasants and allies of the family Phasianidae (sensu del Hoyo 1992-2002, i.e., excluding Tetraonidae and Meleagridae) are frequently kept and bred in zoos; in total 9,731 individuals belonging to 79 species are reported by ISIS. We sorted these species according to size of zoo populations, and selected every even one for further analysis. Next we tested human aesthetic preferences towards these 40 species and found a good agreement among respondents; the first principal component explained 35.2% of the total variation. Species exhibiting elaborated tail feathers and/or loud colours such as Indian peafowl (*Pavo cristatus*), Lady Amherst's pheasant (*Chrysolophus amherstiae*), Reeve's pheasant (*Syrmaticus reevesii*), silver pheasant (*Lophura nycthemera*), Swinhoe's pheasant (*Lophura swinhoii*) were most preferred while short-tailed dull ones such as Cabot's tragopan (*Tragopan caboti*), Salwadori's pheasant (*Lophura inornata*), brown quail (*Coturnix ypsilophora*), Hildebrandt's francolin (*Francolinus* hildebrandti), Natal francolin (*F. natalensis*) were least preferred.

The GLM analysis revealed the human aesthetic preference ($F_{(1,36)}$=16.6, P=0.0002), but not body size ($F_{(1,36)}$=2.6, P=0.1119) or IUCN listing ($F_{(1,36)}$=0.02, P=0.8882), to be a relevant predictor of the zoo population size. The correlation between human aesthetic preference and size of zoo populations was high enough (r=-0.601; P<0.0001) to be worth of conservationists' attention (Figure 5).



*Please note that the higher value of mean rank, the less attractive animal.

Figure 5. Relationship between size of zoo populations and human preferences in pheasants (Phasianidae). Rank of attractiveness = mean square-root arcsin transformed rank. ln zoo population size = log transformed number of individuals of a given species kept in zoos worldwide. R2 = 36.1%, P < 0.0001, y = -8.81 * x -7.29.

Antelopes and Allies

The family Bovidae comprising 138 extant species of antelopes, goats, sheep and buffaloes belong to the hard core of the zoo animals. ISIS recorded 26,794 individuals in zoos belonging to 96 species. Similarly as in the case of pheasants we sorted the species according to the zoo population size and selected a set of 45 species (every even one represented in zoos by more than 12 individuals) for further analysis. The first principal component explained only 26% of the total variance, thus the agreement among the respondents was poorer than in the case of pheasants. Consequently, the GLM analyses revealed that size of zoo populations can be explained neither by human aesthetic preferences ($F_{(1,44)}$=0.31, P=0.5793) nor by IUCN listing ($F_{(1,44)}$=1.87, P=0.1782). Body size has remained the only significant predictor of the zoo population size ($F_{(1,44)}$=5.23, P=0.0270, Figure 6).

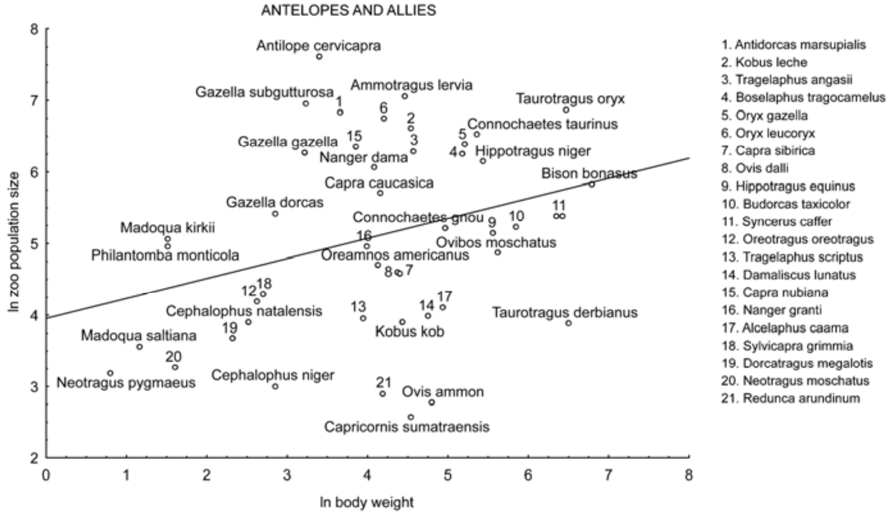


Figure 6. Relationship between size of zoo populations and body size in antelopes and allies (Bovidae). ln zoo population size = log transformed number of individuals of a given species kept in zoos worldwide. R2 = 10.3%, P = 0.0261, y = 3.91 * x +0.29.

Although antelopes and allies vary in their body form and/or in the presence and shape of their horns (Caro et al. 2003), their coloration is rather uniform as in most mammalian taxa. Therefore, body size is the only other stimulus that may influence decision making of zoo visitors and keepers.

Effects of Perceived Attractiveness and Body Size on Higher Taxonomic Scale

The results provided in the previous paragraphs suggest that aesthetic preferences towards particular species are correlated with zoo population size in several vertebrate taxa. Nevertheless, not only the extinction of individual species, but also the extinction of higher taxa poses a major threat to global biodiversity. Therefore, we also carried out similar analyses for presumably monophyletic groups on the family and/or subfamily scale.

For this purpose we split the studied classes of vertebrates into eleven more homogenous groups, each consisting of two or three dozens of families/subfamilies or other monophyletic taxa of comparable level (or more detailed in the case of primates, in accord with Goodman et al.1998). Reptiles were split into three morphologically (for recent phylogenies see Towsend et al 2004, Vidal and Hedges 2005, Uetz et al. 2008) distinct groups: snakes (Ophidia), lizards (tuataras and squamates except snakes) and turtles (Testudines). Birds are a morphologically most homogenous class of terrestrial vertebrates. Moreover, phylogeny (Sibley and Ahlquist 1990, Ericson et al. 2006, Hackett et al. 2008) does not reflect the variability in appearance properly. We analyzed the following groups defined by a combination of the phylogenetic (Ericson et al. 2006) and ecomorphological features: “basal birds” (Paleognathae, Galloanserae and Columbidae belonging to Metaves), “aquatic birds” (belonging to Neoaves and Metaves), “terrestrial birds” (selected Neoaves) and “passerines” (Passeriformes: Passerida; Barker et al. 2004). Mammals were split based on the purely phylogenetic criteria (Murphy et al. 2001, Bininda-Emonds 2007) into following four groups: “basal mammals” (Monotremata, Metatheria, Xenarthra, Afrotheria), ”Glires” (Rodentia and Lagomorpha), ”Euarchonta” (Scandentia, Dermoptera and Primates), and finally ”Laurasiatheria” (Eulipotyphla, Artiodactyla, Perissodactyla, Pholidota and Carnivora; Cetacea and Chiroptera were omitted because of their specific requirements and deviation of typical mammalian life style).

Each of these families/subfamilies was characterized by the total number of individuals kept in zoos worldwide, the number of extant species, the typical body size (i.e., weight for birds and mammals, and length for reptiles) and estimated of human preference. To assess the last variable we randomly selected one (or more) species of each family/subfamily from the complete species list and included them into the set of pictures presented to our respondents (for more details see Data sources and testing procedures). When no relevant picture was available for the particular species, we repeated random selection once again. When pictures of more than one species belonging to the group were included in the test, the data were pooled to avoid pseudoreplication.

Multiple regression, in which log-transformed number of individuals per species (i.e., mean population size) was given as a dependent variable, and log-transformed body size and human preference as independent (explanatory) variables, was computed for each studied vertebrate group. All these eleven models computed for particular vertebrate groups except one (turtles) were significant and explained enough variation to be considered in conservation biology (see Table 3).

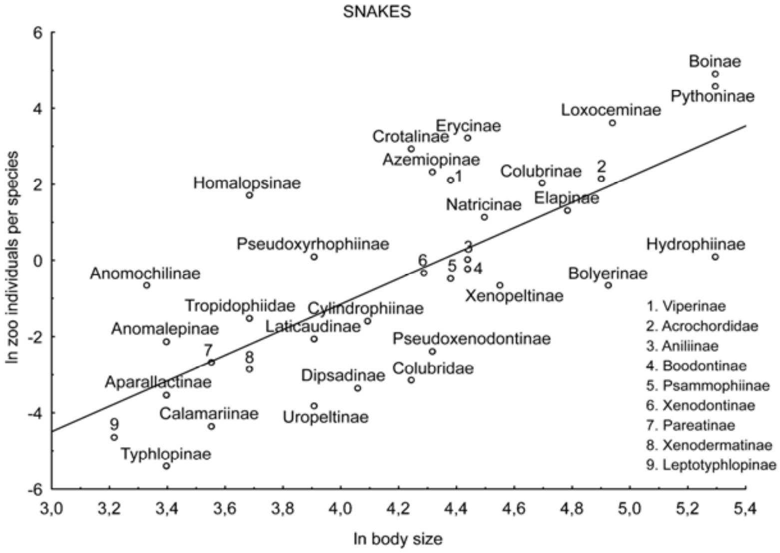
In accord with expectations, body size was the best predictor of the number of individuals per species. Its effect was positive in ten out of eleven analyzed groups (except turtles); nine of these effects were significant ($P<0.05$) and one (group of “basal mammals”) approached significance ($P<0.1$). The larger the typical species of the family/subfamily is, the more individuals per species are kept in zoos. This relationship was really strong within most studied groups, in particular snakes and Laurasiatheria (Figures 7-8, 10-12, 14, 16-18). The only exception were turtles exhibiting even an inverse relationship, which was, however, statistically insignificant.

Table 3. Results of multiple regression explaining zoo population per species (log-transformed) by body size (log-transformed) and human preferences (square root arcsin transformed ranks).

	Body size - median for particular family/subfamily			Rank of perceived attractiveness			Explained variance by PC1	number of respondents	Summary of regression model
Higher taxonomic groups	β	t	p <	β	t	p <	PC1	N	
Reptiles									
Snakes	0.721	5.76	0.0001	-0.024	-0.19	0.8497	48.0%	32	R2=0.5289; $F_{(2.32)}$=18.0; p<.0001
Lepidosauria except snakes	0.536	3.85	0.0001	-0.203	-1.46	0.1548	38.5%	50	R2=0.3429; $F_{(2.34)}$=8.9; p<.0008
Turtles	-0.214	-1.00	0.3319	-0.389	-1.81	0.0868	47.5%	53	R2=0.1788; $F_{(2.18)}$=2.0; p<.1697
Birds									
Basal birds	0.638	4.20	0.0003	-0.273	-1.80	0.0826	24.1%	36	R2=0.3939; $F_{(2.28)}$=9.1; p<.0009
Aquatic birds	0.463	2.86	0.0084	-0.306	-1.89	0.0704	31.6%	36	R2=0.4144; $F_{(2.26)}$=9.2; p<.0010
Terrestrial birds	0.541	3.22	0.0039	-0.353	-2.10	0.0473	32.4%	36	R2=0.3277; $F_{(2.22)}$=6.8; p<.0049
Passerines	0.525	3.20	0.0035	-0.284	-1.74	0.0940	17.2%	36	R2=0.3006; $F_{(2.27)}$=5.8; p<.0080

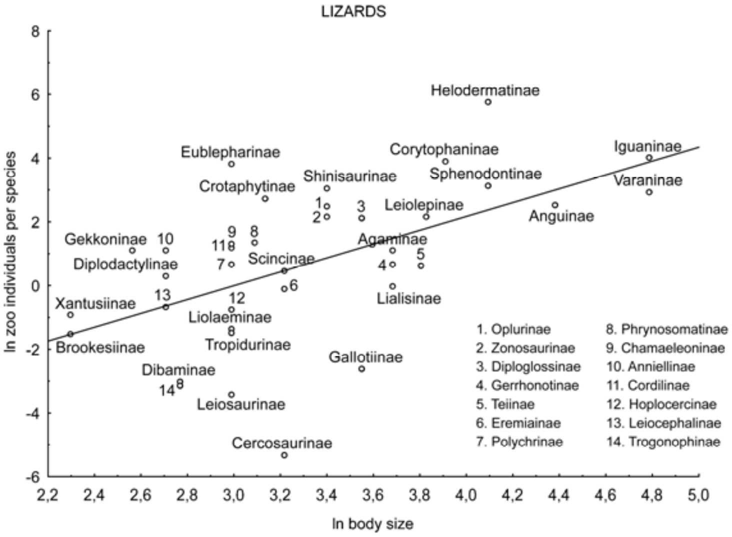
Table 3. (Continued).

Mammals									
Bassal mammals	0.260	1.70	0.0986	-0.417	-2.73	0.0102	28.3%	45	R2=0.2885; $F_{(2.32)}$=6.5; p<.0043
Glires	0.397	2.38	0.0238	-0.242	-1.45	0.1577	42.4%	52	R2=0.1863; $F_{(2.30)}$=3.4; p<.0454
Euarchonta	0.482	2.71	0.0110	-0.150	-0.84	0.4055	21.5%	51	R2=0.1979; $F_{(2.30)}$=3.7; p<.0366
Laurasiatheria	0.663348	5.29177	0.000010	-0.277793	-2.21605	0.034418	20.4%	42	R2=0.5291; $F_{(2.30)}$=16.9; p<.0001



Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Parias flavomaculatus (Crotalinae), Geophis semidoliatus (Dipsadinae), Anilius scytale (Aniliinae), Laticauda colubrina (Laticaudinae), Cercaspis carinata (Colubridae incertae sedis), Atractaspis bibronii (Aparallactinae, Atractaspidinae), Xenopeltis unicolor (Xenopeltinae), Azemiops feae (Azemiopinae), Acrantophis madagascariensis (Boinae), Hydrophis cyanocinctus (Hydrophiinae), Cylindrophis maculatus (Cylindrophiinae), Tropidophis greenwayi (Tropidophiidae, Ungaliophiidae), Vipera ursinii (Viperinae), Acrochordus granulatus (Acrochordidae), Pseudoxenodon macrops (Pseudoxenodontinae), Boulengerina annulata stormsi (Elapinae), Enhydris enhydris (Homalopsinae), Achalinus spinalis (Xenodermatinae), Ialtris dorsalis (Xenodontinae), Anomochilus weberi (Anomochilinae), Pareas monticola (Pareatinae), Psammophis schokari (Psammophiinae), Calmaria schmidti (Calamariinae), Amphiesma platyceps (Natricinae), Antaresia maculosa (Pythoninae), Ithycyphus miniatus (Pseudoxyrhophiinae), Eryx colubrinus (Erycinae), Lycodomorphus bicolor (Boodontinae), Loxocemus bicolor (Loxoceminae), Tantilla coronata (Colubrinae), Rhinophis pillippinus (Uropeltinae), Casarea dussumieri (Bolyerinae), Leptotyphlops humilis (Leptotyphlopinae), Liotyphlops beui (Anomalepinae), Typhlops brongersmianus (Typhlopinae).

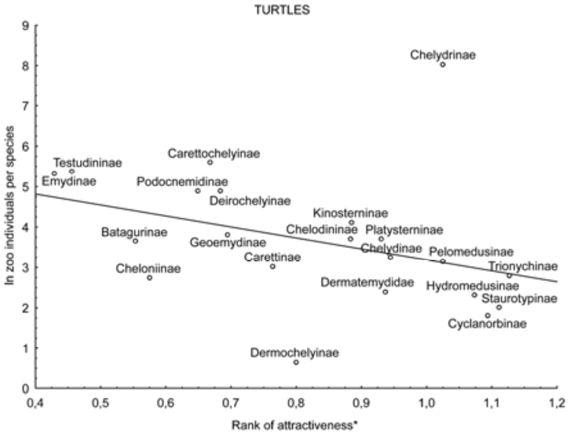
Figure 7. Relationship between size of zoo populations per species and body size in snakes. Ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed length. R2 = 52.8%; P < 0.0001, y = -14.53 * x + 3.35.



Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Chamaeleo rudis (Chamaeleoninae), Oplurus fierinensis (Oplurinae), Microlophus thoracicus (Tropidurinae), Abronia vasconcelosii (Gerrhonotinae), Cnemidophorus gularis (Teiinae), Heloderma suspectum (Helodermatinae), Leiocephalus l. lunatus (Leiocephalinae), Lepidophyma sylvaticum (Xantusiinae), Liolaemus chiliensis (Liolaeminae), Heliobolus spekii (Eremiainae), Ctenophorus fordi (Agaminae), Eublepharis hardwickii (Eublepharinae), Cordylus tropidosternum (Cordilinae), Varanus niloticus (Varaninae), Zonosaurus quadrilineatus (Zonosaurinae), Heteronotia binolei (Gekkoninae), Crotaphytus antiquus (Crotaphytinae), Pristidactylus torquatus (Leiosaurinae), Anolis wattsi (Polychrinae), Corytophanes hernandesii (Corytophaninae), Schinisaurus crocodylurus (Shinisaurinae), Galotia galloti (Galotiinae), Hoplocercus spinosus (Hoplocercinae), Dipsosaurus dorsalis (Iguaninae), Sphenodon punctatus (Sphenodontinae), Saltuarius cornutus (Diplodactylinae), Potamites apodemus (Cercosaurinae), Lankascincus deraniyagalai (Scincinae), Celestus stenurus (Diploglossinae), Sceloporus spinosus (Phrynosomatinae), Rhampholeon boulengeri (Brookesiinae), Ophisaurus atennuatus (Anguinae), Uromastyx aegyptia (Leiolepinae or Leiolepidinae), Trogonophis wiegmani (Trogonophinae), Aprasia rostrata (Lialisinae or Pygopodinae), Dibamus bogadeki (Dibaminae), Anniella pulchra (Anniellinae).

Figure 8. Relationship between size of zoo populations per species and body size in lizards (including tuataras). ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed snout-vent length. R = 30.5%, P= 0.0004, y = -6,52 * x +2,17.

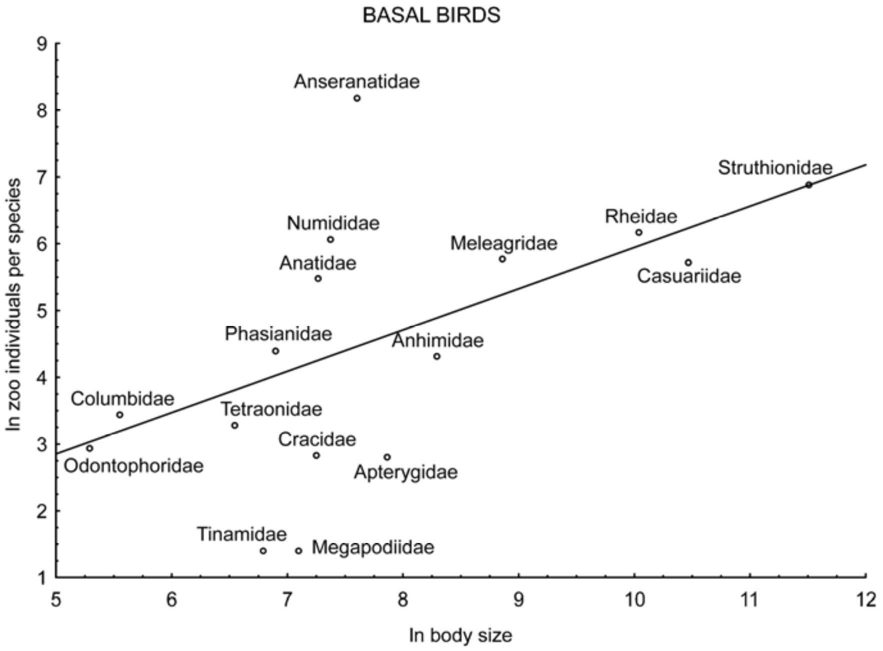
Human preference contributed less apparently to the models explaining the number of individuals per species. Interestingly enough, the effects of ranking were always negative, i.e., the higher the human preference, the better the representation of the given family/subfamily in zoos. However, this factor reached formal statistical significance (P<0.05) only in two mamamlian (”basal mammals” and Laurasiatheria) and one bird (“terrestrial birds”) groups (see Figures 15, 13). In additional one reptile (turtles; Figure 9) and three bird groups (“basal birds”, “aquatic birds” and “passerines”) this factor approached significance (P<0.1).



*Please note that the higher value of mean rank, the less attractive animal.

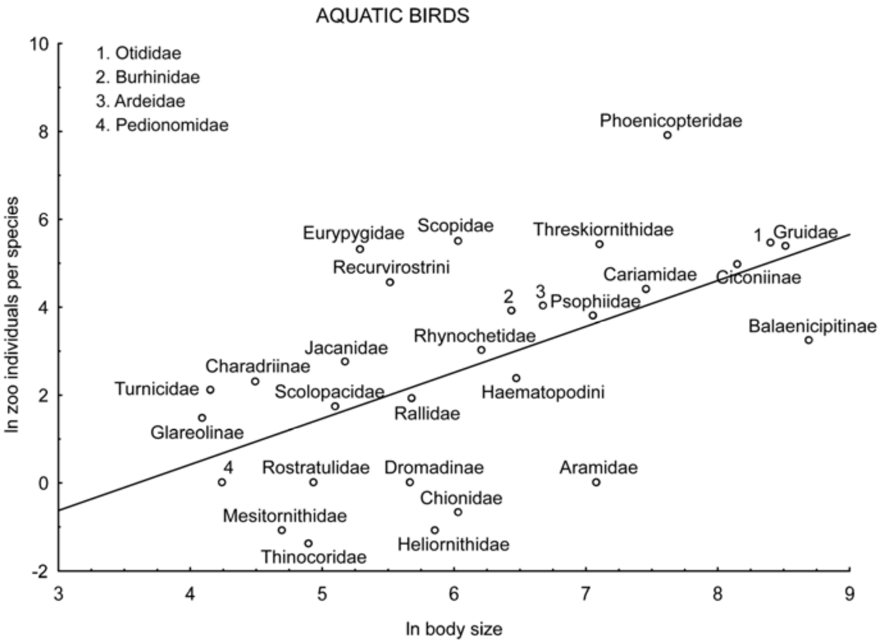
Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Clemmys guttata (Emydinae), Astrochelys yniphora (Testudininae), Malayemys subrijuga (Batagurinae), Chelonia mydas (Cheloniinae), Podocnemis erythrocephala (Podocnemidinae), Carettochelys insculpta (Caretochelynae), Pseudemys nelsoni (Deirochelyinae), Cuora trifasciata (Geoemydinae), Lepidochelys olivacea (Carettinae), Dermochelys coriacea (Dermochelyinae), Elseya albagula (Chelodininae), Kinosternon flavescens (Kinosterninae), Platysternon megacephalum (Platysterninae), Dermatemys mawii (Dermatemydidae), Phrynops hilari (Chelidinae), Chelydra serpentina (Chelydrinae), Pelusios castanoides (Pelomedusinae), Hydromedusa tectifera (Hydromedusinae), Lissemys punctata (Cyclanorbinae), Staurotypus triporcatus (Staurotypinae), Apalone ferox (Trionychinae).

Figure 9. Relationship between size of zoo populations per species and attractiveness in turtles. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. Rank of attractiveness = mean square-root arcsin transformed rank. R2 = 13.35%, P = 0.1034, y = 59.0 * x -2.71.


BASAL BIRDS

Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Apteryx australis (Apterygidae); Chalcophaps stephani, Ptilinopus arcanus, Treron oxyura, Geophaps scripta, Columba delegorguei, Zenaida aurita (Columbidae), Bonasa bonasia (Tetraonidae); Chloephaga poliocephala, Anas undulata, Oxyura maccoa, Tadorna radjah (Anatidae); Rhea pennata (Rheidae); Struthio camelus (Struthionidae); Callipepla squamata, Odontophorus hyperythrus (Odontophoridae); Margaroperdix madagarensis, Tetraogallus caucasicus, Argusianus argus, Gallus sonneratii, Francolinus rufopictus (Phasianidae); Chauna chavaria (Anhimidae); Casuarius casuarius (Casuariidae); Guttera plumifera (Numididae); Ortalis erythroptera, Penelope ortoni (Cracidae); Anseranas semipalmata (Anseranatidae); Nothocercus julius, Tinamus tao (Tinamidae); Meleagris gallopavo (Meleagridae); Megapodius laperouse (Megapodiidae).

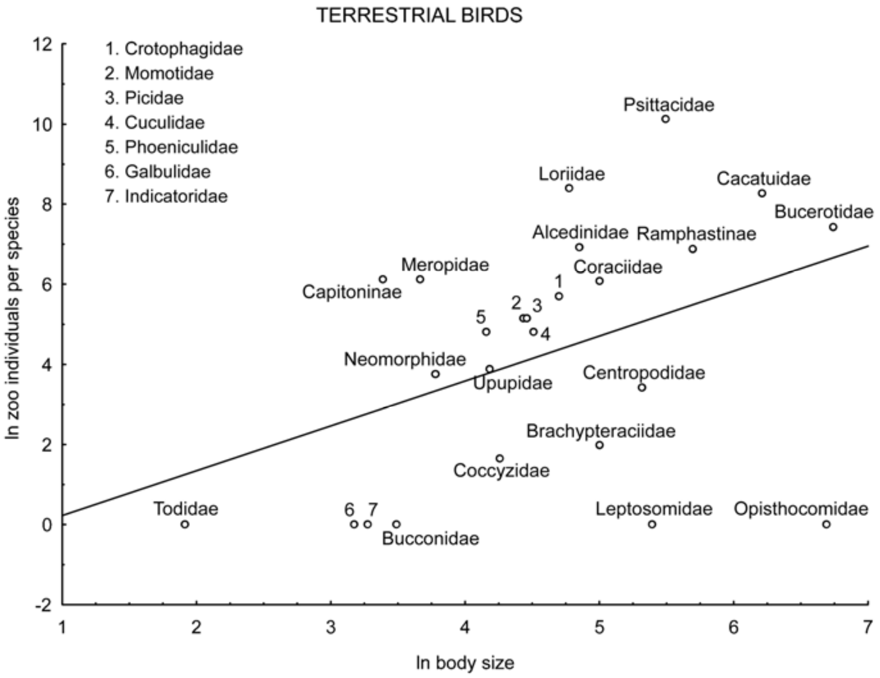
Figure 10. Relationship between size of zoo populations per species and body size in basal birds. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed weight. R2 = 32.4%, P = 0.0008; y = -0.24 * x + 0.62.


AQUATIC BIRDS

Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Phoenicopterus ruber (Phoenicopteridae), Balearica pavonina (Gruidae), Himantopus mexicanus (Recurvirostrini), Aramus guarauna (Aramidae), Ardea humbloti (Ardeidae), Ciconia nigra (Ciconiinae), Dromas ardeola (Dromadinae), Jacana jacana (Jacanidae), Eupodotis caerulescens (Otididae), Eurypyga helias (Eurypygidae), Theristicus melanopis (Threskiornithidae), Balaeniceps rex (Balaenicipitinae), Vanellus melanocephalus (Charadriinae), Rostratula semicollaris (Rostratulidae), Scopus umbretta

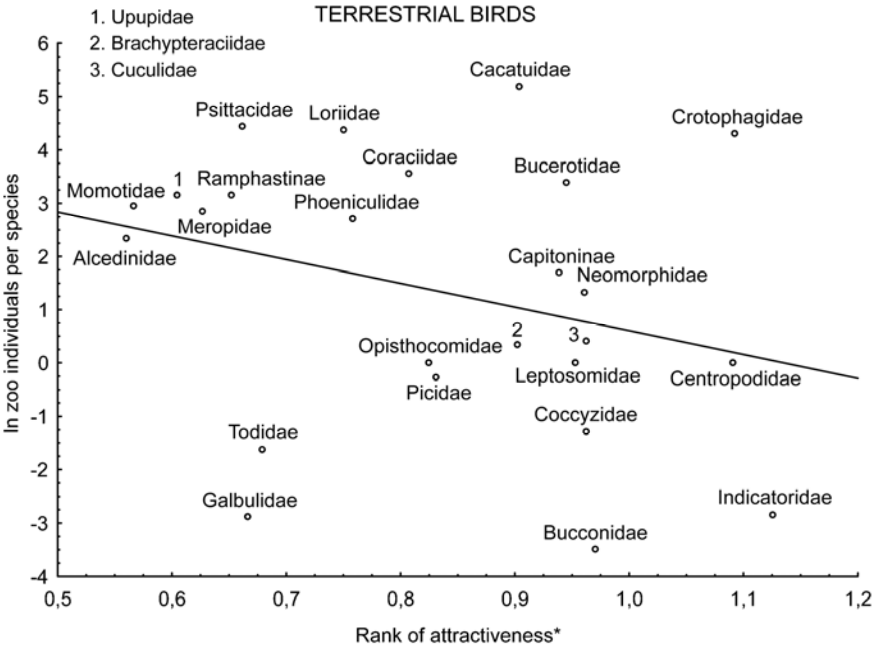
(Scopidae), Glareola ocularis (Glareolinae), Tringa incana (Scolopacidae), Psophia leucoptera (Psophiidae), Heliopais personata (Heliornithidae), Pedionomus torquatus (Pedionomidae), Burhinus recurvirostris (Burhinidae), Haematopus moquini (Haematopodini), Monias benschi (Mesitornithidae), Thinocorus orbignyianus (Thinocoridae), Amaurolimnas concolor (Rallidae), Rhynochetos jubatus (Rhynochetidae), Turnix velox (Turnicidae), Chunga burmeisteri (Cariamidae), Chionis alba (Chionidae).

Figure 11. Relationship between size of zoo populations per species and body size in aquatic birds. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed weight. R2 = 33.4%, P = 0.0010, y = -3.76 * x + 1.05.



Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Alcedo cyanopecta, Halcyon smyrnensis, Megaceryle alcyon (Alcedinidae); Momotus mexicanus (Momotidae); Upupa epops (Upupidae); Merops boehmi (Meropidae); Aulacorhynchus prasinus (Ramphastinae); Ara chloropterus, Bolborhynchus ferrugineifrons (Psittacidae); Jacamerops aureus (Galbulidae); Todus multicolor (Todidae); Charmosyna rubronotata (Loriidae); Phoeniculus staneiceps (Phoeniculidae); Coracias naevia (Coraciidae); Opisthocomus hoazin (Opisthocomidae); Dryocopus pileatus, Picumnus pygmaeus (Picidae); Uratelornis chimaera (Brachypteraciidae); Cacatua alba (Cacatuidae); Tricholaema frontata, Semnornis ramphastinus (Capitoninae); Anorrhinus galeritus (Bucerotidae); Leptosomus discolor (Leptosomidae); Neomorphus geoffroyi (Neomorphidae); Coccyzus lansbergi (Coccyzidae); Eudynamys scolopacea (Cuculidae); Malacoptila rufa (Bucconidae); Centropus violaceus (Centropodidae); Crotophaga sulcirostris (Crotophagidae); Indicator willcocksi (Indicatoridae).

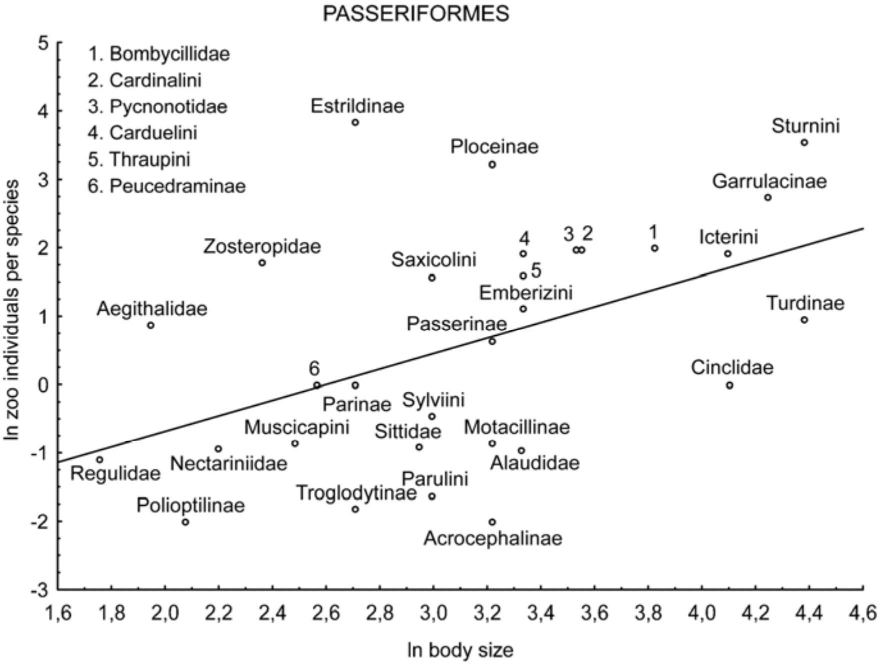
Figure 12. Relationship between size of zoo populations per species and body size in terrestrial birds. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed weight. R2 = 17.1%; P = 0.0399, y = -0,89 * x + 1,12.



*Please note that the higher value of mean rank, the less attractive animal.

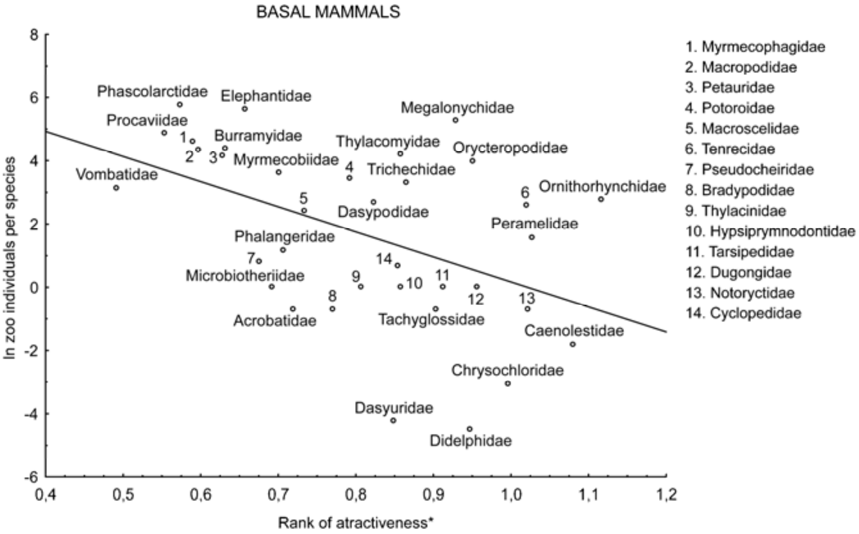
Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Alcedo cyanopecta, Halcyon smyrnensis, Megaceryle alcyon (Alcedinidae); Momotus mexicanus (Momotidae); Upupa epops (Upupidae); Merops boehmi (Meropidae); Aulacorhynchus prasinus (Ramphastinae); Ara chloropterus, Bolborhynchus ferrugineifrons (Psittacidae); Jacamerops aureus (Galbulidae); Todus multicolor (Todidae); Charmosyna rubronotata (Loriidae); Phoeniculus staneiceps (Phoeniculidae); Coracias naevia (Coraciidae); Opisthocomus hoazin (Opisthocomidae); Dryocopus pileatus, Picumnus pygmaeus (Picidae); Uratelornis chimaera (Brachypteraciidae); Cacatua alba (Cacatuidae); Tricholaema frontata, Semnornis ramphastinus (Capitoninae); Anorrhinus galeritus (Bucerotidae); Leptosomus discolor (Leptosomidae); Neomorphus geoffroyi (Neomorphidae); Coccyzus lansbergi (Coccyzidae); Eudynamys scolopacea (Cuculidae); Malacoptila rufa (Bucconidae); Centropus violaceus (Centropodidae); Crotophaga sulcirostris (Crotophagidae); Indicator willcocksi (Indicatoridae).

Figure 13. Relationship between size of zoo populations per species and attractiveness in terrestrial birds. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. Rank of attractiveness = mean square-root arcsin transformed rank. R2 = 09.3%, P = 0.14, y = 5.07 * x - 4.47.



Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Cyanoptila cyanomelaena (Muscicapini), Parus caeruleus (Parinae), Peucedramus taeniatus (Peucedraminae), Parula americana (Parulini), Aethopyga siparaja (Nectariniidae), Passerina ciris (Cardinalini), Uraeginthus angolensis (Estrildinae), Ploceus cucullatus (Ploceinae), Regulus teneriffae (Regulidae), Pycnonotus jocosus (Pycnonotidae), Passer Melanurus (Passerinae), Garrulax pectoralis (Garrulacinae), Phoenicurus auroreus (Saxicolini), Loxia curvirostra (Carduelini), Gracula religiosa (Sturnini), Bombycilla cedrorum (Bombycillidae), Sitta europaea (Sittidae), Zosterops palpebrosus (Zosteropidae), Emberiza citrinella (Emberizini), Bradypterus seebohmi (Acrocephalinae), Cinclus cinclus (Cinclidae), Thryothorus ludovicianus (Troglodytinae), Polioptila caerulea (Polioptilinae), Molothrus ater (Icterini), Catharus guttatus (Turdinae), Anthus campestris (Motacillinae), Sylvia melanocephala (Sylviini) Mirafra erythroptera (Alaudidae), Aegithalos caudatus (Aegithalidae), Coereba flaveola (Thraupini).

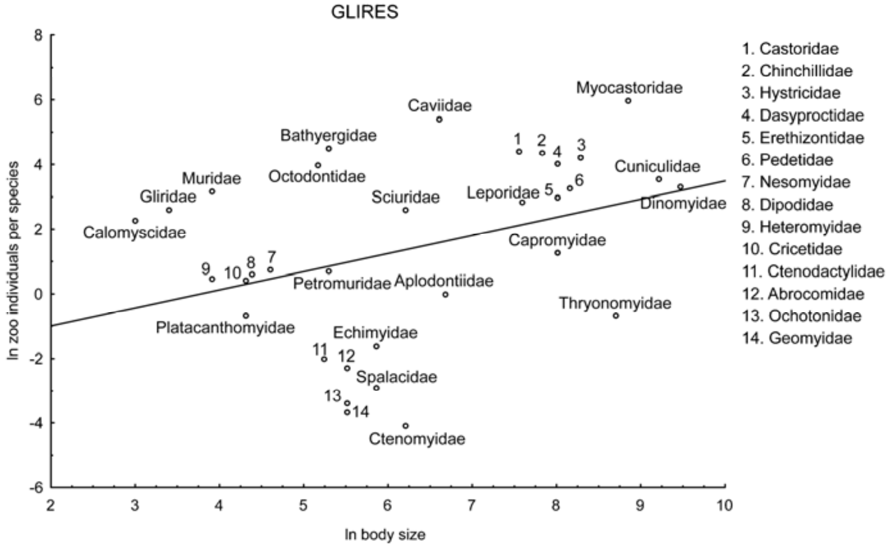
Figure 14. Relationship between size of zoo populations per species and body size in passerines. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed weight. R^2 = 22.3%, P = 0.0085, y = -2.96 * x + 1,14.



*Please note that the higher value of mean rank, the less attractive animal.

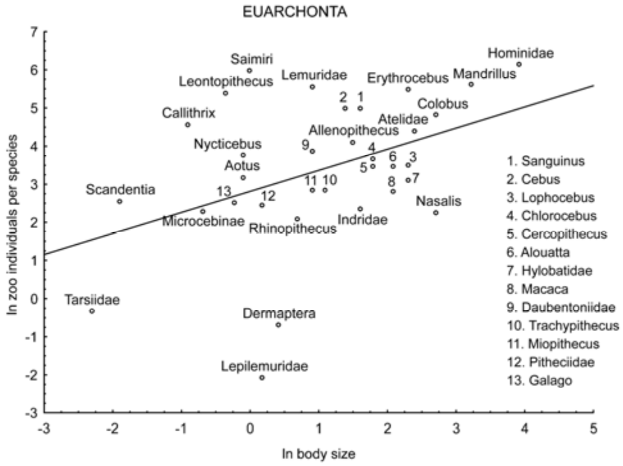
Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Vombatus ursinus (Vombatidae), Dendrohyrax arboreus (Procaviidae), Phascolarctos cinereus (Phascolarctidae), Tamandua mexicana (Myrmecophagidae), Petrogale xanthopus (Macropodidae), Petaurus norfolcensis (Petauridae), Cercartetus nanus (Burramyidae), Loxodonta africana (Elephantidae), Pseudocheirus peregrinus (Pseudocheiridae), Dromiciops gliroides (Microbiotheriidae), Myrmecobius fasciatus (Myrmecobiidae), Trichosurus caninus (Phalangeridae), Distoechurus pennatus (Acrobatidae), Macroscelides proboscideus (Macroscelidae), Bradypus tridactylus (Bradypodidae), Aepyprymnus rufescens (Potoroidae), Thylacinus cynocephalus (Thylacinidae), Chaetophractus vellerosus (Dasypodidae), Sminthopsis murina (Dasyuridae), Cyclopes didactylus (Cyclopedidae), Hypsiprymnodon moschatus (Hypsiprymnodontidae), Macrotis lagotis (Thylacomyidae), Trichechus manatus (Trichechidae), Zaglossus bruijni (Tachyglossidae), Tarsipes rostratus (Tarsipedidae) Choloepus didactylus (Megalonychidae), Marmosa murina (Didelphidae), Orycteropus afer (Orycteropodidae), Dugong dugon (Dugongidae), Cryptochloris asiatica (Chrysochloridae), Microgale taiva (Tenrecidae), Notoryctes caurinus (Notoryctidae), Perameles gunnii, (Peramelidae), Lestoros inca (Caenolestidae), Ornithorhynchus anatinus (Ornithorhynchidae).

Figure 15. Relationship between size of zoo populations per species and attractiveness in basal mammals including Prototheria, Methatheria, Xenarthra and Afrotheria. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. Rank of attractiveness = mean square-root arcsin transformed rank. R2 = 22.4%, P = 0.0041, y = 8.09 * x – 7.92.



Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Ochotona alpina (Ochotonidae), Petromus typicus (Petromuridae), Octodon degu (Octodontidae), Macrotarsomys bastardi (Nesomyidae), Graphiurus kelleni (Gliridae), Sylvilagus obscurus (Leporidae), Dolichotis patagonum (Caviidae), Spermophilus columbianus (Sciuridae), Chaetodipus baileyi (Heteromyidae), Pedetes capensis (Pedetidae), Dasyprocta leporina (Dasyproctidae), Calomyscus (Calomyscidae), Dinomys branickii (Dinomyidae), Platacanthomys lasiurus (Platacanthomyidae), Allactaga elater (Dipodidae), Massoutiera mzabi (Echimyidae), Lagostomus maximus (Chinchillidae), Cuniculus paca (Cuniculidae), Apodemus agrarius (Muridae), Atherurus africanus (Hystricidae), Castor canadensis (Castoridae), Capromys pilorides (Capromyidae), Proechimys guarirae (Ctenodactylidae), Myocastor coypus (Myocastoridae), Ctenomys (Ctenomyidae), Thryonomys swinderianus (Thryonomyidae), Geomys (Geomyidae), Aplodontia rufa (Aplodontiidae), Melanomys caliginosus (Cricetidae), Abrocoma benettii (Abrocomidae), Cryptomys mechowi (Bathyergidae), Coendou prehensilis (Erethizontidae), Spalax leucodon (Spalacidae).

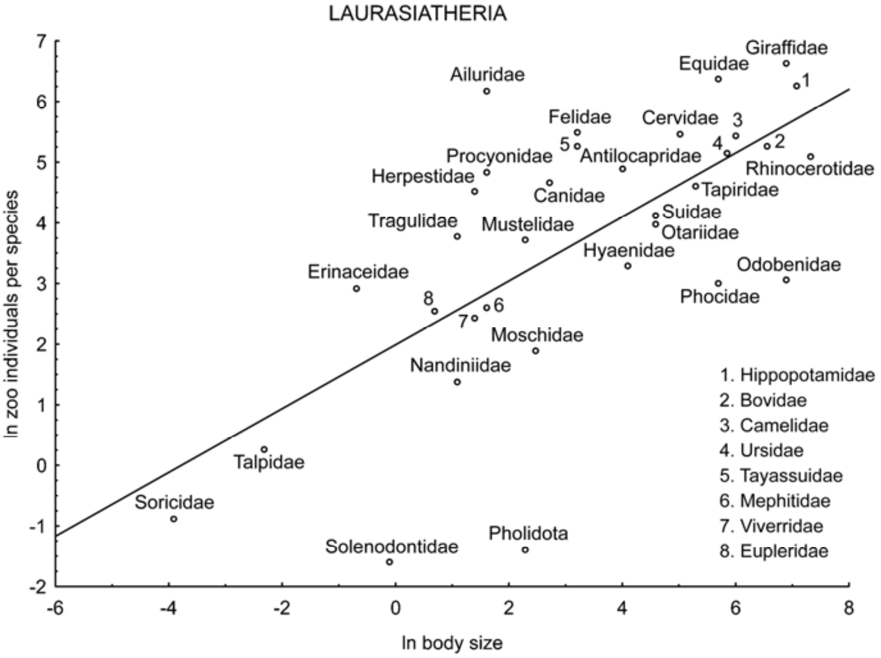
Figure 16. Relationship between size of zoo populations per species and body size in Glires. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed weight. R2 = 12.9%, P = 0.0398, y = -2.12 * x + 0.56.



Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Galago rondoensis (Galagidae: Galago, Euoticus, Otolemur); Microcebus ravelobensis (Microcebinae); Lemur catta (Lemuridae); Nycticebus coucang (Lorisidae: Arctocebus, Loris, Perodicticus, Nycticebus, Pseudopotto); Propithecus edwardsi (Indridae); Leontopithecus rosalia (Leontopithecina: Leontopithecus); Miopithecus talapoin (Cercopithecina II: Miopithecus); Callicebus torquatus (Pitheciidae); Cebus olivaceus (Cebinae: Cebus); Saguinus oedipus (Sanguina: Sanguinus, Callimico); Macaca sylvanus (Macaca); Trachypithecus francoisi (Colobinae: Semnopithecus, Trachypithecus, Presbytis); Pongo abelii (Hominidae); Aotus trivirgatus (Aotidae: Aotus); Alouatta caraya (Atelidae: Alouatta); Tarsius syrichta (Tarsiidae); Nomascus concolor (Hylobatidae); Lepilemur septentrionalis (Lepilemuridae); Saimiri oerstedii (Saimirinae: Saimiri); Lophocebus albigena (Lophocebus, Cercocebus); Callithrix pygmaea (Callithrichina: Callithrix); Daubentonia madagascariensis (Daubentoniidae); Mandrillus leucophaeus (Mandrillus, Papio, Theropithecus); Colobus guereza (Colobina: Colobus, Procolobus); Galeopterus variegates (Cynocephalidae: Dermaptera); Cercopithecus diana

(Cercopithecina V: Cercopithecus); Chlorocebus aethiops (Cercopithecina IV: Chlorocebus); Allenopithecus nigrovirridis (Cercopithecina I: Allenopithecus); Brachyteles arachnoides (Atelidae: Atelidae except Alouatta); Erythrocebus patas (Cercopithecina III: Erythrocebus); Ptilocercus lowii (Ptilocercidae: Scandentia); Nasalis larvatus (odd-nosed II: Nasalis, Simias) Rhinopithecus roxellana; (odd-nosed I: Rhinopithecus).

Figure 17. Relationship between size of zoo populations per species and body size in Euarchonta. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed weight. R2 = 17.9%, P = 0.0142, y = 2.81 * x + 0.55.



Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Ailurus fulgens (Ailuridae), Hemiechinus auritus (Erinaceidae), Ursus arctos (Ursidae), Leopardus pardalis (Felidae), Giraffa camelopardalis (Giraffidae), Vicugna vicugna (Camelidae), Galidictis fasciata (Eupleridae), Manis culionensis (Pholidota), Crocuta crocuta (Hyaenidae), Moschus moschiferus (Moschidae), Erignathus barbatus (Phocidae), Conepatus semistriatus (Mephitidae), Tragulus javanicus (Tragulidae), Rangifer tarandus (Cervidae), Nasua narcia (Procyonidae), Hexaprotodon liberiensis (Hippopotamidae), Diceros bicornis (Rhinocerotidae), Equus grevyi (Equidae), Nyctereutes procyonoides (Canidae), Tayassu pecari (Tayassuidae), Arctocephalus gazella (Otariidae), Genetta genetta (Viverridae), Mungos mungo (Herpestidae), Antilocapra americana (Antilocapridae), Nandinia binotata (Nandiniidae), Sorex minutus (Soricidae), Mellivora capensis (Mustelidae), Odobenus rosmarus (Odobenidae), Talpa europaea (Talpidae), Tapirus bairdii (Tapiridae), Phacochoerus africanus (Suidae), Bos sauveli (Bovidae), Solenodon cubanus (Solenodontidae).

Figure 18. Relationship between size of zoo populations per species and body size in Laurasiatheria. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed weight. R2 = 45.2%, P = 0.00002 y = 1.99 * x + 0.53.

In conclusion, the relationship between human preference and mean size of zoo population was less apparent, but still detectable, when the analyzed units were the families/subfamilies instead of individual species. Obviously, when comparing families/subfamilies several additional differences in their biological features may mask the relationship. Moreover, decreased strength of the relationship may also be attributed to the fact that not all families/subfamilies are homogenous enough to be reliably represented by a picture of the randomly selected species. This is an especially important factor in the case of morphologically highly homogenous groups (e.g. passerines) in which human preferences are highly determined by coloration, i.e., the character sometimes exhibiting considerable variation even among related species as well as parallel evolution of the same patterns (Chiari et al. 2004). The analysis of 54 published datasets carried out by Areekul and Quicke 2006 confirmed that most color characters (except aposematic or mimetic ones) do not provide good phylogenetic signal and suffer from frequent homoplasies.

Preferred Species and Characters

The assessment of human preferences among representatives of families or subfamilies provided us also with additional information.

First, the agreement between the respondents was surprisingly higher for the animal groups least known by the respondent and/or inducing in humans negative rather than positive emotions. The first principal component explained the highest proportion of total variation in such groups as snakes (48.0%), turtles (47.5%), Glires (= rodents and lagomorphs; 42.4%) and lizards (38.5%) are. On the other hand, the lowest agreement among the respondents was recorded in such popular groups as passerines (17.2%), Laurasiatheria (=ungulates, carnivors, pangolins and insectivores; 20.4%) and Euarchonta (primates and allies; 21.5%). Possibly, knowledge or positive attitude towards the animal species may obscure the relationship; while the pictures of unknown animals are ranked solely according to aesthetic rules which are more or less universal (see above).

It is worth of interest, which animals within each particular analyzed group of vertebrates were preferred by our respondents. Top ranking species of each group are listed at the Table 4 and some of them depicted in Figures 19-24. To figure out what taxa/species are perceived by humans as beautiful, indifferent or disgusting, we aligned the set of the pictures according the human's mean ranking in ascending order and tried to interpret the features linked with current position of the picture in whole sequence. Supplementary information was extracted also from remarks of our respondents during the testing.

Table 4. Top ranking species according to human preferences.

Group	The most attractive species	Species perceived as ugly
Snakes	1. Philippine pitviper *Parias flavomaculatus* (Crotalinae)	35. Brongersma's Worm Snake *Typhlops brongersmianus* (Typhlopinae)
	2. Coral Earth Snake *Geophis semidoliatus* (Dipsadinae)	34. Beu's Dawn Blind Snake *Liotyphlops beui* (Anomalepinae)
	3. Coral Cylinder Snakes *Anilius scytale* (Aniliinae)	33. Western Threadsnake *Leptotyphlops humilis* (Leptotyphlopinae)
Lizards	1. Coarse Chameleon *Chamaeleo rudis* (Chamaeleoninae)	37. California legless lizard *Anniella pulchra* (Anniellinae)
	2. Anzamala Madagascar Swift *Oplurus fierinensis* (Oplurinae)	36. Blind Lizard *Dibamus bogadeki* (Dibaminae)
	3. Tschudi's Pacific Iguana *Microlophus thoracicus* (Tropidurinae)	35. Exmouth Worm-lizard *Aprasia rostrata* (Lialisinae or Pygopodinae)
Turtles	1. Spotted Turtle *Clemmys guttata* (Emydinae)	21. Florida Softshell Turtle *Apalone ferox* (Trionychinae)
	2. Madagascan Tortoise *Astrochelys yniphora* (Testudininae)	20. Mexican Giant Musk Turtle *Staurotypus triporcatus* (Staurotypinae)
	3. Snail-eating Turtle *Malayemys subtrijuga* (Batagurinae)	19. Indian Soft-shelled Turtle *Lissemys punctata* (Cyclanorbinae)
Basal birds	1.Brown Kiwi *Apteryx australis* (Apterigidae)	16. Micronesian Scrubfowl *Megapodius laperouse* (Megapodiidae)
	2. Stephan’s Dove *Chalcophaps stephani* (Columbidae)	15. Wild Turkey *Meleagris gallopavo* (Meleagridae)
	3. Hazel Grouse	14. Grey Tinamou

	Bonasa bonasia (Tetraonidae)	*Tinamus tao* (Tinamidae)
Aquatic birds	1. Greater Flamingo *Phoenicopterus ruber* (Phoenicopteridae) 2. Crowned Crane *Balearica pavonina* (Gruidae) 3. Black-Necked Stilt *Himantopus mexicanus* (Recurvirostrini)	29. Snowy Sheathbill *Chionis alba* (Chionidae) 28. Black-Legged Seriema *Chunga burmeisteri* (Cariamidae) 27. Little Buttonquail *Turnix velox* (Turnicidae)

Table 4. (Continued).

Terrestrial birds	1. Indigo-banded Kingfisher *Alcedo cyanopecta* *(Alcedinidae)* 2. Russet-Crowned Motmot *Momotus mexicanus* (Momotidae) 3. Common Hoopoe *Upupa epops* (Upupidae)	25. Willcock‘s Honeyguide *Indicator willcocksi* (Indicatoridae) 24. Groove-Billed Ani *Crotophaga sulcirostris* (Crotophagidae) 23. Violaceous Coucal *Centropus violaceus* (Centropodidae)
Passerines	1. Blue-and-White Flycatcher *Cyanoptila cyanomelana* (Muscicapini) 2. Blue-Tit *Parus caeruleus* (Parinae) 3. Olive Warbler *Peucedramus taeniatus* (Peucedraminae)	30. Common bananaquit *Coereba flaveola* (Thraupini) 29. Long-Tailed Tit *Aegithalos caudatus* (Aegithalidae) 28. Indian Lark *Mirafra erythroptera* (Alaudidae)
Bassal mammals	1. Common Wombat *Vombatus ursinus* (Vombatidae) 2. Southern Tree Hyrax *Dendrohyrax arboreus* (Procaviidae) 3. Koala *Phascolarctos cinereus* (Phascolarctidae)	35. Duck-billed Platypus *Ornithorhynchus anatinus* (Ornithorhynchidae) 34. Incan Caenolestid *Lestoros inca* (Caenolestidae) 33. Eastern Barred Bandicoot *Perameles gunnii* (Peramelidae)
Glires	1. Alpine Pika *Ochotona alpina* (Ochotonidae) 2. Dassie Rat *Petromus typicus* (Petromuridae) 3. Degu *Octodon degu* (Octodontidae)	33. Lesser Blind Mole Rat *Spalax leucodon* (Spalacidae) 32. Brazilian Porcupine *Coendou prehensilis* (Erethizontidae) 31. Giant Mole-rat *Cryptomys mechowi* (Bathyergidae)
Euarchonta	1. Rondo Bushbaby *Galago rondoensis* (Galagidae) 2. Ravelobe Mouse Lemur *Microcebus ravelobensis* (Microcebinae) 3. Ring-tailed Lemur *Lemur catta* (Lemuridae)	33. Golden Snub-nosed Monkey *Rhinopithecus roxellana* (odd-nosed I former Colobinae*) 32. Proboscis Monkey *Nasalis larvatus* (odd-nosed II, Colobinae*) 31. Pen-tailed Treeshrew *Ptilocercus lowii* (Ptilocercidae)

Table 4. (Continued).

Laurasiatheria	1. Red Panda *Ailurus fulgens* (Ailuridae) 2. Long-eared Hedgehog	33. Cuban Solenodon *Solenodon cubanus* (Solenodontidae)

Hemiechinus auritus (Erinaceidae)	32. Kouprey *Bos sauveli* (Bovidae)
3. Brown Bear *Ursus arctos* (Ursidae)	31. Common Warthog *Phacochoerus africanus* (Suidae)

*Colobinae were split into three separate groups according to Sterner et al. 2006.

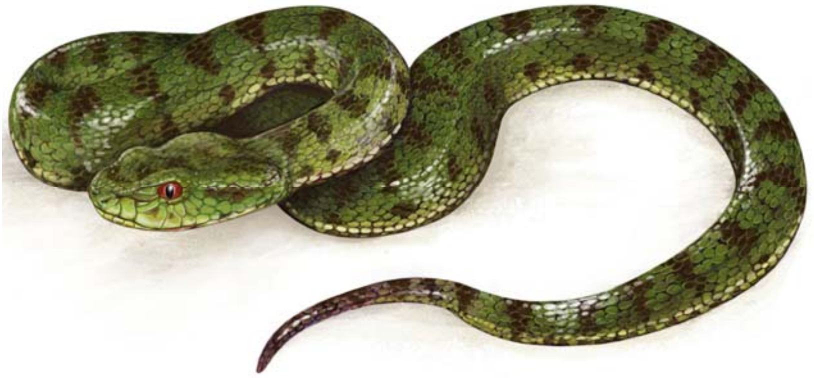


Figure 19. Examples of most preferred species within particular higher taxa according to our respondents. Philippine Pitviper (*Parias flavomaculatus*); Lizards: Crotalinae. Original painting by Silvie Lišková.

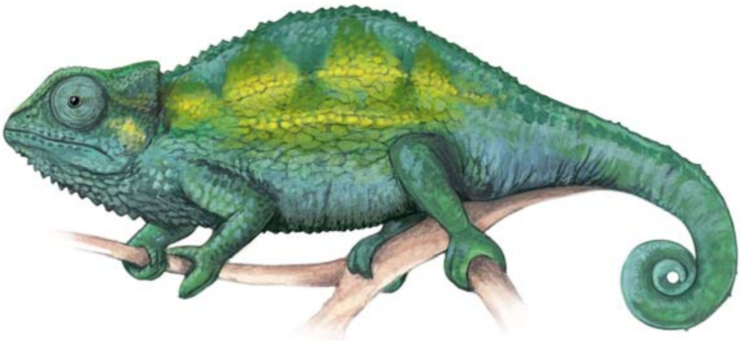


Figure 20. Examples of most preferred species within particular higher taxa according to our respondents. Coarse Chameleon (Chamaeleo rudis); Lizards: Chamaeleoninae. Original painting by Silvie Lišková.

Figure 21. Examples of most preferred species within particular higher taxa according to our respondents. Spotted Turtle (Clemmys guttata); Turtles: Emydinae. Original painting by Silvie Lišková.

Figure 22. Examples of most preferred species within particular higher taxa according to our respondents. Brown Kiwi (*Apteryx australis*); Basal birds: Apterigidae. Original painting by Silvie Lišková.

Figure 23. Examples of most preferred species within particular higher taxa according to our respondents. Greater Flamingo (*Phoenicopterus ruber*); Aquatic birds: Phoenicopteridae. Original painting by Silvie Lišková.

Figure 24. Examples of most preferred species within particular higher taxa according to our respondents. Indigo-banded Kingfisher (Alcedo cyanopecta); Terrestrial birds: Alcedinidae. Original painting by Silvie Lišková.

Figure 25. Examples of most preferred species within particular higher taxa according to our respondents. Blue-and-White Flycatcher (Cyanoptila cyanomelana); Passeriformes: Muscicapini. Original painting by Silvie Lišková.

Figure 26. Examples of most preferred species within particular higher taxa according to our respondents. Common Wombat (Vombatus ursinus); Basal mammals: Vombatidae. Original painting by Silvie Lišková.

Figure 27. Examples of most preferred species within particular higher taxa according to our respondents. Alpine Pika (*Ochotona alpina*); Glires: Ochotonidae. Original painting by Silvie Lišková.

Figure 28. Examples of most preferred species within particular higher taxa according to our respondents. Rondo Bushbaby (Galago rondoensis); Euarchonta: Galagidae. Original painting by Silvie Lišková.

Figure 29. Examples of most preferred species within particular higher taxa according to our respondents. Red Panda (Ailurus fulgens); Laurasiatheria: Ailuridae. Original painting by Silvie Lišková.

Figure 30. Examples of most preferred species within particular higher taxa according to our respondents. Royal Antelope (Neotragus pygmaeus); Antelopes and allies (Bovidae). Original painting by Silvie Lišková.

The preferred traits varied greatly from set to set. Obviously, contribution of coloration on human preferences was important among birds (see Bennett & Owens 2002 for evolution of bird coloration) and reptiles, while it was only marginal among mammals characterized by limited variance in this character (for evolution of mammalian coloration see Caro 2005). We further discuss the observed patterns group by group.

Snakes

The preferred snakes were those with bright background colors: green as Philippine pitviper (*Parias flavomaculatus*, Crotalinae), red as coral earth snake (*Geophis semidoliatus*, Dipsadinae) and coral cylinder snakes *Anilius scytale* (Aniliinae), and bluish as colubrine *Laticauda colubrina* (Laticaudinae). Also stripes or disruptive pattern contributed to beauty. The plain grey or brownish species with snake-typical body plan were placed in the middle of preference scale. Species without clearly differed head and tail were perceived as unattractive: Brongersma's worm snake (*Typhlops brongersmianus,* Typhlopinae), *Liotyphlops beuii* (Anomalepinae), western threadsnake (*Leptotyphlos humilis*, Leptotyphlopinae), Peters' Philippine earth snake(*Rhinophis pillippinus*, Uropeltinae) or southeastern crowned snake (*Tantilla coronata*, Colubrinae).

Lizards and Tuataras

Our respondents preferred green species irrespective to their morphology: coarse chameleon (*Chameleo rudis,* Chameleonidae), Anzamala Madagascar Shift (*Oplurus fierinensis*, Oplurinae), and terrestrial arboreal alligator lizard (*Abronia graminea*, Gerrhonotinae). Species exhibiting whatever distinct color pattern in combination with lizards-typical body plan as were also preferred. Interestingly, those labeled by respondents as “strange” or “fanciful” were perceived as less attractive, e.g. tuatara (*Sphenodon punctatus,* Sphenodontidae), northern leaf-tail gecko (*Saltuarius cornutus,* Diplodactylinae), Egyptian mastigure (*Uromastyx aegyptia*, Leiolepinae) or Boulenger’s pygmy chameleon (*Rhampholeon boulengeri*, Brookesiinae). The animals with reduced limbs as Deraniyagala's tree skink (*Lankascincus deraniyagalai,* Scincinae), Cope's galliwasp (*Celestus stenurus,* Diploglossinae), slender glass lizard (*Ophisaurus atennuatus*, Anguinae) or even worm-like body plan as checkerboard worm lizard (*Trogonophis wiegmani,* Trogonophidae), exmouth worm-lizard (*Aprasia rostrata*, Pygopodinae), blind lizard (*Dibamus bogadeki*, Dibaminae) and California legless lizard *(Anniella pulchra*, Annielinae) were perceived as unattractive or ugly.

Testudines

The most preferred ones were turtles and tortoises with yellow or red pattern on carapax and/or on the head: .spotted turtle (*Clemmys guttata*, Emydinae), Madagascan tortoise (*Astrochelys yniphora*, Testudininae), snail-eating turtle (*Malayemys subrijuga,* Batagurinae), red-headed Amazon side-necked turtle (*Podocnemis erythrocephala*, Podocnemidinae), Florida redbelly turtle (*Pseudemys nelsoni,* Deirochelyinae), three-banded box turtle (*Cuora trifasciata*, Geoemydinae). The list of top ten includes also marine turtles and pig-nosed turtle (*Carettochelis insculpta*, Caretochelinae) with similar appearance. The species placed at the end of the preference scale were labeled by most respondents as “strange” as South-American snake-headed turtle (*Hydromedusa tectifera,* Hydromedusinae) and soft-shelled turtles or “dangerous” and “hostile” as big-headed turtle (*Platysternon megacephalum,* Platysterninae), common snapping turtle (*Chelydra serpentina*, Chelidrinae), or *Staurotypus triporcatus* (Staurotypinae). This feeling of potential danger corresponds also with opinion of many proficient breeders (Figure 9.).

Basal Birds

Favorites of this set were: kiwi (Apteryx australis, Apterygidae), pigeons especially the species with green feathers e.g. Stephan's dove Chalcophaps stephani, negros fruit-dove Ptilinopus arcanus, Sumatran green pigeon Treron oxyura (Columbidae). The species belonging to families Tetraonidae and Anatidae were highly preferred too. The lengths of legs e.g. in lesser rhea (Rhea pennata, Rheidae), ostrich (Struthio camelus, Struthionidae), , northern screamer (Chauna chavaria, Anhimidae) and long tail, e.g., in great argus (Argusianus argus, Phasianidae) or crest as in scaled quail (Callipepla squamata, Odontophoridae) and cassowary (Casuarius casuarius, Casuariidae), are the other observable features increasing the attractiveness of the species/family for humans.

Aquatic Birds

Elegance of shape and length of neck, legs and prominent beaks are the traits of species/families ranked as the most beautiful. Species with short neck, relatively shorter legs and beaks were perceived as unattractive. In this set of pictures, coloration had no marked effect on human ranking.

Terrestrial Birds

Coloration of birds is the most important feature for human aesthetic preference. Brightly colored (blue, red, and green) species from different families were perceived as the most beautiful: e.g. indigo-banded kingfisher *Alcedo cyanopecta,* white-throated kingfisher *Halcyon smyrnensis* (Alcedinidae), russet-crowned motmot (*Momotus mexicanus*, Momotidae) or red-and-green macaw (*Ara chloropterus*, Psittacidae). Also prominent beak (in e.g. Boehm's bee-eater (*Merops boehmi,* Meropidae), Emerald toucanet (*Aulacorhynchus prasinus*, Ramphastinae), great jacamar (*Jacamerops aureus*, Galbulidae) and/or crest e.g. in common hoopoe (*Upupa epops*,Upupidae,) shift the species upwards on the preference scale (Figure 12.). The combination of bright coloration with prominent beak and crest evoke positive emotions reliably. The lengths of the legs or tail are not important.

Passerines

Brightly colored birds with blue e.g. blue waxbill (*Uraeginthus angolensis* Estrildinae), blue-tit (*Parus caerules,* Parinae), blue-and-white flycatcher (*Cyanoptila cyanomelana,* Muscicapini), red e.g. Crimson sunbird (*Aethopyga siparaja,* Nectariniidae), green and yellow or orange colures are perceived as the most beautiful. The black mask on a head e.g. in olive warbler (*Peucedramus taeniatus,* Peucedraminae), village weaver (*Ploceus cucullatus*, Ploceinae) also enhances preferences to the holder. However, the congruence among respondents is low. Probably, human’s cognitive abilities are not adjusted to recognize and classify passerines with such uniform morphology.

Basal Mammals

Characterization of three most preferred basal mammals, i.e., common wombat (*Vombatus ursinus,* Vombatidae), southern tree hyrax (*Dendrohyrax arboreus,* Procaviidae) and *Phascolarctos cinereus* (Phascolarctidae) is quite simple – they all have appearance of lovely Teddy bears with dense fur, shaggy round ears and relatively big eyes. The animals possessing long and shaggy tail as northern tamandua (*Tamandua mexicana,* Myrmecophagidae), yellow-footed rock-wallaby *Petrogale xanthopus* (Macropodidae), squirrel glider *Petaurus norfolcensis* (Petauridae).are preferred too. Interestingly, elephant (*Loxodonta africana*) occupies just the eighth position on the scale of preferences. Subterranean, mouse-like animals and duck-billed platypus are placed on the tail of humans’ preferences.

Glires

This set of the pictures was unpopular among our respondents. Some students even tried to avoid evaluation of this set and expressed wisdom to arrange sets consisting of other animals. Most preferred species resemble approximately “Mickey Mouse” body scheme e.g. Alpine pika (*Ochotona alpina*, Ochotonidae), degu (*Octodon degu*, Octodontidae) or lesser big-footed mouse (*Macrotarsomys bastardi*, Nesomyidae). The length shaggy tail, big ears and bigger body size are preferred traits in this group. As in the previous group, the subterranean species e.g. giant mole-rat (*Cryptomys mechowi*, Bathyergidae) or lesser blind mole rat (*Spalax leucodon,* Spalacidae) and those resembling rat were unequivocally perceived as ugly.

Euarchonta

It is obvious that respondents prefer small nocturnal species with big eyes and ears e.g. rondo bush baby (*Galago rondoensis*, Galagidae), ravelobe mouse lemur *(Microcebus ravelobensis*, Microcebinae) or slow lori (*Nycticebus coucang,* Lorisidae). The primates with long and shaggy tail, e.g., ring-tailed lemur (*Lemur catta*, Lemuridae), Milne-

Edwards's (*Propithecus edwardsi,* Indridae), golden lion tamarin (*Leontopithecus rosalia,* Leontopithecina, Calitrichidae) or collared titi (*Callicebus torquatus,* Pitheciidae) are highly preferred too, similarly as in other groups (see above Basal mammals and Glires). Surprisingly, great apes represented by orang-outan (*Pongo abelii,* Hominidae) were placed to thirteenth position only on preference scale. The species placed at the end of the preference scale were in some aspect different from apish typical appearance e.g. pen-tailed tree-shrew *Ptilocercus lowii* (Ptilocercidae), proboscis monkey (*Nasalis larvatus,* Colobinae).

Laurasiatheria

In these set again bear-like animals as red panda (*Ailurus fulgens*, Ailuridae) or really bears brown bear (*Ursus arctos*, Ursidae) were preferred. Again species with dense fur, shaggy round ears animals long-eared hedgehog (*Hemiechinus auritus*, Erinaceidae) and/or apparent color pattern e.g. leopard (*Leopardus pardalis,* Felidae) or giraffe (*Giraffa camelopardalis*, Giraffidae) were perceived as charming or beautiful. For the list of unattractive species see Table 4.

Conclusion

Worldwide net of zoos supports considerable proportions of living species, at least in the case of terrestrial vertebrates as mammals, birds and reptiles. This collection may play role of valuable Noah's Ark providing that following conditions are fullfilled.

1) It is reasonable selection of species to keep that may help to cover all major clades and species/taxa under the most apparent risk of extinction. This requires application of both phylogenetic approach and actual information on conservation status of concerned species.
2) It is necessary to reflect the fact that economics and space essentially limits the size of zoo populations. We clearly demonstrated that zoo populations of most species (including those actually going to extinction in nature) are too small to be sustainable even in the short-time perspecive. Thus management of these insufficient populations should be promptly introduced to this alarming situation. This especially requires blurring boundaries between captive and wild populations (cf. Dickie et al. 2007) as well as those between zoo animals and populations kept by other respectable breeders (including private and NGO collections). Surplus animals in zoos should not be further castrated or killed as dictated by defenders of animal rights and wellfare ethics, but preferably moved from hard core of studbook populations kept in zoos and professional breeders into its periphery, e.g., private breeders, NGOs, reintroduction programs, etc. Simultaneously, priming, coordination and methodical role of zoos and their breeding programs should be extended. Conservation ethics (Hutchins 2007) evaluating survival of the species as moral priority have to be used to overcome administrative barriers and popular preconceptions.
3) Decisions, which species is the right one to keep and breed in large numbers, have to follow conservation needs rather than popularity of the species. Only 187 out of 23,582 living species of higher vertebrates have worldwide zoo population exceeding 500 specimens. Even more alarming is that only 49 out of these 187 species are those actually endangered.

We confirmed that zoo collections are biased in favor of the birds (higher numer of captive species) and mammals (larger population sizes), while reptiles are underrepresented. Thorough analyses of zoo population sizes suggest that body size is without any doubt the most prominent factor increasing the representation of given species or higher taxon in zoos. Although large animals are disproportionally more expensive to keep they are frequently preferred, probably due to visitor's preferrence.

In addition to body size, there is appearance of the animal per se. Some animals are perceived as more attractive than the others. Our respondents were exposed to the sets of pictures depicting different animal species and asked to rank the species according to their beauty. We were surprised by the high degree of congruence among the responses of different persons. Nevertheless, the characters contributing to human preferences varied greatly among studied sets of pictures. Conspicuous coloration was prominent factor in some birds and reptiles taxa, while preferred body proportions varied among studied taxa. Most comparisons carried out among related species showed the strong effects of beauty on size of zoo populations. In contrast, when not species, but families/subfamilies were compared this effect has remained significant within particular animal taxon only (basal mammals, Laurasiatheria, terrestrial birds). Obviously, characters matching human aesthetic criteria are distributed across different animal taxa. Thus, human preferences towards particular species belonging to the same family/subfamily may sometimes differ considerably. This may help zoos to find the species satisfying aesthetic criteria of the visitors and keepers in almost every clade of animals worth of ex situ conservation effort.

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Mammalian Collection on Noah's Ark: The Effects of Beauty, Brain and Body Size

Daniel Frynta*, Olga Šimková, Silvie Lišková, Eva Landová

Department of Zoology, Faculty of Sciences, Charles University in Prague, Prague, Czech Republic

Abstract

The importance of today's zoological gardens as the so-called "Noah's Ark" grows as the natural habitat of many species quickly diminishes. Their potential to shelter a large amount of individuals from many species gives us the opportunity to reintroduce a species that disappeared in nature. However, the selection of animals to be kept in zoos worldwide is highly selective and depends on human decisions driven by both ecological criteria such as population size or vulnerability and audience-driven criteria such as aesthetic preferences. Thus we focused our study on the most commonly kept and bred animal class, the mammals, and we asked which factors affect various aspects of the mammalian collection of zoos. We analyzed the presence/absence, population size, and frequency per species of each of the 123 mammalian families kept in the worldwide zoo collection. Our aim was to explain these data using the human-perceived attractiveness of mammalian families, their body weight, relative brain size and species richness of the family. In agreement with various previous studies, we found that the body size and the attractiveness of mammals significantly affect all studied components of the mammalian collection of zoos. There is a higher probability of the large and attractive families to be kept. Once kept, these animals are presented in larger numbers in more zoos. On the contrary, the relative mean brain size only affects the primary selection whether to keep the family or not. It does not affect the zoo population size or the number of zoos that keep the family.

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* E-mail: frynta@centrum.cz

Introduction

Nowadays, mankind covers about 83% of the Earth's land surface [1], causing global biodiversity to decline due to a quick loss of natural habitats of many species [2]. The proportion of potentially threatened species is rapidly increasing, leaving only very few species safe from a possible extinction [3]. It is therefore important not to miss any potential chance for animal conservation, including both in-situ and ex-situ conservational efforts. The world's zoos, aquaria, botanical gardens, and gene banks provide insurance for species and genetic diversity [4]. According to the ISIS (International Species Information System) online database, more than 7 million individual animals are kept in 872 zoos and aquariums (as recorded by the date of 12th January 2011). The high potential of zoos to serve as wildlife reservoirs, coupled with the rapid destruction of nature that we have faced in the last few decades, led [5] to frame the landmark Ark Hypothesis. The role of zoos as an ark proved viable in the case of amphibians (the "Amphibian Ark") that suffered a rapid population decline due to the chytridiomycosis disease. In response to this threat, The World Association of Zoos and Aquariums (WAZA), the IUCN/SSC (The International Union for Conservation of Nature/Species Survival Commission) Amphibian Specialist Group, and the IUCN/SSC Conservation Breeding Specialist Group (CBSG) worked together to collect a large number of species [6]. Moreover, in 1993 the EU recognized this conservation potential of zoos during the Convention on Biological Diversity (CBD), and obliged the zoos to manage the ex-situ and in-situ conservational role under the CBD's requirements [7], regardless of the lack of the government's systematic financial or other support [8]. EAZA (American Association of Zoos and Aquariums) and AZA (American Association of Zoos and Aquariums) supervise many specific ex-situ conservation programs such as Species Survival Plans and European Endangered Species Programmes. Moreover, they cooperate with CBSG, TAGs (Taxon Advisory Groups) and use various studbooks and data management systems, notably ISIS, to maintain the breeding of a variety of species which may also raise the effectiveness and possibility of species survival through captive breeding [9–11].

However, although the space to accommodate wild animals in zoos worldwide altogether is large, it is still very limited when compared to the list of all extant species. Only a small fraction of the world's animal population can board the Ark. In the year 2009, the Ark provided space for about 152 thousand individual mammals belonging to 990 species (18.5% of extant species) within a median worldwide zoo population size of 34.5 individuals. Empirical studies suggest that the minimum population size necessary for short-time captive maintenance of animal species/breeds under controlled conditions is about 50 [12], and populations over about 500 individuals are usually not affected by inbreeding depression [13]. Although these thresholds are only rough estimates because the effect depends on both effective population size and frequency of deleterious recessive mutations (cf. [14–16]). The zoos worldwide maintain 416 mammalian species represented by more than 50 individuals, which is 7.8% of all extant species. For the threshold of 500 individuals, the numbers count only 79 mammalian species, representing 1.5% of the extant mammalian diversity [17]. Similar numbers were confirmed in an independent study from April 2010 [18], finding that out of all 142 threatened mammalian species belonging to the IUCN categories Endangered, Critically Endangered, and Extinct in the wild, 68 species are being kept in zoos in more than 50 individuals, out of which 30 species are kept in more than 250 individuals.

Such small numbers point out that, even theoretically, if zoos tried to keep and breed endangered species, the space would be limited to hold only a tiny fraction of needful species at populations large enough to sustain a long-term captive breeding program of animals while avoiding an inbreeding depression. However, the presence of just a few unrelated individuals in zoos may occasionally save the species if the captive population is immediately expanded when necessary, e.g., after an unexpected crisis of the wild populations (but see [19] for negative effects of bottlenecking). This suggests that cooperative ex-situ conservation can help restore animal populations once the threat has diminished. Although many authors have questioned this assumption ever since (i.e., [20–24]), many researchers find the theoretical role of zoos in reintroduction programs as feasible (for a review of the limitations and solutions of availability of captive populations in reintroduction, see [25]; e.g., disease risk, behavioral competence of captive-reared individuals such as reduced ability to avoid predators or find food resources and attachment to humans; changes in genetic compositions, etc.), and a notable contribution of zoos to animals ex-situ breeding can be demonstrated by successful reintroductions which reduced the threat level of particular species. Species such as the Przewalski horse (*Equus ferus przewalskii*; [26]), the American bison (*Bison bison*; [27]), the European wisent (*Bison bonasus*; [28–30]), Pére David's deer (*Elaphurus davidianus*; [31]), or Arabian oryx [32] may serve as examples of successfully maintained zoo animal populations released back into the wild. Other notably successful reintroduced animals were the Asiatic wild ass (*Equus hemionus*; [33]), the golden lion tamarin (*Leontopithecus rosalia*; [34]), and the black-footed ferret (*Mustela nigripes*). The latter recovered from a very small population of only eighteen remaining individuals ([35]).

Moreover to the ex-situ breeding role of captive zoo populations, these groups might contribute to conservation purposes in other ways that do not necessarily demand high captive population densities. A very important role of today's zoological gardens presents education, especially promotion of increased public and political awareness of the need for in-situ conservation [36].

A single popular animal (or a small group of these) might serve as a flagship species and help its endangered relatives in the wild, or their natural habitat and its residents, to gain the necessary financial support from the public [37]. Another significant role of zoos resides in training specialists with the right knowledge about the breeding and care of the animals [38]. International studbooks running under the World Association of Zoos and Aquariums (WAZA) and collaboration with the ISIS database include husbandry and veterinary guidance for as many species as possible (www.waza.org). However, keeping a few individuals of a rare species, or their relatives, may help to retain the right specialists for future needs. The experience of staff and researchers working with living animals is irreplaceable by studbook information and guidelines, and their presence may help to save the species. Similarly, imagine a well-educated surgeon with no experience with real patients to perform operations on living humans.

The situation is complicated due to the fact that conservation activities are not the only purpose of the zoos. In fact, it is an issue discussed more intensively during the last several decades [38]. Zoos are vitally dependant on the funds gained from visitors [39]. Guests come to zoos mainly for recreational activities, expecting to see large, attractive, and active animals [40–42]. This may seemingly lead to the conclusion that there is a trade-off of which animals to keep in zoos to satisfy both conservational purposes and the visitors' recreational desires. The species' conservational status according to the IUCN was not the key factor for the selection of species to be included in the worldwide zoo collection (see [17,18] for terrestrial vertebrates; [43] for parrots, [44] for boid snakes). A question thus arises: is it the attractiveness and/or factors connected with the attractiveness of the animals that determines the composition of the collection of zoo animals around the world?

Balmford et al. [45] hypothesized that it is the size of the animal that determines its presence in a zoo and we confirmed this relationship in almost all examined taxa of terrestrial vertebrates in our previous papers [17,43,44]. Additionally, we found that attractiveness of the animals to human respondents also affects the world's zoo population numbers in some clades, namely snakes [44], parrots [43], terrestrial birds (grouping followed [46], excluding Accipitriformes, Strigiformes, Trogonidae and Coliidae; Psittaciformes, Opisthocomus and Cuculiformes were added), basal mammals (Monotremata, Marsupialia, Xenarthra and Afrotheria), and mammals of the carnivore-ungulate clade (Laurasiatheria, [17]).

On principle, larger animals are more conspicuous and visible to potential zoo visitors. This leads to the assumption that size can be difficult to separate from attractiveness, yet still there is more to beauty than size itself. In this paper, we measured separate data of attractiveness perceived by human respondents for a nearly complete set of mammalian families. We hypothesized that both size and attractiveness of mammals are good predictors of the size of their captive zoo populations (World Zoo Collection; further referred to as WZC).

Moreover to the above-mentioned physical properties, the brain size may modulate the attractiveness of animals to zoo curators and visitors. Adolf Portmann, the well-known Swiss biologist of the 20th century, hypothesized that humans categorize animals into the "higher" and "lower" ranked animal groups [47], and that this categorization, reflecting the brain size of the animal, affects the perceived attractiveness. Accordingly, we hypothesized that the brain size is a good predictor of behavioral attractiveness of mammalian species.

In this paper, we aimed to analyze the effect of body size, brain size, and attractiveness of mammalian species from almost all recent families to several variables explaining the WZC. We elaborate the previously-questioned number of individuals in the WZC in separate analyses to ask which factors determine whether the animal is present in any zoo or not, and to ask how many zoos actually keep those selected ones, and in how large or small numbers. There is a possibility that rather than species recognized by current taxonomists, taxa closer to genera or families represent the primary units of human spontaneous categorization [48]. Thus, the species within a family may compete with each other for the space available on the Ark (e.g., a zoo might select just one "mouse" or "rat" to keep in its collection instead of all 715 species of the family Muridae). Because of that, we included the species richness of the family as another factor to explain the analyzed WZC variables.

Materials and Methods

The dataset used for statistical analyses (see Appendix S1) includes 123 rows referred to as families. There were 119 families recognized by [49] and four infraorders (i.e., Microchiroptera, Megachiroptera, Mysticeti, Odontoceti). Cetaceans and chiropterans were pooled into infraorders because these specialized aerial and marine taxa deviate considerably from the typical mammalian body plan and their representation in zoos is rather poor.

Dependent variables

Information about the numbers of mammalian species and individuals kept in zoos worldwide was obtained from the ISIS (International Species Information System) online database (http://www.isis.org) covering more than 800 zoos and aquariums from 76 countries. We excluded hybrids, ambiguous genera, and domestic species/forms (see Appendix S2) from the dataset. We analyzed the following four variables derived from this dataset (accessed on 12th January 2011):

1. **Proportion of zoo species.** The number of species kept in the WZC scaled to the total number of extant species of a given family. This binomial variable reflects the mean probability that a species is kept at least in one zoo.
2. **Mean population size.** The world zoo population size (square-root transformed) per species present in the WZC (the families not represented in the WZC were excluded).
3. **Number of zoos.** The natural log-transformed mean number of zoos keeping the species (species and families not represented in the WZC were excluded).
4. **Number of conspecifics per zoo.** The mean number of conspecifics per zoo keeping the species (the families not represented in the WZC were excluded).

Explanatory variables

Species richness. The number of extant species of each family was log-transformed. In the case of infraorders, the number of extant species was divided by the number of families belonging to the infraorder.

Body size. We gathered body weight records (in grams) for representatives of most mammalian genera from literary sources (mostly from [50]). These values were naturally log-transformed and used for computation of family means.

Brain size. The relative brain size was substituted by an encephalization quotient. This variable, introduced by [51–53] and then repeatedly used as a measure of relative brain size (e.g. [54]), is a natural log-transformed ratio between observed brain weight and theoretical brain weight predicted by an allometric equation for mammalian species of the given body size. We performed an ordinary least square regression to calculate the allometric relationship between brain and body size. We gathered the primary data on brain and body weights for 1309 mammalian species from various literary sources (see Appendix S3). Because the individual families were unequally represented in the dataset, we employed a weighting by the variable inversely proportional to the number of included species belonging to the particular family (Figure 1). The resulting empirical allometric equation ($\ln B = -0.6601 * \ln M - 2.4100$; B = brain mass, M = body mass) was used for a calculation of the encephalization quotients.

Attractiveness. For the purpose of data collection, we defined four sets of 123 pictures depicting species from each family. Species representing individual families in each partial set were selected by a two-step (first genus then species) random choice process from the list of extant genera and species ([49]; domestic forms were excluded). Thus, duplicated presence of identical genera and species was avoided whenever possible. In monotypic families, the species was represented by different pictures. Sets coded as A, B and C consisted of illustrations while D consisted of photographs. The main sources of the pictures were [55–58]. In order to avoid possible effects of body size and background on rating, we adjusted the pictures with a white background and we resized them so that the pictured mammals were of a similar relative size (for illustration, see Figure 2).

The aesthetic attractiveness of the families was examined by presenting pictures of mammalian species to human volunteers (following [44]). The respondents were Czech citizens, mostly university students within the age range of 19–29 years. One can argue that as far as age, sex, and ethnic composition is concerned, our respondents did not properly represent the full scope of zoo visitors. The Czech Republic belongs among the least socially stratified countries in the world as demonstrated by the Gini index (GI) measuring the extent to which the distribution of income among individuals within an economy deviates from a perfectly equal distribution (0 corresponds to perfect equality while 100 to perfect inequality). The GI of the Czech Republic is 31 which corresponds to the 110 rank of 137 countries included in a comparison provided by the World Bank ([59]; compare, e.g., with GI = 45 for the USA which places them to the 41st position in the ranking; the higher the rank, the higher is the equality in society). Thus, we expected the Czech students to possess aesthetic preferences for animals comparable to the rest of the society, including zoo visitors (but see [60,61] who found socio-economic and educational differences in preferences, but their method did not focus purely on aesthetics). Since we preferred a homogenous example of respondents well motivated to performing the task, in which we could focus on the variables related to the tested stimuli rather than respondent characteristics, the students presented a good testing sample for the experiments evaluating human-perceived animal attractiveness.

Moreover, our previous studies revealed that the aesthetic ranking of animal species is highly stable with the factors of age, sex and ethnic composition having only a marginal effect ([43]). This is especially surprising in the case of cross-cultural comparisons, e.g., in such different cultures as are those in Europe and Papua New Guinea ([62,63] and new unpublished data; see also the agreement in physical attractiveness ratings of female faces across cultures [64], but see [65]). Note that the sample of respondents from non-European countries differed greatly in age and/or socioeconomic rank but their preferences for the examined animals still highly corresponded to those of the Czech students.

During the experiment, each respondent was exposed to one set of 123 pictures that were placed on a table in a random assemblage. Their objective was to “pack the photographs in an order corresponding to the beauty of the depicted species from the most beautiful to the least beautiful one”, as we asked them. The order of the pictures in the pack was then coded by numerals from 1 (the most beautiful one) to 123, further referred to as ranks. Although no explicit time limit was given, all the respondents performed the task in about 30 minutes. Each set of pictures was evaluated by a comparable number of respondents: 77 (25 men), 85 (31), 77 (27) and 75 (25) for sets A, B, C and D, respectively. Altogether, we gathered data from 314 respondents; 206 of which were women and 108 were men.

All respondents agreed to participate in the project voluntarily. Each subject provided a written informed consent and additional information about gender, age and their affinity to mammals. The age and gender had no effect on the preferences (MANOVA, all

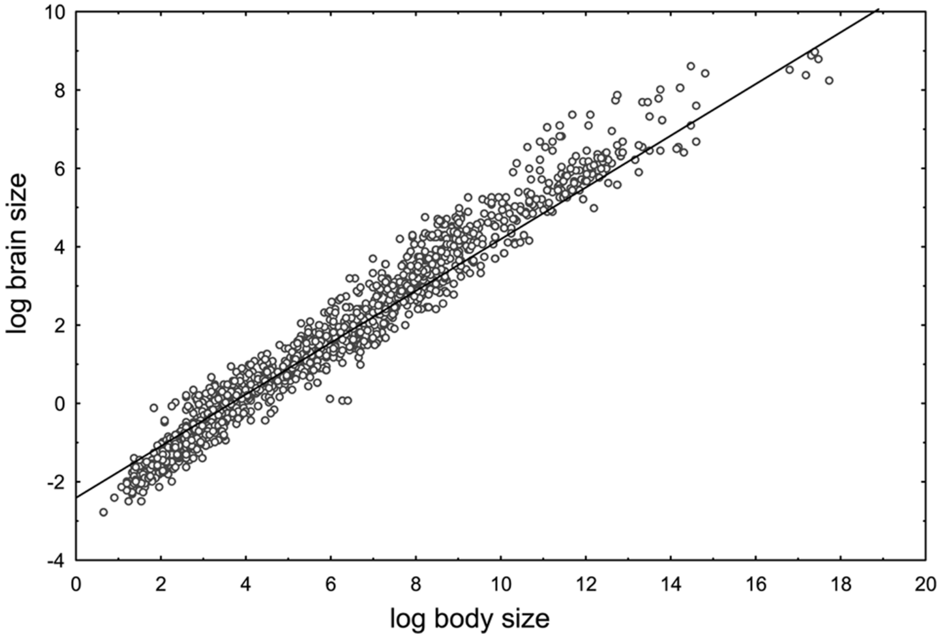

Figure 1. The allometric relationship between the brain and body sizes in 1309 mammalian species. Because the families were represented by an unequal number of data points (species), each family was given an equal weight when calculating the ordinary least-square regression. This correction for biased representation of the families resulted in a line seemingly unfitting the data points (representing species and not families). This adjusted regression line is considerably more reliable for further GLM analyses performed between family level, though. Allometric equation: ln(brain mass) = −0.6601 * ln(body mass) − 2.4100.
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Ps $>$ 0.05), which allowed us to pool the data. The affinity to mammals exhibited too low of a variance (91.85% respondents reported positive affinity to mammals, 8.15% neutral and 0 negative) to allow reliable testing. The experiments were performed in accordance with the European law and were approved by The Institutional Review Board of Charles University, Faculty of Science (No. 2009/2).

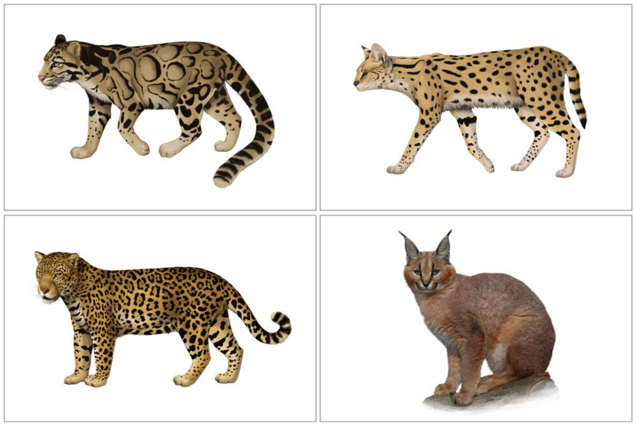

Figure 2. The pictures of the representatives of the family Felidae (the second most preferred family out of 123 examined ones). It illustrates the variation of body positions among four tested sets of pictures (for details see under Materials and Methods): clouded leopard *Neofelis nebulosa* (top left), serval *Leptailurus serval* (top right), jaguar *Panthera onca* (bottom left; pictures painted by Silvie Lišková) and caracal *Caracal caracal* (bottom right; photo from the archive of the Zoo Prague).
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In order to quantify and test congruence in species ranking provided by different respondents and/or to compare sets composed of different species, we adopted Kendall's Coefficient of Concordance (W) as implemented in SPSS v.16.0 [66]. There was considerable congruence among the respondents in all four sets of pictures; W coefficients were 0.206, 0.264, 0.224 and 0.334 for sets A, B, C and D, respectively (all $p < 0.001$).

Prior to further analyses, the raw ranks were transformed as follows: each value was divided by the number of evaluated families (123) and square-root arcsine transformed to improve its statistical distribution. Next, we computed the mean transformed rank for each set and family. Mean transformed ranks computed for individual sets were mutually significantly correlated ($r^2 = 0.334$, 0.450, 0.401, 0.324, 0.449 and 0.420 for A vs. B, A vs. C, A vs. D, B vs. C, B vs. D and C vs. D, respectively; all $p < 0.0001$). This allowed us to compute family means from the mean preference ranks obtained for partial sets of pictures and to further use this variable as a simplified measure of aesthetic attractiveness of the family for humans. The numeric values of this variable were positivized (multiplied by -1) to make the explanation of the results more intuitive.

We included another explanatory variable in preliminary analyses: whether the family is mainly diurnal or nocturnal/fossorial. However, this variable correlates with the body size ($r = -0.51$), and when the influence of body size is removed, the factor itself explains neither of the analyzed dependant variables. As such, we removed it from further analyses.

Statistical treatment

In order to examine the effects of species richness, body size, attractiveness, and brain size on dependent variables, we generated General Linear Models (GLMs) in R 2.8.0 [67]. In the case of the proportion of zoo species, we adopted the binomial model with logit link function and Chi – square tests. We used the Gaussian distribution with identity link in remaining analyses. AIC criterion was used to reduce the original full models. The simplified model was also compared to the previous model by the ANOVA test to verify that the change in residual deviance was not significant ($P>0.05$).

Because species data are not independent as a result of shared phylogeny among more closely related taxa [68], we also carried out a phylogenetically controlled analysis using the independent contrast method [69]. For the purpose of this analysis, we used a phylogenetic tree of families compiled from recent studies dealing with molecular phylogenies. The main branching was adopted from Bininda-Emonds [70] and Arnason et al. [71], while specialized studies were used to improve the branching of partial crown taxa: Marsupialia [72], Xenarthra [73], Cetartiodactyla [74], Carnivora [75], Madagascar carnivores [76], Rodentia [77], Hystricognathi [78], Platacanthomyidae [79], Muridae [80], and Primates [81]. When phylogenetic information was equivocal, we resolved the tree in accordance with the conventional taxonomy. The independent contrasts of the arcsine-transformed mean preference rank, log-transformed WZPS, species number and body mass were computed using COMPARE, version 4.6b [82]. All branch lengths were set to 1 because the corresponding estimations were not available. Thus, for the contrasts analysis, we assumed the applicability of the punctuational model of evolution. The diagnostic proposed by [83] revealed that the contrasts were appropriately standardized. The multiple regression analyses based on independent contrast scores were performed in Statistica 6.0. [84] and constrained to pass through the origin [83].

Results

The analyzed zoos kept 179 868 mammals belonging to 1048 species and 103 families. The most represented families belonged predominantly to the carnivore-ungulates, primates and Xenarthra-Afrotheria clades (Appendix S1).

The highest aesthetic attractiveness was found in the large sized mammals (families Ailuridae, Felidae, Phascolarctidae, Ursidae, Giraffidae, Elephantidae, Equidae, Macropodidae, Mephitidae, and Cervidae). In contrast, the least preferred mammals (families Notoryctidae, Bathyergidae, Chrysochloridae, Spalacidae, Caenolestidae, Solenodontidae, Talpidae, Ctenomyidae, Geomyidae, and Dasypodidae) were predominantly small subterranean (fossorial) creatures with reduced eyes.

Proportion of zoo species

GLM revealed that the proportion of zoo species is associated positively with body size, attractiveness, and brain size, and negatively with species richness (all $Ps<0.0001$). This result was confirmed when the original variables were replaced by their independent contrasts and treated by a multiple regression through the origin (Table 1a, Figure 3).

Mean population size

Mean population size of zoo species was associated positively with body size ($P=0.0001$) and attractiveness ($P=0.0008$). Only the effect of attractiveness was confirmed by the independent contrast analysis ($P<0.0001$; Table 1b, Figure 4a,b).

Number of zoos

Both GLM of original data and multiple regression of independent contrasts agreed that the mean proportion of zoos keeping the species was significantly predicted by the body size ($P<0.0001$ and $P=0.0104$, respectively) and attractiveness ($P=0.0045$ and $P=0.0002$, respectively) of the animal (Table 1c, Figure 4c,d).

Number of conspecifics per zoo

GLM revealed negative effect of body size ($P=0.0016$) on the mean number of conspecifics kept in a zoo. This effect was confirmed by multiple regression of independent contrasts ($P=0.0002$). The latter analysis also revealed negative effect of species richness ($P=0.0318$; Table 1d, Figure 4e,f).

Discussion

We analyzed the representation of mammalian species in the WZC in the year 2011 and we found that it was very poor and highly selective, comparable to its state in 2009. [18] The list of currently recognized mammalian species [49] contains 5334 extant species, but only 1048 of them (16%) were actually present in the WZC. There were twenty families that were entirely absent in the WZC. Such selectivity may not only affect the putative conservation value of zoo populations, but it may also warn us about the existence of a large bias in species selection for conservation in general.

The selection of species into the WZC is determined by decisions made by humans, and although the selection criteria might be different, we may still assume that the psychological drives behind such selection are the same or similar to those for the selection of species for conservation and reintroduction. Such conclusion is supported by the fact that, between the years 1992–2009, out of the 12 evaluated reintroduced mammalian families, 11 of them are in the top-half when taking brain size (EQ) or attractiveness into account (for the list of reintroduced families with detailed published results, see Appendix S4). The "intelligent" and "beautiful" animals seem to be favored in human decision-makings. Moreover, many conservation programs strongly depend on financial support by the public, and it is most appropriate to assume that their decisions which species to support and which not to is driven by similar factors. Therefore, a deeper understanding of the factors that affect various aspects of the WZC is very important.

It was previously demonstrated that large species selectively attract human attention and conservation efforts [85,86]. We confirmed that the body size affects fundamentally all components of mammalian representation in the WZC. Mammalian species characterized by a large body size have a higher probability to be included in WZC. They tend to be represented by more numerous populations and they are also kept by more zoos. Because the material cost of keeping animals increases with the body size of the animal (Balmford 1996), the preferential representation of large mammals in the WZC is an interesting phenomenon. The metabolism (and thus the amounts of food and feces) and the required area of enclosure exponentially increase with the body size to about ¾ (0.72; [87,88]; for review see [89]) and 2/3 (i.e., the length of the suggested enclosure is roughly proportional to the body length of the animal in breeder's guidelines, e.g., [90]), respectively. The fact that keeping a large species is constrained by the available space and expenses is further illustrated by our results suggesting that the number of conspecifics per zoo tends to be smaller in species of a larger body size. However, it seems that the zoos are able to overcome these constraints and selectively keep large animals because these attract more visitors and thus secure countervailing income ([91]).

In our previous study, we performed a separate analysis of the WZC of selected mammalian clades and we demonstrated that human preferences affect the WZC positively in basal mammals

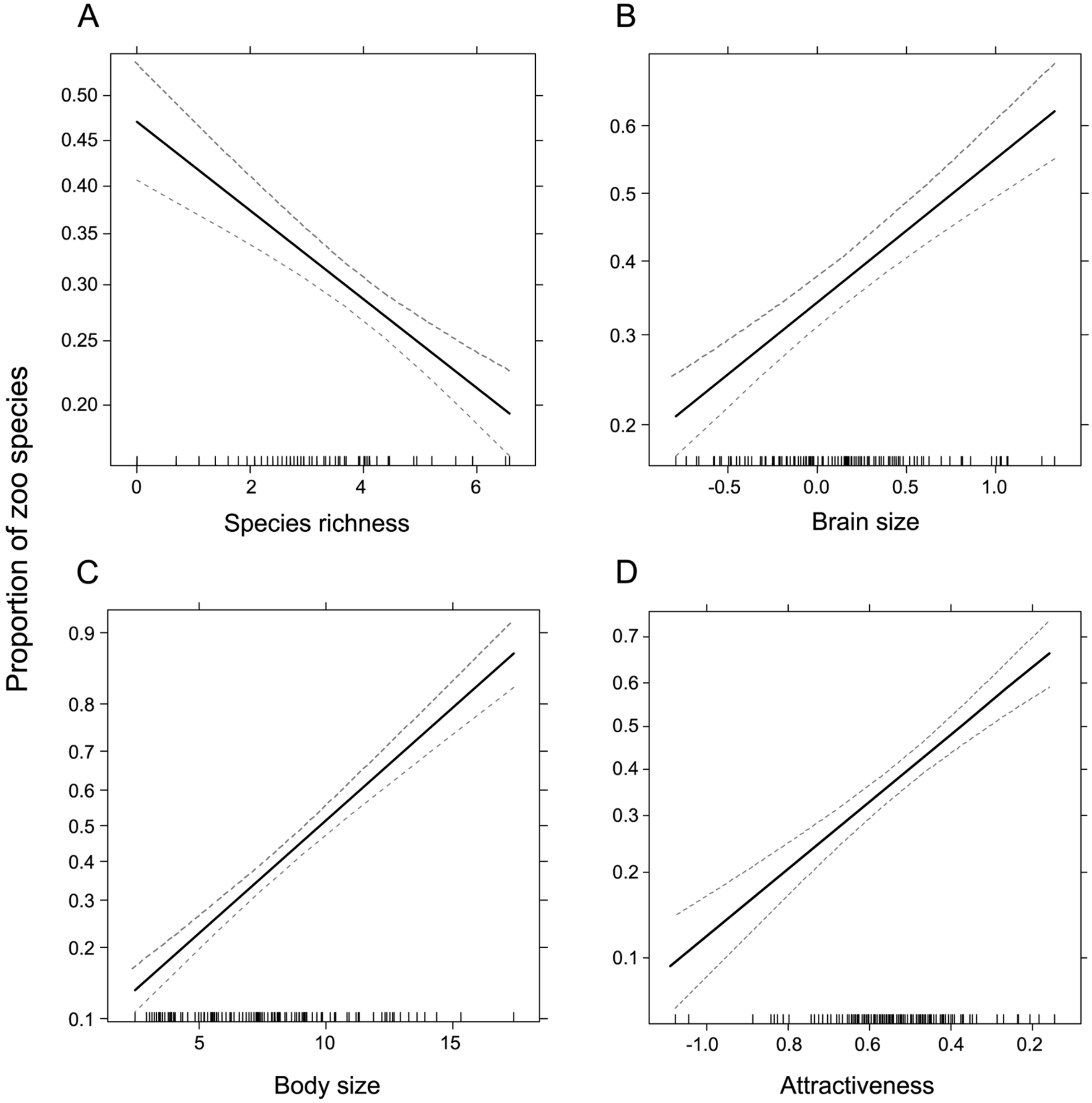

Figure 3. The proportion of zoo species as predicted by GLM. The effects of species richness (a), brain size (b), body size (c), and attractiveness (d). The dependent variable is the number of species kept in WZC scaled to the total number of extant species of a given family. This binomial variable reflects the mean probability that a species is kept in at least one zoo. For the definition and transformation of the explanatory variables see under the Material and methods section.
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and Laurasiatheria [17]. The results of this study first show this relationship across all mammalian families; the species belonging to aesthetically attractive families have a higher probability to be included in the WZC, and they tend to be represented by more numerous populations as well as being kept by more zoos.

The positive effect of the encephalization index on the representation of mammalian species in the WZC predicted by [47] was only confirmed in the case of the proportion of zoo species. Apparently species of small-brained clades have a higher probability to be entirely omitted by the world zoos and their managers and curators. In agreement with Portman, the overall brain size (non-human primates: [92]), relative brain size (executive brain size: [93]; residuals: [94]) or the encephalization quotient, $EQ = E_a/E_e$, indicate the extent to which the brain size of a particular species E_a deviates from the expected brain size E_e, and are, to some extent, good predictors of so-called ''intelligence'' of a mammal (for a review, see [95]).

However, the exact definition of the term ''intelligence'', or higher cognitive abilities, is ambiguous. There are two main conflicting views: the adaptive specializations theory [96], saying that ''intelligence'' includes various learning and memory processes, which lead to adaptations for specific ecological task resolutions; and the general process view of ''intelligence'', described by the existence of general associative-learning abilities, which differ quantitatively among species [97]. A new, consensual theory describes ''intelligence'' as a behavioral flexibility [95] manifested in quick problem-solving task or number of innovations [94]. Fagen [98] assumed that the number of innovations and play

Table 1. The parameters of the reduced general linear models examining the effects of species richness, body size, brain size and attractiveness on dependent variables reflecting the representation of mammalian species in WZC.

A.	Anova					Coefficients	Independent contrasts		
	Df	**Deviance**	**Resid.Df**	**Resid.Dev**	**P**	**Estimate**	**Beta**	**B**	**p-level**
NULL	122	1855.22							
(Intercept)						−0.447			
Taxonomic uniqueness	1	333.04	121	1522.18	<0.0000	−0.199	−0.309	−0.063	0.0001
Body size	1	770.76	120	751.42	<0.0000	0.257	0.363	0.059	<0.0000
Brain size	1	81.73	119	669.69	<0.0000	0.861	0.176	0.165	0.0221
Attractiveness	1	71.33	118	598.36	<0.0000	3.178	0.242	0.582	0.0020

B.	Anova					Coefficients	Independent contrasts		
	Df	**Sum Sq**	**Mean Sq**	**F value**	**P**	**Estimate**	**Beta**	**B**	**p-level**
(Intercept)						11.152			
Body size	1	383.31	383.31	16.9380	0.0001	0.468			
Attractiveness	1	272.03	272.03	12.0210	0.0008	12.499	0.389	16.375	<0.0000
Residuals	100	2263	22.63						

C.	Anova					Coefficients	Independent contrasts		
	Df	**Sum Sq**	**Mean Sq**	**F value**	**P**	**Estimate**	**Beta**	**B**	**p-level**
(Intercept)						2.336			
Body size	1	44.23	44.23	38.2475	<0.0000	0.188	0.237	0.145	0.0104
Attractiveness	1	9.75	9.75	8.4308	0.0045	2.366	0.350	3.416	0.0002
Residuals	100	115.65	1.16						

D.	Anova					Coefficients	Independent contrasts		
	Df	**Sum Sq**	**Mean Sq**	**F value**	**P**	**Estimate**	**Beta**	**B**	**p-level**
(Intercept)						3.663			
Taxonomic uniqueness							−0.209	−0.152	0.0318
Body size	1	11.02	11.02	10.5723	0.0016	−0.129	−0.370	−0.193	0.0002
Attractiveness	1	2.17	2.17	2.0789	0.1525	−0.001			
Residuals	100	104.20	1.04						

a) Proportion of extant species kept in WZC.
b) World zoo population size per species in WZC.
c) Proportion of zoos keeping the species.
d) Individuals per Zoo Keeping the species.

The results of the phylogenetically adjusted analyses (multiple regression of independent contrasts performed through the origin) are also included. For the definition and transformation of the variables see under the Material and methods section.

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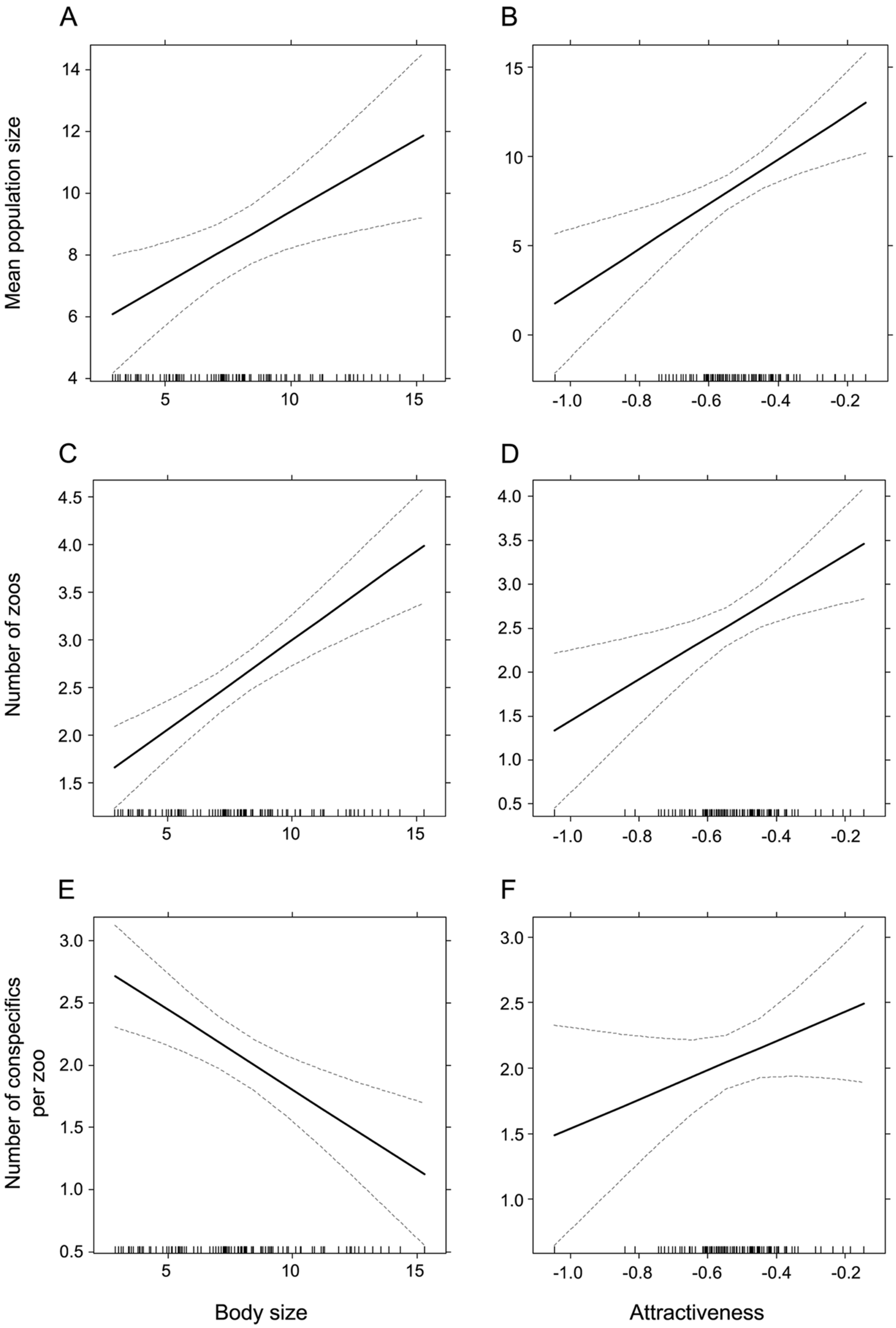

Figure 4. The effects of body size and attractiveness. The effects of body size and attractiveness on the mean population size (a,b), number of zoos (c,d) and number of conspecifics per zoo (e,f). The mean population size: The world zoo population size (square-root transformed) per species present in WZC. The number of zoos: The natural log-transformed mean number of zoos keeping the species. The number of conspecifics per zoo:

The mean number of conspecifics per zoo keeping the species. The families not represented in WZC were excluded from the analyses. For the definition and transformation of the explanatory variables see under the Material and methods section.
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has close or causal relationship. In mammals, the large-brained taxa are more likely to contain species that play more often [99], and playful and active animals are more attractive to zoo visitors (e.g., Felidae: [100]). The attractiveness of animals with interesting behavior was also confirmed in [60], which reported higher willingness to support birds with special behavioral characteristics, e.g., courtship rituals.

Species richness of a family has a negative effect on the proportion of zoo species, the mean population size, and the number of conspecifics per zoo. Thus, the zoo curators tend to avoid simultaneous keeping of species belonging to the same family. This can be explained by human tendency to categorize mammals into primary cognitive categories frequently joining multiple scientific species into a single unit. Ethnobiologists repeatedly demonstrated that the primary units of human categorization of animals correspond to so-called "generic names" (for a review see [48]). These are one-word terms describing a typical species of a "genus"; additional species names are derived by adding the adjectives.

The knowledge of the factors affecting the selection of animals in the WZC might be applicable to a broad array of efforts influenced by human-induced selection of species. Once we become aware of it, we may adjust future planning of conservation projects to lead them into a better success, saving both time and finances along the way. Zoo curators may intentionally try to select unattractive, but needful, endangered species along with the attractive ones to be included in their collection to fulfill both the advisable ex-situ conservation role and the expectation of zoo visitors. For example, the least attractive mammalian family of the marsupial moles (Notoryctidae) includes only two species, both endangered according to the IUCN status. They are not kept in any zoo at present, and their future is very insecure unless selectively focused on, going against the unwanted bias. Another way to fulfill both of the roles is to select the most attractive species out of a list of species with a similar threat status. For example, there are both attractive and unattractive species within some animal families, as shown by Frynta et al. [43], on all 367 parrots of the family Psittacidae. From within such families, endangered yet attractive animals could be included in the WZC.

Whatever the conservation priorities are ([101]), if there is an existing tendency to prefer the conservation of some species over the others, the factors affecting this tendency should be known. Nowadays, the preservation of biodiversity is a widely accepted priority for species conservation (e.g., [102,103]). This priority is in conflict with human tendency to pay the proper attention selectively to large and attractive animals. However, the awareness of this selectivity may help the conservationists to improve their strategies. There are many small and/or unattractive species that are phylogenetically significant and thus key for biodiversity preservation. With only little or no support received, these species could be lost forever. A good example of possible application of species attractiveness assessment is in the case of the EDGE species (Evolutionarily Distinct and Globally Endangered [104]) – a selection of threatened species with high biodiversity value. Once known, the unattractive species putatively lacking public awareness and support could receive special attention by conservation specialists.

Moreover, knowing that the attractiveness of an animal itself plays a major role in a human's decision-making, they may be able to intentionally select the "beautiful" species not only to raise the zoo's popularity among visitors, but also to use such species in educational programs, or present them as flagship species for further in-situ protection of wildlife. A reasonable definition of flagship species was proposed by Verissimo et al. [105] (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". Smith et al. [106] found that large bodied mammalian species with forward-facing eyes are most frequently used as flagships by non-government conservational organizations (NGO) and, based on these characteristics, they suggested five critically endangered species with a strong potential to serve as good flagship species: the African wild ass, tamarau (dwarf buffalo), pygmy raccoon, Talaud bear cuscus and Pennant's red colobus. When compared with our results, four of these animals belong to attractive mammalian families positioned in the top-half rank of the attractiveness (up to the fifth position; Equidae 7, Bovidae 20, Procyonidae 38 and Phalangeridae 50). The high attractiveness of threatened species per se may further increase the potential of these or similarly selected species to serve as flagships. In contrast, the Pennant's red colobus belongs to the family Cercopithecidae which appeared to be rather unattractive (placing the 94th rank position). However, this family contains a large number of species the attractiveness of which may vary. A more detailed analysis on a species level could help to determine the actual attractiveness of the red colobus, or help find a species with similar attributes but higher attractiveness to be used as a flagship instead.

A properly selected flagship species may convince the public to donate more money for conservation, just as demonstrated by [107]. In their study, the respondents were willing to pay more for the conservation of an otter than that of a water vole. This is in accord with our finding that otters from the family Mustelidae are more attractive to humans, placing 34th in the preference ranking, than water voles from the family Muridae, which placed as far as 73rd (See Appendix S1). Also, when lumped together into one conservation program, these two animals received less support than otters alone [107]. This may be explained either by the sole presence of the unattractive animal in the program, which pushes the respondents back, or by the rising complexity of the message that was presented to the respondents. Either way, if conservationists select a single highly attractive animal to be presented to the public as a messenger for conservation planning, it may raise the success of the project. This may be caused both by raising the financial support of the project by people living far away from the place of question, or by local people who may re-think their view of the natural riches surrounding them [37]. Furthermore, we found that the attractiveness of snakes as perceived by humans is shared among such different cultures as Europeans and villagers from Papua New Guinea [62]. Another study confirmed these results on people from the five main inhabited continents [63]. If applicable to other animal taxa, the message from a single flagship species could touch people worldwide as well as people local to the conservation project. Although local communities face various problems with potential flagships that trigger conflicts as predatory animals, competitors or pests ([108,109]), the attractiveness may play its role when the flagship is selected from harmless, non-conflicting species. In case of highly attractive animals, the attractiveness may even outweigh the possible conflict. The family Equidae placed 7th rank of attractiveness in our study and the reintroduction of the Przewalski horse was well-accepted by local people in Mongolia (Hustain Nuru; Kůs E., Zoo Prague, personal communication) despite it being a competitor for domestic horses ([26]).

In conclusion, this study shows that the predictors associated with human attention, especially body size and aesthetic attractiveness, have a substantial effect on the composition of the WZC. In the 21st century, it is of an utmost importance to pay attention to the biodiversity preservation, and it might be up to the worldwide zoological gardens to play a significant role in this task. This is especially because zoos have the capacity to hold numerous species, a capacity larger than any other institution, together with the knowledge about the breeding of various species and properly managed studbooks. Whether they utilize this potential is a vision of the future. However, for the zoos and conservationists whose intentions are to conserve biodiversity, our study reveals one of many factors – the human factor – that may fundamentally affect the conservation efforts. Thus, conservation biologists should consider these psychological factors for proper management of the "Ark".

Supporting Information

Appendix S1 The dataset used for statistical analyses, sorted by attractiveness from the most attractive family to the least attractive one. (See under the Materials and methods section for the definition of the variables.)
(XLS)

Appendix S2 The forms and species listed in the ISIS database that were excluded from (or added to) the analysis.
(PDF)

Appendix S3 The literary sources of brain size data.
(PDF)

Appendix S4 Review of mammals reintroduced during the years 1992–2009. We collected journals and book sources of mammalian reintroductions within the years 1992–2009 with detailed information about the reintroduction events.
(PDF)

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Author Contributions

Conceived and designed the experiments: DF EL. Performed the experiments: DF OS SL EL. Analyzed the data: DF OS SL EL. Wrote the paper: DF OS SL EL.

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