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Ph.D. thesis

Human preference to animal species and its impact on species conservation

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Prohlašuji, že jsem se v uvedených publikacích a rukopisech podílela na všech fázích přípravy, od sběru dat až po sepsání rukopisu, společně se školitelem. U prací IV, V, a VII také ve spolupráci s Mgr. Evou Landovou, Ph.D. a VII s Mgr. Silvií Liškovou. Ostatní spoluautoři přispěli zejména sběrem primárních dat.

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Introduction

The dissertation thesis deals with the phenomenon of human perception of animal attractiveness. I tested human aesthetic preferences to selected groups of animals across major vertebrate taxa, and snakes in particular, and compared preferences of people belonging to distant cultures/ethnics. The aim was to bring new knowledge to the little studied area of human aesthetic approach to other kinds and to test its suspected consequences to species conservation.

Animals have been an integral component of the human environment and culture from the very beginning of our species and perception of their aesthetics has become part of our attitude to them. The oldest known art are pictures of animals on the walls of the Chauvet Cave in France. Hundreds of pictures date back to 35,000 years ago (Z 2011) and contain at least 13 different species of animals. Some of the animals were typically hunted or used by Palaeolithic hunters, such as horses, cattle, and reindeer. However, others were mostly predatory animals including some rarely or never found in other ice age paintings: cave lions, panthers, bears, owls or cave hyenas. The high proportion of depicted species of hardly any utilitarian value suggests that the Upper Palaeolithic hunter-gatherers awarded some animals with ritual or magical aspect and these animals played a predominant role in their mental world. Appearance and aesthetics of animals, as well as their ecology and abilities, already likely determined the position of the species in human cultures.

Aesthetic judgements are a pervasive element of human perception that eases dealing with diverse and complex environment. We have evolved shared preferences for a range of evolutionary relevant stimuli such as appearance of other humans or favourite landscapes. Wilson (1984) dealt with human attachment to living things and aesthetic feelings to nature and other kinds in his “biophilia” theory. The importance of other animal species to humans is underlined by the fact that we devote an increased attention to animals over other stimuli (Lipp et al. 2004, New et al. 2007), and have virtually the same object processing efficiency (accuracy and speed) of animals and human faces (Rousselet et al. 2004). Moreover, humans likely possess an innate concept of the structure of the animal world. Illiterate hunter-gatherers are able to name and categorize animal species in a very similar way as contemporary scientists (Berlin 1992). As young infants as three months already show categorical perception of animals (Eimas and Quinn 1994) and four year olds already consider internal properties of animals to be more important than superficial ones when deciding what animals are of the same kind (Diesendruck 2001). Evolutionary psychologists suggest that our mind is evolutionarily prepared to respond to animal stimuli (Barkow et al. 1992). If aesthetic preferences to other kinds were part of the human mind that evolved prior to geographic and cultural diversification of our species, people of distant cultures would probably share their aesthetic preferences to animals. One of the aims of this thesis was to test this assumption.

When it comes to the attractiveness of other living kinds to humans, we conspicuously tend to like some taxonomic groups better than others (e.g. Morris 1967, taxonomic bias in reintroduction programmes: Seddon et al. 2005). Even very young infants already prefer attractive animal faces to unattractive ones (Quinn et al. 2008). Many hypotheses were proposed (e.g., Morris 1967) to explain the unequal attractiveness of animal species for humans: most studied the effects of juvenile body proportions (Gould 1979, Pittenger 1990), form close to an average appearance (Halberstadt and Rhodes 2003) and conspicuous coloration (e.g., Van Hook 1997, Stokes 2007). We have also analysed the preferences for certain body traits and effects of colouration on the perceived attractiveness. Although colour perception is a highly complex phenomenon, influenced by the context (Clydesdale 1993), we may (committing a gross generalisation) abstract that people positively evaluate bright colours and negatively dark ones, and this is more pronounced in females than males (Hemphill 1996; Boyatzis and Varghese 1994). Adults tend to like the most blue colour, followed by green (usually second) and red third. In comparison, children like better yellow and rank lower green colour (see review Crozier 1997). Perceptual categorisation is another factor shaping colour preferences (Goldostone 1995). Leaving apart the conflict between Whorfian linguistic relativists (cf. Whorf 1956) and Berlin and Kay (1969) with their successors who advocate for universal perceptual constrains, we shall particularly take this factor into consideration in cross-cultural comparisons. For example, colour perception is known to differ significantly between Papua and Europe (Kay and Regier 2007), the two regions where we tested and compared human aesthetic preferences to snakes. Furthermore, terminology devoted to animal patterns in a given language is known to affect their discrimination (Goldstein and Davidoff 2008).

To determine human aesthetic preferences to other animal species, I used snakes as a pilot taxonomic group. Snakes are desirable experimental objects as they do not display much variance in morphotype but they still vary in appearance (colour and pattern that may be coded), and lack anthropomorphic features that are known to modify human preferences. Importantly, snakes represent valid biological stimuli; according to Isbell (2006) snakes, especially the constrictors, were the primary source of predation in early primate evolution. Humans are assumed to devote preferential attention to snakes over other objects (e.g. Őhman and Mineka 2001, LoBue and DeLoache 2008) although this has been criticised in methodical grounds by authors who bring evidence for an increased attention to animals in general (e.g. Lipp et al. 2004, New et al. 2007). Eight months old infants are able to distinguish between snakes and flowers (LoBue and DeLaoche 2010) but not between snakes and other animals (DeLaoche and LoBue 2009). This may also support the theory that we possess rather animal-specific mechanisms that drive our attention. I believe that an increased attention eases the assessment of animal beauty and enhances the congruence among people. Undoubtedly, snakes belong to the most feared animals among adults (Arrindell 2000, Davey 1994) as well as children (Morris 1967), and they are one of the most common causes of human phobias (Davey 1995, Öhman and Mineka 2003). We share an easy elicitation and learning of snake fear with many primates, e.g. macaques (Ramakrishnan et al. 2005; Coss et al. 2007) tarsiers (Gursky 2005, 2006), or marmosets (Clara et al. 2008). According to Bracha (2006), humans have shared a general snake phobia with most simians and such a fear of snakes has already been present in the common ancestor. Herzog and Burghardt (1988) explain ophidiophobia by the conditions of African savannas where it might be difficult to quickly identify whether the encountered snake is poisonous or not. This thesis deals with the question, whether the fear affects human aesthetic appreciation of the snake species, and also explores the meaning of warning aposematic colouration to humans.

Last but not least, I would like to make an introduction into practical consequences of human selective interest and aesthetic preferences to other species. Their study forms about a third of this thesis. In the course of the last few thousands of years, these consequences dramatically differed. Some species gained protection being sacred, others, having supposedly magical powers, rather suffered (and suffer) from hunting for magical or medical purpose. The existence of some attractive species in the wild has been threatened by human interest in them (e.g. hunting for skin, trophy, captive breeding). While this still holds true in some rather rare cases, at present much more danger to most species poses loss of habitat (Bennett and Owens 2002) combined with the lack of human interest. 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, and vulnerable species inevitably compete for it.

Distribution of any conservation effort and willingness to support the species varies greatly from species to species. Funding decisions by FWS (The U.S. 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 and 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 (Gunnthorsdottir 2001), larger in size and resembling humans (Samples et al. 1986). Animal taxa also differ in their social construction and political power (expressed as, e.g. a 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).

The situation of zoological gardens worldwide is somewhat similar. Although, human-animal relationships in zoos is a more complex phenomenon (Hosey 2008), the popularity of zoo animals may be successfully explained by simple traits as body size (Ward et al. 1998). With respect to the excess of species in need of protection and the fact that the accommodation capacity of zoos is strictly limited (Soulé 1986, Wilson 1992, Tudge 1995), we may see zoos as luxury hotels in the world full of animal refugees. The winners may be the species that satisfy human aesthetic and emotional requirements, rather than those most vulnerable. To test this suspicion we analysed the zoo population sizes worldwide and studied possible bias in favour of certain taxonomic groups, endangered species or larger or more attractive species. We obtained some interesting straightforward results.

Although the 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 a small number of compared species. This thesis aims to provide quantitative studies carried out on a finer taxonomic scale.

Summary of results

The thesis cosists of five publications in peer reviewed journals (mean $\mathrm{IF}_{5\text{-year}}$: 2.4), a manuscript and a book chapter. Roman numerals refer to the particular study; for the list, please see table of contents.

I have focused on human aesthetic requirements on other species and the main aims of my research are to address the questions: (**A**) Do humans share aesthetic preferences to animal species? (**B**) What animal traits account for human preferences? (**C**) In what way does the aesthetic evaluation happen? (**D**) What are the consequences of human aesthetic preferences to species conservation?

As the topic has never been studied before, the first thing to say is that a consistent human aesthetic preference to animal species (hereafter referred as preference) proved to exist in all our experiments. The congruence among respondents depends on the taxonomic group evaluated and also on the studied population. Nevertheless, the respondents always significantly agreed with each other on what species are beautiful and what are ugly. Contrary to expectations, I generally did not find sex differences in preference. To measure the perceived beauty I used sets of live animals and standardised photographs/pictures and each respondent viewed one set at a time (16 pictures in case of children up to 34 pictures in case of adult respondents). Respondents were instructed to sort the animals in rank order corresponding to the perceived beauty. The control experiments ruled out the effect of snake's body position in the picture and within-species variation (**I**) and 2D representations of snakes proved to be an equivalent substitute for live animals (**V**).

(**A**) Do humans share aesthetic preferences to animal species?
Being sure that the preferences exist and having a reliable method of quantifying them, we focused on the question whether aesthetic ranking of snake species is broadly shared among human cultures. The question stems from the hypothesis that we may have inherited relevant emotional and perceptual mechanisms (forming preference) from our ancestors (whose fitness and social status may have been enhanced by possession of certain animals or their body parts). To test this hypothesis we examined human preferences to 32 boid species in populations of five continents: Czech Republic and Papua New Guinea (**I**), Bolivia, Philippines, India – Rajasthan and Delhi, Malawi and Morocco (**II**). These populations/ethnics obviously possess distant and disparate cultures and differ in their attachment to nature and experience with snakes. It seems reasonable to expect at least slight cross-cultural differences in the aesthetic value of snake species. We found a small but significant effect of population and European data (Czech Republic) contributed the most to the cross-cultural differences (**II**). On contrary, correlation of Czech and Papuan preference seems almost perfect and accounts for 76% of variation (**I**). This appears as a very interesting result, considering profound differences of the two cultures, distant gene pools (Cavalli-Sforza et al. 1994) or different colour categories (Kay and Regier 2007) and thus colour perception. Not to mention the fact that five of the tested species are distributed in Papua New Guinea and Papuan

respondents were genuinely experienced with snakes. To be able to compare the correlation coefficients among the eight populations, mean preferences in each particular population were correlated with corresponding measures computed from the pooled remaining data. All resulting correlations were close, positive and statistically significant (**II**) and especially Bolivia, Papua New Guinea and Philippines formed a coherent group.

We can conclude that there are cultural differences in the aesthetic preference to other kinds, but these are surprisingly small considering the differences mentioned above. Observed congruence seems to rather support the theory that we share a considerable component of aesthetic preferences to certain living kinds. However, such a congruence may apply to objects other than snakes/animals too. Similar cross-cultural studies have been done on aesthetics of commercial products and cross-cultural differences were usually reported (e.g. Limon et al. 2009, Pearce et al. 2010). However, these experiments cannot be easily compared to ours, because they were designed to detect the differences. At present I prefer the interpretation that humans share a deep-rooted emotional concept of animals and follow common cues when judging their aesthetics. And this probably increases the cross-cultural agreement. Regardless the cause (adaptive or not), the revealed cross-cultural congruence in aesthetic preferences is substantial and non-trivial. Its phylogenetic interpretation is that the preference has remained unchanged during last dozens of thousands of years.

Exploring limits of human aesthetic preferences to animals, I also attempted to determine to what extent these are present in childhood. I tested preferences of pre-school children aged 4-6 years and compared them to adult preferences (**III**). All respondents evaluated 56 boid species according to perceived beauty. For restricted abilities of children, I had to split the pictures in four blocks. I am aware of the statistic weakness of this setting, however, I did not find better method suitable for young children. There was a significant congruence among children. Although MANOVA revealed small age differences, mean preferences of children and adults significantly correlated in individual blocks (except for one) and in the pooled data. As in any attempt to prove and measure similarities (cross-cultural similarities included), it is very hard to settle on the point where lies the boundary between difference and congruence. In the light of the level of attention of nursery children during task which performance evoked process of randomisation, the results appear like congruence. Regarding the factors reliable for the observed age differences, I will go into more detail in the following paragraphs.

(**B**) What animal traits account for human preferences?

What is it in the animal that we see as beautiful? I have explored the issue at two different levels: (i) within a coherent group of snake species and (ii) across major vertebrate taxa except amphibians and fish.

(i) Study of preference to animals on a fine taxonomic scale allows coding of animal traits and statistical analyses of their effect. I focused on boid snakes (**III**) and in more detail on milk snakes, both live (**V**) and depicted (**IV**, **V**).

In boid snakes we coded body size, coefficients of body shape and presence of colours, pattern and shine (**III**). Adult respondents preferred animals with bright colours, relatively slim neck and presence of pattern (the strongest predictor) and the GLM model explained 68.8% of variance. Adults and children significantly differed only in their preference of relative neck width. Children preferred species with relatively thick neck and inconspicuous head. These were usually also small species (e.g. Erycinae), harmless to children. On the other hand, snake proportions preferred by adults characterise rather bigger species that probably posed more danger to children than adults during our evolution in African savannas.

In the experiment with live milk snakes we used the body weight, presence of black, red and white/yellow colours and striped pattern to explain the aesthetic preference and also the perceived fear (**V**). As more attractive were found bigger animals with higher proportion of red and lower proportion of black colour. The fear of live snakes increased with snake's size and higher proportion of black colour. Aposematic pattern was sometimes perceived as attractive and usually as dangerous. Having no co-evolutionary experience with deadly coral snakes (milk snakes are their mimics), it may be explained by social learning or a universal perception of a warning black-and-white/yellow-red signal that we share with other mammals. Interestingly, the perceived fear does not interact with perceived beauty, the respondents evaluate the species according to the two emotions independently.

We also studied aesthetic preferences to milk snakes using pictures of whole snakes, their heads and skin patterns (**IV**). Although the set differed from the experiment with live snakes in species composition, the results were very similar. Interestingly, the aposematic pattern was liked when seen in a whole snake and considered repellent when only head or skin fragment was being evaluated. There are alternative (not mutually exclusive) explanations. The picture of whole snake may evoke safe distance (aposematic pattern does not matter), repetitive nature of aposematic signal can be distinguished only as whole (attractiveness of repetitive signals), and/or in a detailed view other disruptive patterns (invisible from distance) may appear more attractive.

(ii) We carried out a large analysis of human aesthetic preferences within reptile, bird and mammal taxa (**VII**) and used these data to explain zoo populations worldwide (which is described later). At this scale we only observed following tendencies without statistical analyses. Attractiveness increased with bright colours and pattern, especially in groups that exhibit comparably lower variability in morphology: snakes, lizards, turtles, and most of all terrestrial birds and passerines. Morphology played role as well, i.e. as ugly were perceived snakes with unclearly shaped head, lizards without limbs or turtles with big head (e.g. Platysternidae, Chelydridae). In birds, long legs, long tail, prominent beak, a crest and overall elegance often win our sympathy. The situation of mammals is more complicated; a charming representative of basal mammals or Laurasiatheria looks like a teddy bear (or at least a bear), has a dense fur, round ears and big eyes (Vombatidae, Ailuridae, Ursidae). Apparent colour pattern is also favourable (e.g. leopard, giraffe). Surprisingly, similar tendency repeats in Euarchonta, where nocturnal species with big eyes and ears (e.g. Galagidae, Lorisidae) are more preferred than big apes.

(**C**) In what way does the aesthetic evaluation happen?

This question turned out to have a complex and very interesting answer. The data revealed distinct clusters of species instead of a continuous gradient of the perceived emotion, although the respondents were never asked to categorize the snakes. The classification occurred according to two dimensions and the process resembled an unsupervised categorization (**IV**). In milk snakes, the main clusters were the uniformly black forms (most distinct group), those basically black/brown coloured, and red banded (this groups splits into a small cluster of greyish species and main group of species with aposematic pattern). The species grouped this way in all experiments, with live (**V**) and depicted (**IV**) animals, and irrespective of the evaluated emotion, i.e. whether the perceived beauty or fear was assessed (**V**). This basal branching pattern has also remained virtually unchanged when separate analyses of whole snakes, heads and skins pattern datasets were carried out and/or the clustering methods were altered (**IV**). As this classification structure reflecting the aesthetic preference resembles the one constructed from a matrix of objectively defined characters, it seems that subjective cognitive categories reflect unconsciously but properly the objective similarities.

The respondents categorize the species along two dimensions, but just one of them determines the agreement about what is beautiful and what is ugly (i.e. this axis corresponds to the mean preference – respondents agree also on the polarity of the axis). The interesting point is that the respondents probably categorize first and then establish the polarity of the beautiful-ugly axis (for more detail, please see **IV**).

(**D**) What are the consequences of human aesthetic preferences to species conservation? We focused on species conservation expressed as ex-situ breeding by zoos worldwide. These institutions have the potential to keep sufficient populations of (at least some) species that are substantially endangered in wild to be able to reintroduce them eventually. We asked whether they use this potential or prefer species that best attract visitors. Again, analyses occurred at two levels, (i) within closely related groups of species, and (ii) within higher taxa of mammals, birds and reptile.

(i) We studied zoo populations of boid snakes (**VI**), turtles, pheasants, and antelopes and allies (**VII**) and explained these by species' body size, human aesthetic preference and degree of endangerment (IUCN listing). In case of boid snakes, no significant effects of the conservation status was found. On the other hand, zoo population increased with preference and body length, both factors associated with visual stimulation of visitors (**VI**). We found similar pattern in other groups too. The size of zoo population can be explained only by the human preference in case of turtles, and pheasants and allies, and only by the body size in case of antelopes and allies. The IUCN listings had no significant effect and zoos did not seem to systematically prioritise species with regard to their degree of endangerment.

(ii) Effects of preference and body size on zoo population on a higher taxonomic scale (**VII**). The size of zoo population per species (for all snakes, lizards and tuataras, testudines, basal birds, aquatic birds, terrestrial birds, passerines, basal mammals, glires, Euarchonta and Laurasiatheria) was by far the best explained by the body size. The larger the typical species of the family/subfamily, the more individuals per species are kept in zoos (with the only exception of turtles and basal mammals). On contrary, the aesthetic preference does not seem to play such a crucial role as on a finer taxonomic scale (see paragraph above) – it significantly predicts the size of zoo population only in case of one bird (terrestrial birds) and two mammalian groups (basal mammals, Laurasiatheria). At this scale the effect of attractiveness may be masked by other differences in biological features and the fact that not all families/subfamilies are reliably represented by a randomly selected species.

Zoo collections are clearly biased in favour of birds (higher number of captive species) and mammals (larger population sizes), while reptiles are underrepresented (**VII**). Most of them are kept in very low numbers, the mean size of zoo population is 13 animals for reptiles, 15 for birds and 30 for mammals. The size of zoo population is higher for endangered species in case of birds only, and still such numbers can never make survival of the species in captivity possible. However, it is necessary to reflect the fact that the economics and space available inevitably limit the size of zoo population. Keepers and conservationists may directly benefit from this research by carefully selecting the species to breed, so that they meet both, aesthetic and conservation criteria.

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Ethology

RESEARCH PAPERS

We all Appreciate the Same Animals: Cross-Cultural Comparison of Human Aesthetic Preferences for Snake Species in Papua New Guinea and Europe

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Abstract

We examined the aesthetic perception of animal species in two culturally contrasting societies. Students from the Czech Republic and villagers from Papua New Guinea were asked to rank photographs of the python and boa species according to the perceived beauty of the depicted snake. The ranking of the species in Europe and Papua tightly correlated in spite of ethnic differences that were significant in the case of six species. This result suggesting basic similarity in animal beauty perception between two distant ethnic groups is not only a partial argument for perceptual unity of humankind. This cross-cultural congruence may be important for conservation policies as humans may be predetermined to appreciate and thus support some species more than others.

Introduction

Animals have been an integral component of the human environment and culture from the very beginning of our species. Thus, our mind should be evolutionarily prepared to respond specifically to animal stimuli. Manifestation of this may be innate tendency of humans to affiliate with other species that was recognised by Wilson (1986) and named as 'biophilia'. Nevertheless, we share not only interest in animal species, but also ability to categorize them in a similar way. Even illiterate hunter-gatherers are able to name and categorize animal species in a very similar way as contemporary scientists (Berlin 1992 and references herein). We addressed the question whether cross-cultural congruence also applies to the aesthetic perception of animal species. For this purpose we compared aesthetic preferences towards snake species in European students and Papuan villagers. As a model group we chose snakes that represent biologically valid stimuli and are known to selectively capture human attention even in complex visual displays (Öhman & Mineka 2003).

Papuans have entirely different cultural background than Europeans, and moreover, live in much closer contact with wild animals including snakes. In Papua New Guinea, as everywhere in Australian zoogeographic area, most snake species belong to the family Elapidae and are highly poisonous (O'Shea 1996). Therefore, we expected that aesthetic apprehension of tested species recovered by our research would significantly differ between people from Europe and Papua.

Methods

We collected 32 photographs of boas and pythons, each depicting a typical individual of its species. We set each of the snake bodies on a black background regardless of real size of the animal and printed in format 10 × 15 cm. Our respondents were undergraduate students of the Charles University in Prague (63 men and 20 women born in the Czech Republic) and villagers from Papua New Guinea (63 men and 20 women from Madang and Chimbu provinces) who voluntarily agreed to participate in the project. Each study subject was shown the set of photographs in a random assemblage and asked to rank the species according to the perceived beauty.

The congruence among the respondents was evaluated by non-parametric Kendall's test of concordance that is appropriate for rank-order data (Sheskin 2004). This procedure was computed in SPSS version 16.0 (SPSS Inc. 2007). The ranks of particular species provided by individual respondents were divided by 32 and square root arcsine transformed prior to multivariate analyses and ANOVA. To assess multivariate structure of the data we performed principal component analysis (PCA) in which transformed species rankings were treated as variables. We used discriminant function analysis (DFA) to reveal possible variance between sexes and ethnic groups, applying its combination as grouping variable. Combination of sex and ethnic group Species displaying the highest variance within ethnic groups (*Corallus caninus*) was excluded from multivariate analyses to avoid the problem of predetermination of the last rank. Most computations were made in STATISTICA 6.0. (StatSoft 2001).

We were conscious of possible hidden effects of the position of snakes on the pictures (rolling the body), within-species variation and many different characteristics of the pictures on respondents' apprehension and resulting ranks. The assessments could be also influenced just on the part of respondents' state of mind. We carried out additional testing in Czech respondents to exclude these influences. To check consistency of results, we asked 25 respondents to rank two different sets of pictures ($n = 30$) according to perceived beauty of depicted animals. The sets consisted of the same 30 boid species but differed in the depicted individuals (exhibiting an apparently different position). The picture background was black in both sets and each respondent had 24–48 h break between testing and retesting. Different individuals of the same species obtained nearly the same ranks (Spearman $r = 0.97$; $p < 0.0001$). Thus we concluded that the position of the snake body and qualities of the photograph do not significantly affect resulting ranks (Marešová & Frynta 2008) and if there is any influence of respondents' mood or immediate state, it is trivial.

Results

There was a good agreement among the respondents in ranking the snake species. Non-parametric Kendall's test of concordance was highly significant (Kendall's $w = 0.345$, 0.360 and 0.325 for Czech men, women and pooled sexes, respectively; $w = 0.204$, 0.228 and 0.193 for Papuan men, women and pooled sexes, respectively; all $p < 0.001$). To further explore the data we performed PCA; the first principal component (PC1) accounted for 39.0%, 26.0% and 30.9% in the Czech Republic, Papua New Guinea and pooled data, respectively. The loadings of most respondents (i.e. 166 individuals except for six Papuans and five Czechs) contributed to PC1s in one direction. Moreover, there were tight correlations between PC1s and mean ranks of particular species obtained in Europe, Papua and pooled samples (Spearman $r = 0.97$; 0.99 and 0.99, respectively; all $p < 0.0001$). Thus PC1s may be interpreted as perceived beauty and for further analyses we used mean ranks that we find more intuitive than PCs.

We computed mean species ranks for Czech and Papuan respondents separately and then correlated with each other. This correlation explained 76% of variation ($r = 0.87$; $n = 32$; $p < 0.0001$; Fig. 1). The congruence between Czech and Papuan respondents is reflected also by non-parametric Kendall's coefficient of concordance in a pooled sample ($w = 0.239$; $p < 0.001$). Nevertheless, DFA in which combinations of sex and ethnic group were used as a grouping variable (Wilks' $\lambda = 0.3178$; $F_{(93,395)} = 1.99$; $p < 0.0001$) revealed small but significant sex differences within the European sample ($F_{(31,132)} = 1.92$; $p < 0.0059$). It also uncovered slight differences between ethnic groups ($F_{(31,132)} = 2.28$; $p < 0.0007$ for men and $F_{(31,132)} = 2.36$; $p < 0.0004$ for women); however, these groups overlapped considerably. A total of 16.9% of Czech respondents and 22.9% of

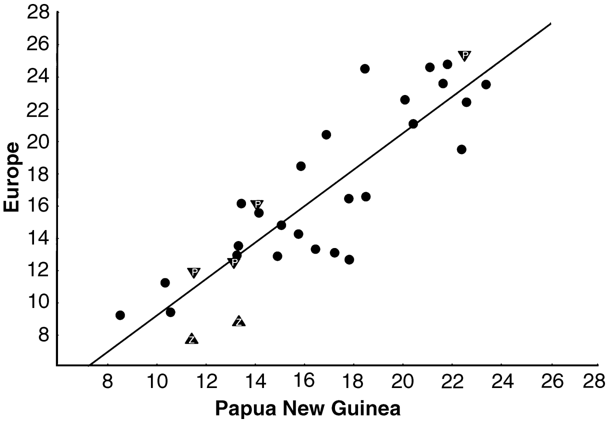

Fig. 1: Relationship between the mean ranks (human preference) of snake species ($n = 32$) obtained in Europe (Czech Republic) and Papua New Guinea. ▼P= species living in Papua, ▼Z= species most represented in zoos.

Papuan respondents were misclassified into the other ethnic group. Separate ANOVAs for each particular species (Bonferoni adjusted) were then performed to test the effects of ethnic group, sex and its interaction on ranking. Significant effect of sex was found in two species: *Corallus annulatus* (more preferred by women) and *Epicrates angulifer* (more preferred by men). Ethnic differences were significant in the case of six species: the Papuans prefer more *C. annulatus, Eryx johni* and *Python timorensis*, whereas the Czech respondents prefer more *Python sebae, Liasis childreni* and *Eryx conicus*.

Discussion

It is almost self-evident that two human populations possessing completely different cultures and distant gene pools (Cavalli-Sforza et al. 1994) should at least slightly differ in aesthetic preferences. We confirmed this hypothesis, however, the rankings of the snakes provided by European and Papuan respondents' exhibit surprising similarity (Fig. 1). Moreover, the slight disparity in ranking the species is not explicable by personal experience and/or the role of the particular species in the local culture, as four of the tested species are distributed in New Guinea and none of them played a significant role in ethnic differences. Thus, not only classification of the animal kingdom but also considerable component of aesthetic preferences for animal species may be universal across humankind. This conforms with the view of evolutionary psychology (Barkow et al. 1992) claiming that the human mind evolved prior to geographic and cultural diversification of our species.

The above-discussed findings suggest that both studied ethnic groups share nearly the same perception of animal beauty. Nevertheless, shared preferences may result from more general perceptual processes that are not specific for animals and/or snakes. There is a question whether respondents really evaluated the animals rather than just the colourful pictures. We have noticed that in particular the Papuan respondents saw the depicted animals as living creatures and discussed a lot about them. Nevertheless, even the congruence in colour preferences would be of relevance as colour perception is known to differ considerably between Papua and Europe (Kay & Regier 2007). If we look at the colouration of the species that were significantly more preferred by one ethnic group, we are not able to trace up the characters responsible for the difference. The appearance of three species that are preferred more by Papuans is quite similar and comparable with the look of those three preferred more by Europeans. The situation is similar with respect to observed sex differences in two species. There are known sex differences in colour preferences (Hemphill 1996) that are, however, not applicable to our results.

Of course, we are aware of the fact that snakes have special meanings for humans. Easy elicitation and learning of snake fear evolved in humans and many other primates (Öhman & Mineka 2002; Ramakrishnan et al. 2005; Coss et al. 2007) as snakes may have signified deadly threats for our primate ancestors. Fear may increase human attention but on the other hand it may interfere with beauty perception.

Even if we are not able to determine causes of detected congruence in animal beauty perception, this phenomenon deserves further research. It seems reasonable to perform similar comparison concerning perception of other animal groups as well as abstract pictures. Moreover, native ethnic groups from other continents should be also included. This may allow us to verify the generality of our results.

In present situation, endangered species of many taxa compete with one another for financial and political support provided within conservation projects. The winners of the competition for human support tend to be the species that are attractive to humans (Gunnthorsdottir 2001), larger in size (Metrick & Weitzman 1998), considered as 'a higher form of life' (Metrick & Weitzman 1996) and those that resemble humans (Samples et al. 1986). As far as tested group of boid snakes is concerned, the number of individuals of particular species kept in zoos worldwide is highly correlated with human preferences, but not with species rarity or conservation status (Marešová & Frynta 2008).

Another approach is to estimate the effort that humans would devote to save a given species. It is possible to quantify economic value of the species by means of willingness to pay (WTP). In a hypothetical market, people expressed in questionnaires their maximum WTP for protection of the species/biodiversity (e.g. Thayer 1981; Randall et al. 1983). Results of this method are generally in conformity with studies mentioned above. Martín-López et al. (2008) in their meta-analysis of 60 recent papers on economic valuation of biodiversity proved that WTP increases in favour of conservation species with anthropomorphic and anthropocentric (e.g. larger eye-size) characteristics instead of scientific factors; e.g. listing in International Union for Conservation of Nature categories did not have any influence on WTP.

If further testing proves the phenomenon of wildly shared preference for certain animal types within a group of related species, it is imaginable that in global conservation network this might lead to selective protection/neglecting of some species and thus contribute to the species composition of future biota.

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Cross-Cultural Agreement in Perception of Animal Beauty: Boid Snakes Viewed by People from Five Continents

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Introduction

Humans seem to have evolved relatively universal cognitive, perceptual and emotional mechanisms that enable them to appropriately react to other animal species. Strong evidence has been accumulated that they even share an innate concept of the structure of living world. 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) employing universal principles (Berlin *et al.* 1973). Even young children view animal categories as objectively defined (Rhodes and Gelman 2009), and these are less influenced by linguistic and cultural factors than human or artefact categories (see review Diesendruck 2003). Humans devote considerably more attention to animals as opposed to other stimuli (Lipp *et al.* 2004; New *et al.* 2007) and have literally the same object processing efficiency (accuracy and speed) of animals and human faces (Rousselet *et al.* 2004). People also inherently tend to affiliate with other species (e.g. the "biophilia" theory) and employ aesthetic judgements in their attitude to animals (Thornhill 1993).

Animals are vital stimuli to humans, and adaptive explanations are readily available. Particular emotional and perceptual mechanisms may be inherited from early humans, whose fitness and social status increased with possession and identification of certain animals or their body parts. Our ancestors thus may have developed an adaptive sense of "animal attractiveness" and preference to animal species that became part of the human mind before geographic and cultural diversification of our kind (Barkow *et al.* 1992). To test this hypothesis we study aesthetic preferences within an integral taxonomic group, boid snakes, in several distant cultures: Bolivia, Philippines, India – Rajasthan and Delhi, Malawi and Morocco, and compare them to our previous results from the Czech Republic and Papua New Guinea (Marešová *et al.* 2009a and new data). So far only a few studies on human attitude to animal species have been conducted cross-culturally and they focused mostly on negative emotions such as fear and disgust (Davey *et al.* 1998). Moreover, animals representing distant taxa were compared with each other (e.g. a leech versus a bat).

We chose boid snakes to test human preferences within a coherent animal group because they vary in appearance (color and pattern), and lack anthropomorphic features that are known to modify human preferences. Importantly, snakes represent valid biological stimuli; according to Isbell (2006) snakes, especially the constrictors, were the primary source of predation in early primate evolution. Large constrictors still represent a potential threat to members of some indigenous cultures and snakes in general

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belong to the most feared animals (Arrindell 2000; Davey 1994; Morris 1967). Despite that, humans are consistently able to provide two independent rankings of the same set of snake species – that of perceived beauty and evoked fear. These rankings are not mutually correlated (Landová *et al*. 2011) and therefore snakes can be considered as valid objects of beauty assessment as any other animal group without emotional connotations.

We have previously found a striking agreement between European and Papuan respondents in their preferences to boid snakes (Marešová *et al*. 2009a). Surprisingly, we found that species' ranking was not influenced by the fact that some of the tested species are distributed in Papua New Guinea and local participants very likely had direct experience with them and with other snake species. However, the examination of more cultures was required to test the hypothesis about the universality of human aesthetic preferences to animals.

The aim of this paper is to test the hypothesis that the aesthetic ranking of snake species is broadly shared among human cultures. In that case, the main axis of aesthetic preferences would be similar across humankind despite very substantial cultural differences.

Materials and Methods

As stimuli we used 32 photographs of boas and pythons, each depicting a representative adult individual of its species. The selection was carried out to cover maximum diversity in appearance within the taxa. Photographed individuals were borrowed from private keepers and zoos or belonged to the authors' collections. In the case of rare species, photographs were adopted from a book (Walls 1998a, b). In comparable experiments with animal aesthetics photographs were proved to fully substitute for live snakes (Landová *et al*. 2011). To standardize the photographs, all snake bodies were set on black background regardless of the snake's real size and printed in format 10×15 cm. Although we attempted to photograph the snakes in a comparably packed position, the posture (the extent and way of curling the body) was impossible to standardise. However, neither posture nor within-species variation affected resulting ranks when tested in Europe (Marešová and Frynta 2008).

People from Bolivia (24 men and 6 women from Cochabamba, mean age 22 years), Philippines (46 men and 28 women, mostly from Bohol, mean age 34 years), Delhi in India (14 men and 10 women, mean age 28 years), Rajasthan in India (32 men and 25 women, mean age 31 years), Morocco (10 men and 9 women, villagers from South East of the country, mean age 19 years) and Malawi (23 men and 16 women from the South of the country, mean age 28 years) participated in the experiment. Corresponding results from the Czech Republic (63 male and 61 female undergraduate students, mean age 21 years) and Papua New Guinea (63 men and 20 women from villages in Madang and Chimbu provinces, mean age 25 years) were compared (Marešová *et al*. 2009a and new data for the Czech Republic). Respondents voluntarily agreed to participate in the project. Each participant was shown a set of 32 photographs in a random assemblage and received following instructions "Please, sort the photographs in rank order corresponding to the beauty of the depicted snake from the most beautiful to the least beautiful one". The order of the photographs in the pack was then coded by numerals from 1 (the most beautiful one) to 32, hereafter referred to as ranks. In most cultures the respondents tent to discuss the stimuli in the way that indicated that they viewed the snakes as living creatures rather than just colorful images.

The ranks provided by individual respondents were divided by 32 and square root arcsin transformed to achieve normal distribution and further used as measures of perceived beauty. Most computations were performed in STATISTICA (StatSoft 2001); effect of sex and ethnic group was tested in MANOVA and partial correlations of individual populations were computed in Discriminant Funcion Analysis (DFA). Congruence among respondents was quantified by Kendall's coefficient of concordance (W, ranges from 0 to 1), a non-parametric test traditionally used for ordinal data. The contribution of individual ethnic groups to the cross-cultural variability was examined and visualised in Redundancy Analysis (RDA) as implemented in CANOCO (ter Braak and Smilauer 2002).

Results

The respondents agreed on which species are beautiful and which are ugly (Kendall's coefficient of concordance: W, df=31; Bolivia: W=0.142; Czech Republic: W=0.329; Delhi: W=0.109; Rajasthan: W=0.146; Morocco: W=0.111; Malawi: W=0.226; Philippines: W=0.200; Papua New Guinea: W=0.193; all $p<0.001$).

MANOVA revealed small, but significant effect of population ($F_{(155,999)}=1.27$, $P=0.021$), and no effects of sex ($P=0.236$) and their interaction ($P=0.476$). This result allowed us to pool sexes in further analyses. Multivariate test (DFA) revealed only two significant partial comparisons between populations: Malawi differed from both Rajasthan ($F_{31,207}=2.21$, $P<0.001$) and Philippines ($F_{31,207}=1.84$, $P=0.007$). Mean beauty measures of pooled data were closely correlated with those reported in our previous paper (Marešová *et al*. 2009a and new data) from Papua New Guinea ($r=0.94$, $P<0.001$; Fig. 1) and Europe (Czech Republic, $r=0.74$, $P<0.001$; Fig. 2).

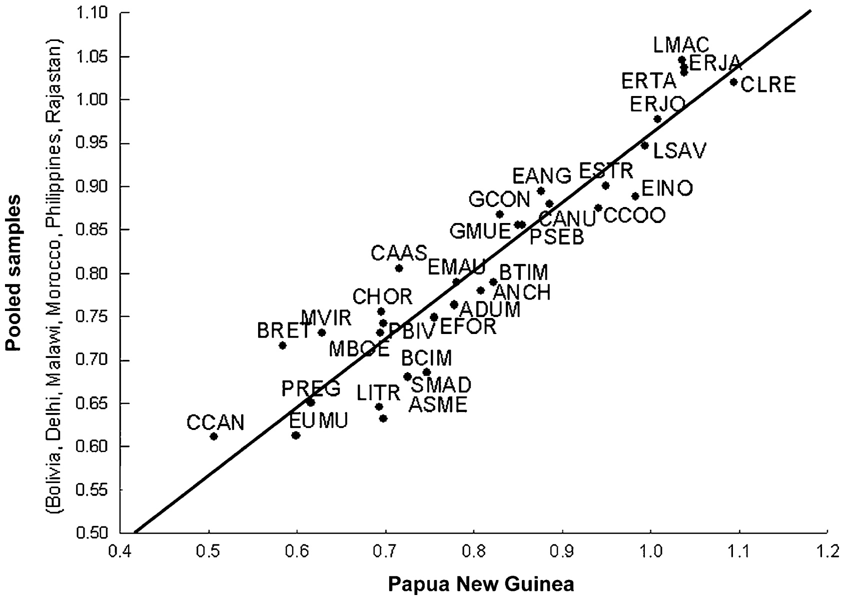

Fig. 1 Relationship between mean measures of perceived beauty of the pooled data (Bolivia, Delhi, Malawi, Morocco, Philippines and Rajasthan) and corresponding values obtained in Papua New Guinea (Marešová *et al.* 2009a). Please note that the higher value, the less preferred species. Species abbreviations as follows: ADUM – *Acrantophis dumerili*, ANCH – *Antaresia childreni*, ASME – *Aspidites melanocephalus*, BCIM – *Boa constrictor imperator*, CANU – *Corallus annulatus*, CCAN – *C. caninus*, CCOO – *C. cooki*, 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 jacculus*, ERJO – *Eryx johni*, 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. timorensis*, SMAD – *Sanzinia madagascariensis*

Permutation test (RDA) confirmed significance of between-population differences (F=18.2 and F=3.7 for the first and all canonical variables, respectively; both P< 0.001). Nevertheless, the first three multivariate axes reflecting between population differences accounted for only 4%, 0.5% and 0.3% of variation, respectively (compare with 16.7%, 12.1% and 9.8% explained by corresponding PCA axes referring to between-individual agreement). The projection of populations into the RDA axes revealed that the European results (Czech Republic) contribute the most to cross-cultural differences (Fig. 3). When this population was excluded, the contribution of the first three canonical axes dropped to 1.4%, 0.7% and 0.4% of variation, respectively, but still remained significant (F=

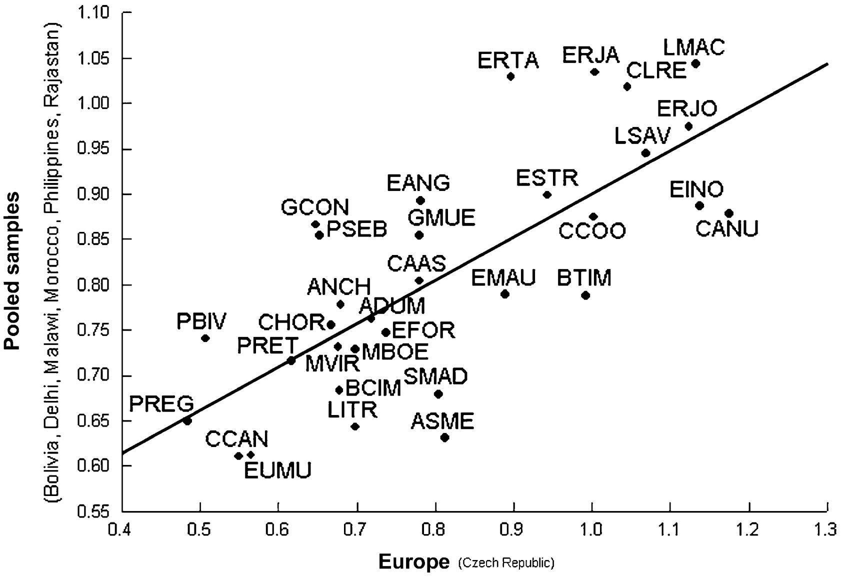

Fig. 2 Relationship between mean measures of perceived beauty of the pooled data (Bolivia, Delhi, Malawi, Morocco, Philippines and Rajasthan) and corresponding values obtained in Europe (Marešová *et al.* 2009a and new data). The higher value, the less preferred species. For species abbreviations, please see Fig. 1

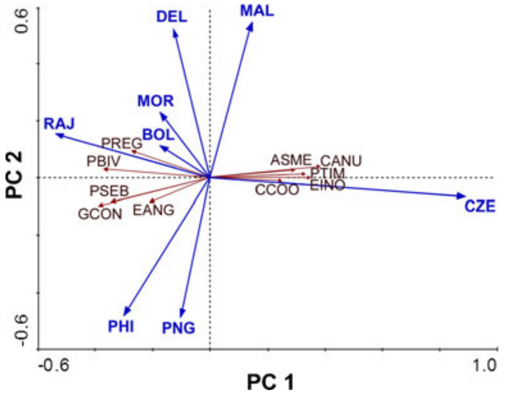

Fig. 3 Results of RDA; projection of populations and snake species into the first two canonic axes. BOL = Bolivia, DEL = Delhi; RAJ = Rajasthan; MOR = Morocco, MAL = Malawi; PHI = Philippines, PNG = Papua New Guinea, CZE = Czech Republic. Data concerning Papua New Guinea and Czech Republic were adopted from Marešová *et al*. (2009a). For abbreviations of species that contributed to the first two canonic axes, see Fig. 1

4.6 and $F=1.7$ for the first and all canonical axes, respectively; both $P<0.001$).

Next, Pearson correlation coefficients following leave one sample out procedure were computed to quantify similarities of snake ranking across studied populations. Mean measures of perceived beauty in each particular population/ethnic group were correlated with corresponding measures computed from the pooled remaining data; alternatively, only non-European data were included (Table 1). All resulting correlations were close, positive and statistically significant (all $P<0.001$). The lowest coefficients of determination were found in the case of the smallest data set (Morocco; 19 respondents): 0.51 and 0.57 for all and non-European data, respectively.

Table 1 Results of leave one sample out comparisons. Coefficients of determination (r^2) of the relationships between mean measures of perceived beauty in the particular ethnic group and corresponding values computed from all remaining data pooled (r^2; left column). The values computed exclusively for non-European data in the reference pooled dataset (r_{NE}^2) are given in the right column. * Data from Marešová *et al*. (2009a), new data added for the Czech Republic

Ethnic group	N	r^2	r_{NE}^2
Morrocco	19	0.513	0.566
Czech Republic*	124	0.602	0.602
Malawi	39	0.812	0.653
Rajastan	57	0.493	0.677
Delhi	24	0.703	0.719
Bolivia	30	0.804	0.877
Papua New Guinea*	83	0.901	0.88
Philippines	74	0.812	0.916

Discussion

Studied populations possess very distinct and disparite cultures. They differ in their uses and perceptions of their local habitats as well as vary in their knowledge and general attitudes regarding snakes. They also vary greatly in direct experience with snakes. The species tested exhibit a great variety of colors and patterns, perception of which is known to be modulated through linguistic categories (for colors: Kay and Regier 2007; Roberson *et al*. 2000; for animal patterns: Goldstein and Davidoff 2008). Moreover, the meaning of colors and their emotional charge may also be culturally dependent. Therefore, it is reasonable to expect that ethnic groups will at least slightly differ in their perception and appreciation of these species of animals. Our results confirm this intuitive assumption but also show evidence of considerable cross-cultural similarities in aesthetic preferences to snakes species. Observed congruence seems to be consistent with the theory that snakes are exceptionally strong aesthetic stimuli for all or most humans and/or we share a considerable component of aesthetic preferences to certain living kinds on a fine taxonomic scale. However, we have to consider an alternative explanation that the revealed cross-cultural congruence applies to aesthetic preferences irrespective of the nature of the objects evaluated. Specifically designed experiments are needed to be able to weigh these competing hypotheses. Nonetheless, studies on the aesthetics of commercial products often report significant cultural differences (e.g. Limon *et al*. 2009; Pearce *et al*. 2010). Thus, we do not wish to over generalize our results and prefer a more constrained interpretation that humans share a deep rooted emotional concept of animals and follow common cues when judging their aesthetics. This may increase the cross-cultural agreement. Regardless the cause, the revealed cross-cultural congruence in aesthetic preferences is substantial and non-trivial. The phylogenetic interpretation of such a pattern is congruent with the idea that the preference has remained unchanged during last dozens of thousands of years, i.e. the period characterized by a rapid cultural, technological and ecological diversification of human kind.

The congruence among respondents within an individual culture was highly significant in all cases, and its level varied within expected limits (Marešová *et al*. 2009b). The small cross-cultural differences that we revealed are dependent on the statistical method used and hard to quantify. Despite that, there are a few reasonably robust observations. Europe seems to be a likely candidate for the most distinct perception of snake aesthetics. Measures of perceived beauty obtained in the Czech Republic correlated with the pooled data relatively loosely (Table 1) and its significant contribution to the cross-cultural variability is clearly shown in the RDA projection (Fig. 3). We may speculate that European participants differ from other populations in their minimal direct encounters with live snakes), while they may be the most influenced by media. The overall lowest coefficient of determination was found in Moroccan data set and probably results from the small number of respondents (Table 1). This was followed by Rajasthan where respondents disagreed the most with European participants (Table 1 and Fig. 3). Independently of the method used Bolivia, Papua New Guinea and Philippines form one very coherent group which might be an interesting result inviting further research. When judging the importance of detected cross-cultural differences, it is useful to compare them with the relatively high inter-individual differences that may be caused by personality, individual experience, mistakes or other factors not controlled for.

Our findings are not only important for better understanding of human perception of other species but they may also have implications for conservation practice. People across cultures seem to infer values from external features, often applying the rule “what is beautiful is good” (Dion *et al*. 1972), e.g. customers across cultures make assumptions about the nature and quality of products from their packages (Limon *et al*. 2009). Similar perceptual shortcuts seems to apply to our apprehension of other living kinds. Attractiveness is an important determinant in perceptions of endangered species (Gunnthorsdottir 2001; Knight 2008), and people more willingly allocate funds for conservation of species that they like (Martin-Lopez *et al*. 2007). Taxonomic bias has also been documented in conservation research literature (Clark and May 2002). Present conservation resources are extremely limited with respect to the number of threatened or endangered species, and we can view animal’s appearance as a package that they bring to a highly competitive market. In case of boid snakes, human preferences are a good predictor of conservation efforts devoted to captive breeding of particular species in zoos worldwide, unlike its conservation status or present range size (Marešová and Frynta 2008). Similar evidence has been brought in case of parrot species (Frynta *et al*. 2010) and other vertebrate taxa (Frynta *et al*. 2009). If we assume that we inherently share an idea of what is beautiful and desirable in an animal, it is easy to imagine selective support or neglect of endangered species. It would affect ongoing anthropogenous macroevolutionary processes thereby influencing the composition of future biota.

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Are adult preferences to snake species already present in childhood?

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Abstract.

Humans share not only cognitive and emotional mechanisms devoted specifically to animals but also a considerable component of aesthetic appreciation of other species. This has been shown in adults and supported by cross-cultural evidence. The study explores aesthetic preferences towards boa and python species in pre-school children (aged 4-6) and adults, and compares the two groups. Despite children's restricted abilities to rank large number of tested species, they significantly agreed with each other on what species are beautiful and what are ugly. We found significant positive relationship between the mean ranks provided by children and adults ($r = .54$, $P < .001$). These results support the view that we inherently share aesthetic preferences to other animal kinds on a fine taxonomic scale. The difference between children's and adult's ranking was predicted by a single body feature, relative neck width. Children preferred species with relatively thick neck and inconspicuous head. These were usually also small species (e.g. Ericinae), harmless to children. On the other hand, snake proportions preferred by adults characterise rather bigger species. Large pythons probably posed more danger to children than adults during our evolution in African savannas and we may speculate that young children possess tendency to avoid large snake species, which is reflected by their aesthetic preferences.

Key words: cognition; aesthetic preferences; child; snake; colouration

Introduction

Aesthetic preferences are a pervasive element of human perception that eases dealing with diverse and complex environment. Perhaps not surprisingly, we judge aesthetics of natural objects and those created by man in a different manner (De Sousa, 2004; Halberstadt & Rhodes, 2000, 2003). We have evolved shared preferences for a range of evolutionary relevant stimuli such as appearance of other humans or favourite landscapes. Aesthetic feelings are also involved in our attitude towards other animal species (Thornhill, 1993).

Animals are vital stimuli to humans because appropriate reaction to them enabled our ancestors to survive or increase their fitness. As a result, we devote increased attention to animals over other stimuli (Lipp, Derakshan, Waters, & Logies, 2004 ; New, Cosmides, & Tooby, 2007) and have virtually the same object processing efficiency (accuracy and speed) of animals and human faces (Rousselet, Mace, & Fabre-Thorpe, 2004). Moreover, humans likely possess an innate concept of the structure of animal world. Illiterate hunter-gatherers are able to name and categorize animal species in a very similar way as contemporary scientists (Berlin, 1992), and as young infants as three months already show category perception of animals (Eimas & Quinn, 1994). Four year old children already consider internal properties of animals to be more important than superficial ones when deciding what animals are of the same kind (Diesendruck, 2001), which has been confirmed cross-culturally (Waxman, Medin, & Ross, 2007). Furthermore, young children view animal categories as objectively defined and as they get older, they start to perceive them as more conventional, just like older children and adults (Rhodes & Gelman, 2009). In this light, it may seem surprising that children demonstrate very little knowledge about general look of animals in the photographs compared to the appearance of their body parts (Davidoff & Roberson, 2002). However, adults with minimum experience with pictorial materials in Africa exhibit similar pattern when recognising depicted animals. They firstly devote their attention to particular characters (horns, ears, legs, tails) and than recognise the whole animal (Deregowski, Muldrow, & Muldrow, 1972; Deregowski, 1976; for other examples see review Bovet & Vauclair, 2000).

We have chosen boa and python snakes as a study group because they represent valid biological stimuli, exhibit variance in their appearance can be coded and they lack anthropomorphic features. Humans are assumed to devote preferential attention to snakes over other objects (e.g. Őhman & Mineka, 2001; Isbell, 2006; in children: LoBue & DeLoache, 2008) although this has been criticised on methodical grounds by authors who bring evidence for an increased attention to animals in general (e.g. Lipp et al., 2004; New et al., 2007). Unquestionably snakes belong to the most feared animals among adults (Arrindell, 2000; Davey, 1994) as well as children (Morris, 1967). It has been previously proved that people are able to evaluate both perceived beauty of the snakes and fear the species elicit and these emotions are independent. Resulting ranks from the two tasks are not mutually correlated (Landová, Marešová, Šimková, Cikánová, & Frynta, 2012). Snakes are one of the most common causes of human phobias (Davey, 1995; Öhman & Mineka, 2003). In children animal phobia enables faster detection of the feared stimulus (Waters & Lipp, 2008) and triggers extreme behaviour that results in avoidance of the stimulus (King, Ollendick, Murphy, & Muris, 2000). We share this tendency to fear snakes with many primates, e.g. chimpanzees (Herzog & Burghardt, 1988), macaques (Cook & Mineka, 1989; Coss, McCowan, & Ramakrishnan, 2007) tarsiers (Gursky, 2005, 2006) or marmosets (Clara, Tommasi, & Rogers, 2008). Herzog & Burghardt (1988) explain ophidiophobia by the conditions of African savannas where it might be difficult to quickly identify whether the encountered snake is poisonous or not.

However, human share also aesthetic perception of snake species (Marešová, Krása, & Frynta, 2009a). Villagers from Papua New Guinea and Czech students ranked boa and python species according to the perceived beauty in a very similar way, irrespective of the fact that four of the tested species are distributed in Papua and local people are very likely closely experienced with them as with other snake species. It may be of interest from evolutionary, anthropological as well as conservation point of view to explore the nature and origin of cross-culturally shared aesthetic preferences towards snake species. Even very young infants are known to prefer attractive animal faces to unattractive ones in similar way as adults (Quinn, Kelly, Lee, Pascalis, & Slater, 2008). These facts bring up the question to what extent human aesthetic preferences to animal species are present in childhood and perhaps innate.

The aims of this study are to (1) quantify the preferences toward boas and pythons in pre-school children and adults, (2) compare the age groups, and (3) attempt to explain the preferences by the body traits of the species.

Materials and Methods

We selected for our experiment 51 species and 5 subspecies of pythons and boas, covering 19 currently recognised genera, with the only exception of Apodora (the single species *Apodora papuana* can be hardly distinguished at first sight from *Liasis olivaceus* and the letter species was included). The species/subspecies were selected to cover the most of natural variety in colouration and pattern within the taxa.

To test beauty preferences, we used standardised set of photographs. The snakes were photographed in a moderately packed position and in the case of rare species, photographs were adopted from a book (Walls, 1998a, 1998b). We digitally set the snake bodies on black background regardless their real size and printed in format 10x15 cm. The full set consisted of 56 standardised photographs of boas and pythons each depicting a typical individual of its species. We split the photos into four separate blocks, each consisting of 16 photographs, so that small children were able to oversee and evaluate all species within one block at one time. Eight species/photos were present in two copies, and used to balance the blocks for variability in appearance. Ranks of these doubled pictures were removed before analyses to avoid the problem of pre-determination of the last rank.

The visceral traits of each species were coded from the photographs. These were presence of main colours (white, grey, yellow, red, reddish brow, brown, black, and green; coded 0-not present to 3-covers most of the body), pattern (coded 0,1), gloss (coded 0,1), neck width (mm) and maximum width of the body (mm). In addition, the photograph area covered by the snake body was measured (mm^2) and the quality of photograph was evaluated by six independent respondents (coded 0,1). The neck width scaled to maximum body width is further referred to as relative neck width, and body width scaled to total area of the body is referred as body shape. In our previous work, we tested and ruled out the influence of body position (whether and how the snake is packed) and intra-species variability on respondents' preferences (Marešová & Frynta, 2008).

Our participants were undergraduate students of the Charles University (9 males and 38 females) and children from two nurseries (13 males and 26 females; aged 4-6). Approval was granted by the institutional ethical committee. Photos of snakes have been previously successfully used in fear tasks with children (e.g. LoBue & DeLoache, 2008; Waters & Lipp, 2008) and photographs proved to fully represent live snakes in both fear and beauty tasks (Landová, Marešová, Šimková, Cikánová, & Frynta, 2012). Four year old children are already able to recognise pictures as 2D representations of real objects (DeLoache & Burns, 1994), which is further facilitated by the frequent contact with pictorial stimuli (Bovet & Vauclair, 2000).

Each respondent was exposed to one block, i.e. 16 photographs, placed on a table in a random assemblage. To maintain children's attention, we asked the respondents only to rank order five most liked and five least liked species. The respondents were instructed: "Please, pick up the most beautiful snake…then second most beautiful…up to the fifth one". The order of the photos was coded by numerals from 1 (the most beautiful one) to 5, further referred to as ranks. Afterwards, the respondents repeated the task with five least liked species, starting with the ugliest one. These were coded by numerals from 16 (the ugliest) to 12. The six species that were not selected by the respondent were given a mean rank 8.5. All respondents completed all four blocks in sequence and they did not show any troubles when performing the tasks.

The ranks of species provided by individual respondents were divided by 16 and square root arcsin transformed to achieve normal distribution. The variables showing lognormal distribution (body size, neck width and maximum body width) were transformed by natural logarithm prior to the analyses. We performed most calculations in Statistica 6.0. (StatSoft., 2001). The agreement among the respondents was quantified by Kendall's coefficient of concordance as implemented in SPSS (Statistical Package for the Social Sciences), version 16.0.

Results

Congruence among the respondents.

In order to quantify agreement among the respondents, we computed Kendall's coefficient of concordance (W; df = 15) separately for each combination of age and block. The results revealed that adult respondents agreed on which species are beautiful and which are ugly
(W = .454, .380, .470, .408 for individual blocks of species, respectively; all P < .001). The congruence among children was less apparent but still significant (W = .177, .103, .123, .225, all P < .001).

The effect of respondents' age and sex on their preferences.

Next we performed MANOVA to test the effects of the age and sex of the respondents. The preferences for snake species were marginally explained by the age (F(54,18) = 2.73; P = .0109) but not sex (F(54,18) = .73; P = .8151) and their interactions (F(54,18) = 1.56; P = .1503), which allowed us to pool sexes in further analyses. Nevertheless, mean ranks provided by children and adults were significantly correlated in individual blocks (r = .54, .66, .54, respectively; all P < .05), except for one (r = .44, P = .087), and in the pooled data (r = .45, P < .001; when *Charina bottae* was excluded as outlier: r = .54; Fig. 1).

To identify species that substantially contributed to the age differences, we performed MANOVA, and the levels of significance were Bonferroni corrected. From the total of 56 snake species, children significantly differed in their preferences from adults in 10 cases. They liked better *Eryx johni*, *Charina bottae* and *Bothrochilus boa*, whilst they ranked lower than adults *Eunectes noteus*, *Epicrates inornatus, Boa c.constrictor, Gongylophis conicus, Acrantophis madagascariensis, Broghammerus reticulatus, and Python regius*.

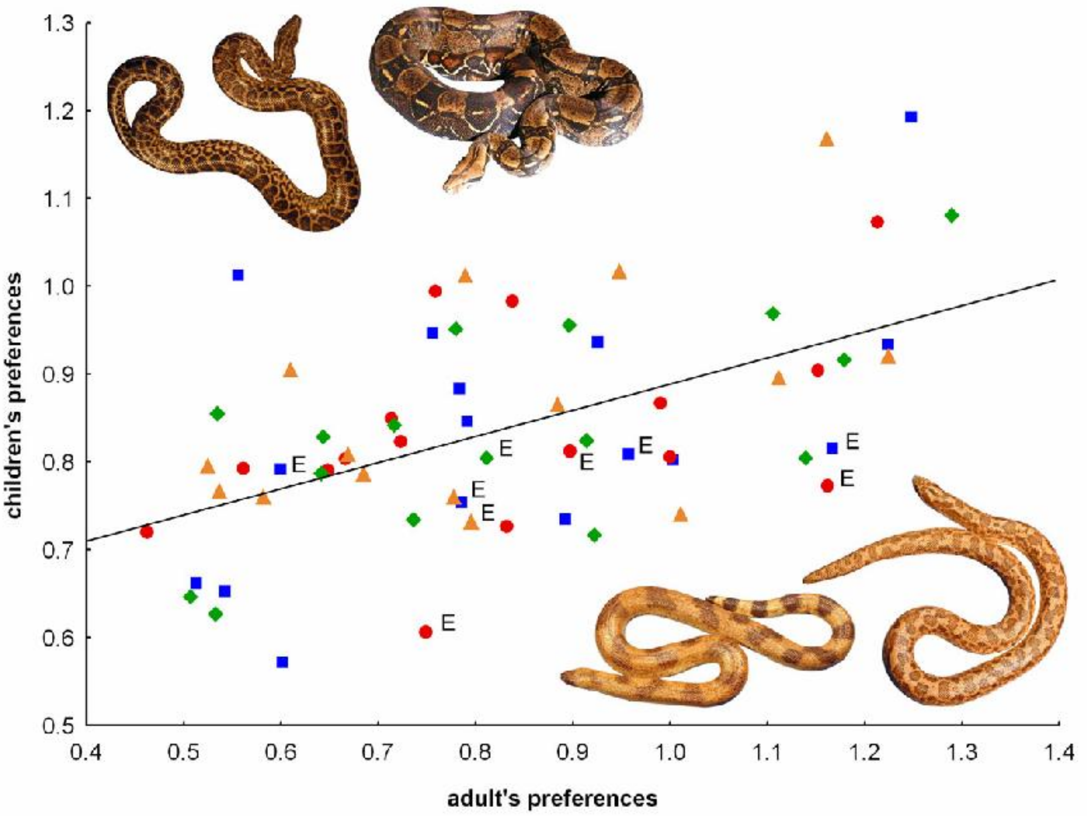

Fig 1. Relationship between beauty evaluation by adults and children. Axes show adults' and children's arcsin transformed mean ranks of the species; the lower number the more preferred species. Symbols (■, ●, ▲, ♦) mark individual blocks of photographs. Photos above the fit line: *Eunectes noteus* and *Boa c.constrictor*– evaluated more positively by adults; below the line: *Eryx johni* and *Eryx jacculus* – preferred more by children. E – Sand boas (*Erycinae*)

Explanation of age differences in beauty perception by visceral traits of the species.

Presence of the main colours, pattern, gloss, relative neck width, body shape and quality of the photograph were adopted as explanatory variables in General Linear Models (GLMs) to explain preferences of adults and children. Adults showed preferences towards animals with green, yellow and red colour (F(1,43) = 13.08, 6.29, 4.49, respectively, all P < .04), presence of pattern (F(1,43) = 29.10, P < .001) and relatively slim neck (F(1,43) = 7.17, P = .0104), and the whole model explained 68.8% of variance. The presence of pattern appeared to be the strongest predictor of adult preferences (accounted for 33.2% of variance in adult preferences). Children's preferences were significantly explained only by the presence of bright colours, i.e. yellow, red and green (F = 6.88, 6.30, 5.94, respectively, all P < .02). Full and reduced models explained 45.9% and 25.7% of variance, respectively. The strongest predictor of children's preferences was yellow colour.

In order to interpret the revealed differences, residuals of the correlation between children and adults were computed and further treated as dependent variable in GLMs. Full model revealed only the effect of relative neck width (F(1,43) = 7.15, P = .0106) on the residuals, and explained 47.5% of variance. The relative neck width itself accounted for 23.2% of variance (F(1,43) = 16.32, P < .0001) and children preferred species whose neck was relatively thick.

Discussion

Adult respondents are able to reliably rank quite large number of species, even within a taxonomic group that shows limited variance in appearance (Marešová, Landová, & Frynta, 2009b). Consistently with these results, adults reached a good congruence in their preferences in the present study. Agreement among pre-school children was much less pronounced but still significant in all four blocks. In the light of further evidence, such as very similar preferences of adults and children for colour traits of the animals and comparable range of mean ranks, we ascribe relatively low congruence among children rather to their constrained abilities to perform the task (e.g. oversee all pictures at a time or maintain attention), than to the absence of a shared opinion on snake beauty.

We have found no sex differences in any age group which is in agreement with our previous findings on adult preferences towards boas and pythons (Marešová & Frynta, 2008). In contrast, sex differences have been repeatedly confirmed for colour preferences (e.g. Boyatzis & Varghese, 1994; Dittmar, 2001; Hurlbert, Ling, & Sweeting, 2003) and they also seem to be an ubiquitous element of human attitude to different taxonomic groups (Brown, 2000; Herzog, Betchart, & Pittman, 1991; Herzog, 2007). Particularly less attractive species tend to be evaluated relatively higher by males (Kellert, 1993; Hills, 1993).

Children and adults showed similar preferences towards snake species (Fig 1), although small systematic differences were revealed. They best preferred the same colours, i.e. green, red and yellow, which is in congruence with previous results that adults (Hemphill, 1996) and children (Boyatzis & Varghese, 1994) evaluate bright colours positively. It should be noted that children of this age already use colours symbolically, i.e. preferred ones to draw a positive figure and vice versa (Burkitt, Barrett, & Davis, 2003). Crozier (1997) found that children like better than adults yellow colour and less green colour. Congruently, the presence of yellow colour was the strongest predictor of children's preferences in the present study.

Presence of pattern, in some cases highly structured and complex, seemed to be highly important to adults. They evaluated species with no pattern lower, which is in agreement with adult preferences for symmetry and high complexity of visual stimuli (Rentschler, Juttner, Unzicker, & Landis, 1999) and repetitive signals (Kenward, Wachtmeister, Ghirlanda, & Enquist, 2004). Adults demonstrably preferred snakes that had relatively slim neck and thus distinctively defined head shape. We observed the opposite in children who tended to like better snakes with less expressed shape of head, especially Sand boas (see Fig. 1). The relative neck width was the only significant factor explaining differences in children's and adult's preferences. This result may not be accidental and have evolutionary relevance. A snake with thick body, slim neck and distinctive head is also likely to be big, while species with uniform body shape and inconspicuous head, such as Sand Boas, are usually smaller. Although the snakes were depicted on photographs regardless their real size, children's preference for small species and dislike for large ones is evident from the range of species that contributed to age differences (for a list please see results). Large pythons probably posed more danger to children than adults during our evolution in African savannas and we may speculate that young children possess tendency to avoid large snake species, which is reflected by their aesthetic preferences. Adult preference for "proper snakes" with distinctive heads may be influenced by their symbolical meaning (Murphy & Henderson, 1997) and usual image of snake body shape in the given culture.

Despite relatively low congruence among children and inverse preference for certain features of snake's body shape, we find that considerable component of aesthetic preferences is shared by children and adults. It was previously shown that beauty perception of snake species is highly consistent across distant cultures (Marešová, Krása, & Frynta, 2009a; Frynta, Marešová, Řeháková-Petrů, Šklíba, Šumbera et al., 2011), and present results further support the theory that we inherently share not only attachment to certain taxonomic groups but also aesthetic preferences towards animal kinds in finer taxonomic scale. However, such a simple fact may have considerable implications. Affective factors play an important role in biodiversity conservation (Marešová & Frynta, 2008; Metrick & Weitzman, 1996, 1998; Samples et al., 1986), and we are more willing to protect, and invest to, species that we like (Gunnthorsdottir, 2001; Martin-Lopez, Montes, & Benayas, 2007). Concerning studied boid snakes, the number of individuals of particular species kept in zoos worldwide is highly correlated with human preferences, but not with species rarity or conservation status (Marešová & Frynta, 2008). Our preferences are likely to shape the composition of future biota, and they should be further explored and considered in education and conservation decisions.

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ORIGINAL PAPER

What makes some species of milk snakes more attractive to humans than others?

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Abstract Animals are ancestrally important stimuli for humans who pay disproportional attention to animal objects and exhibit an outstanding ability to categorize animal species, especially those most relevant to them. Humans as well as other primates perceive snakes as ambivalent stimuli that elicit unspecific arousal and attention. We assessed human aesthetic preferences toward milk snakes, the traditional model for studies of Batesian mimicry. The genus is fairly uniform in size and shape, but includes a great variety of color forms; some possessing aposematic patterns while others being rather cryptic. This provides an opportunity to test which features are responsible for positive aesthetic evaluation of the species. We asked the respondents to rank 34 pictures of milk snakes according to perceived beauty. The sets (whole bodies, heads, and skin fragments) covered most of naturally occurring variation in milk snake appearance. While ranking the beauty, the respondents spontaneously classified the species according to two dimensions. In each set, one of the dimensions corresponds to perceived beauty. The respondents' ranking revealed several distinct clusters of species instead of a continuous gradient. The species clustered in a similar way irrespective of evaluated set. One dimension of the ranking associated with the relative representation of red color and the number of transversal stripes, the other corresponded to a low proportion of red and a high proportion of black color. When the whole body of the snake is evaluated, aposematic coloration contributes to its perceived beauty. In conclusion, humans showed a surprising ability to classify milk snake patterns; they repeatedly formed the same distinct groups of species, thus completing a process that resembles unsupervised categorization.

Keywords Human cognition · Aesthetic preferences · Categorization · Aposematic signal · Mimicry · *Lampropeltis*

Introduction

Aposematic coloration advertises the unprofitability of its bearer as a prey to its potential predator. Deadly poisonous snakes such as the red-yellow-black-ringed coral snakes are the most popular example of extremely dangerous aposematic prey. Avian predators living in sympatry with the coral snakes, but not those living in allopatry, have evolved innate avoidance of these dangerous animals (Smith 1975, 1977, 1980). It was experimentally demonstrated that even aposematic plasticine replicas of coral snakes are avoided by avian predators, thus the tricolor coral snake pattern and partly also bicolor striped pattern may provide efficient protection against predation in natural situations (Brodie 1993; Brodie and Janzen 1995; Hinman et al. 1997; Buasso et al. 2006).

In contrast to birds, olfactory oriented mammalian predators such as coatis and opossums do not respond well to warning coral snake patterns (Beckers et al. 1996; Brodie 1993). Nevertheless, snakes elicit fear and/or antipredator behavior in many primates, e.g., tarsiers (Gursky 2005, 2006), marmosets (Clara et al. 2008), macaques (Ramakrishnan et al. 2005; Coss et al. 2007), and humans (Hunt

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et al. 2006; Wright et al. 2002; Őhman et al. 2007). Reaction of primates to warning coral snake pattern is complicated by different ability of color vision. Most New World monkeys living in sympatry with coral snakes and their mimics are allelic trichromatics. Red and green discrimination in these species is restricted only to females heterozygous in specific opsin gene localized on X chromosome (Jacobs and Neitz 1987; Hiramatsu et al. 2005; for review see Jacobs et al. 1996; Jacobs 2007; Surridge et al. 2003). In contrast, Howler monkeys of the genus *Alouatta* as well as all species of Old World monkeys and apes including human beings share fully developed routinely trichromatic color vision (Dulai et al. 1999; Rowe 2002) and thus both sexes can perceive aposematic patterns similarly as other visually orienting predators, e.g., birds.

Moreover, primates can easily learn to fear snake stimuli when they are encountered in aversive contexts (Őhman and Mineka 2003). In spite of this, humans and other primates were seldom experimental subjects in studies devoted to the function of coral snake coloration. This paper examines responses of human subjects to aposematic coral snake patterns. As humans have not evolved in sympatry with coral snakes that occur exclusively in the New World range, they are unlikely to have innate fear of coral snake pattern. Nevertheless, humans are able to recognize general aposematic patterns as had been demonstrated in studies modeling artificial evolution of aposematic forms (Sherratt and Beatty 2003; Beatty et al. 2004). On the other hand, coral snake patterns possess complexity and bilateral symmetry, the main factors responsible for human visual preference (Rentschler et al. 1999).

Humans devote increased attention to animal stimuli in general (New et al. 2007) and to snakes in particular (Mineka and Őhman 2002; Isbell 2006; LoBue and DeLoache 2008; Waters and Lipp 2008). In our previous paper, we developed a reliable procedure for the evaluation of aesthetic preference for animal species using standardized photographs and demonstrated that humans are perfectly able to rank boid snakes according to perceived beauty (Marešová and Frynta 2008). Surprisingly, the evaluation of snake species is highly congruent across cultures, nearly the same rankings were provided by European students and villagers from Papua New Guinea (Marešová et al. 2009). Moreover, this ranking is a good predictor of conservation efforts devoted to captive breeding of particular species in zoos worldwide. Boid snakes exhibit considerable variation in shape, size, pattern, and color. To analyze factors underlying human preferences, we searched for another snake group exhibiting uniform external morphology and simplified color and pattern variation. Thus we paid attention to coral snake pattern that has a clear biological function and consists of distinct repetitive elements that may be coded into simple character states.

To assess human attitudes to coral snake patterns, we used as experimental stimuli milk snakes of the genus *Lampropeltis* instead of true coral snakes. These colubrine snakes are a classic example of Batesian mimicry (Bates 1981). Some species/populations of these non-venomous snakes evolved color patterns resembling highly venomous coral snakes of the genus *Micrurus* (Elapidae) enabling them to deceive visually oriented predators, mostly birds of prey, and thus to avoid predation pressure (Brodie and Brodie 2004). Of course, current and/or historical experience of the predator with the model species of coral snake is required for successful function of Batesian mimicry.

Milk snakes are obviously of North American origin and have expanded southwards as far as the Colombian Andes and Venezuela (Navarrete and Rodriguez-Acosta 2003) where they have met their model—the true coral snakes. In spite of their presumably North American origin supported by the fossil record, coral snakes radiated in South America. Molecular phylogenies revealed that the North American species of the genus *Micrurus* are descendants of the derived South and/or Central American clades. The typical aposematic tricolor pattern is an ancestral character state within coral snakes (Savage and Slowinski 1992; Gutberlet and Harvey 2004) and, it is mimicked not only by some species of *Lampropeltis* but also by numerous other non-venomous snakes (e.g., *Urotheca, Elapsoides, Scaphiodontophis*) throughout the geographic range (e.g., Greene and McDiarmid 1981; Pough 1988; Savage and Crother 1989; Savage and Slowinski 1996; Brodie and Brodie 2004). Besides the Batesian mimetic species there are species/populations of milk snakes with cryptic or non-aposematic color pattern. This variability of patterns within the genus *Lampropeltis* provides a good opportunity for testing the effects of particular elements of the aposematic pattern on its evaluation by human respondents.

The aims of this paper were (1) to assess aesthetic preferences of human respondents toward pictures depicting a representative set of milk snakes; (2) to identify the main axes of variation in human preferences; (3) to classify the studied *Lampropeltis* patterns according to human responses; (4) to compare this classification with that based on color characters; (5) to evaluate the correspondence between human preferences and aposematic pattern; (6) to correlate attractiveness reported by the respondents with other measures of human attention devoted to respective forms of milk snakes.

Materials and methods

Matrix of 32 color characters for 54 forms (species/subspecies/populations) of milk snakes was compiled from Markel (1994). Presence/absence of a particular color or trait on respective area of depicted snake was coded 1/0. Following characters were included. Characters recognized on dorsum: (1) dark brown color; (2) black color; (3) red color; (4) white or yellow stripes; (5) light brown color; (6) gray color; (7) small white/yellow spots; (8) longitudinal stripes; characters recognized on ventrum; (9) white or yellow color; (10) gray color; (11) red color; (12) dark brown color; (13) black color; characters recognized on head; (14) dark brown/black background color; (15) light brown background color; (16) gray background color; (17) dark brown/black spots; (18) red spots; (19) yellow spots; (20) white spots; (21) spots present outside the rostrum; (22) spots present on the rostrum; characters recognized on the neck; (23) yellow color; (24) white color; (25) lunets; (26) transversal stripe; characters concerning striping pattern: (27) dark melanine transversal stripes (rings); (28) dark stripes of lunet like form; (29) wide dark stripes; (30) wide red stripes; (31) wide yellow/white stripes; (32) number of light stripes coded in ordinal scale 0–2.

Next, we selected 34 subspecies of the genus *Lampropeltis* to cover most of naturally occurring variation in color patterns and compiled three sets of pictures depicting these snakes. The first set (further referred as snakes) consisted of color photographs of the snakes. We digitally set all the snake bodies on white background regardless of their real size and printed in the format 10 × 15 cm. The second and the third sets (further referred as heads and skins) were color pictures from Markel (1994) depicting the head and segment of mid-body skin, respectively.

Our respondents were undergraduate students of Charles University (Faculty of Sciences), who agreed to participate in the project. Each person was exposed to one set, i.e., 34 photographs, placed on a table in a random assemblage. Then we asked her or him: “Please, pack the photographs in an order corresponding to the beauty of the depicted snake 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 34, further referred to as ranks. Each subject provided a written consent and additional information about age, sex, attitude toward snakes (positive, neutral, negative, phobic), experience with snakes and other pets, and knowledge of the presented species. Although no explicit time limit was given, all the respondents performed the task within a few minutes.

The sets “snakes”, “heads”, and “skins” were evaluated by 60 (41 women and 19 men), 60 (48 women and 12 men), and 62 (41 women and 21 men) respondents, respectively. The ranking of species provided by individual respondents was divided by 34 and square root arcsine transformed to achieve normal distribution. The transformed data were further analyzed by Principal Component Analysis (PCA) and/or Cluster Analysis (CA) to visualize the multivariate structure of our data sets. Manhattan (City-block) distance was selected as metrics and unweighed pair-group average as clustering method for CA. To evaluate difference between the sexes we performed Multivariate Analysis of Variance (MANOVA) in which sex, set, and its interaction were taken as factors. This procedure revealed no significant effects of sex ($F_{33,146} = 1.53$, $P = 0.0526$) and sex*age interaction, which allowed us to pool sexes in further analyses.

Means of transformed preference ranks and/or PC scores computed for each analyzed picture as dependent variables were further analyzed by linear regression and/or GLMs. As explanatory variables we adopted color and pattern characters assessed on test photographs, i.e., the number of red (or light) stripes; arcsine transformed relative proportion of red, black/brown, gray/light brown, and white/yellow surface. Alternatively, we correlated PC scores and preference ranks with the variables reflecting human attention toward particular species: the number of specimens kept in zoos worldwide, the number of hits in Zoological Records database, and finally the number of hits on Google search for text or pictures with Latin name of the snake (or Latin and English name).

The numbers of individuals kept in zoos were obtained from the International Species Information System online database (www.isis.org; downloaded on 1 January 2008) covering over 730 zoos and aquariums worldwide. The variables showing lognormal distribution (number of individuals kept in zoos, numbers of hits in databases) were transformed by natural logarithm prior to the analyses. We performed most calculations in Statistica 6.0. (StatSoft 2001).

Results

Phenetic tree constructed from color and pattern characters

First, we classified studied species according to objective characters defined without regard to further respondents’ evaluation. On the basis of 32 color and pattern characters we constructed Manhattan dissimilarity matrix (further referred as objective matrix) and performed cluster analysis including 54 taxa of milk snakes. We adopted this statistical procedure to uncover the main groups of the taxa on the basis of character similarity and visualize them in the resulting phenetic UPGMA tree (Fig. 1). This tree revealed several distinct and meaningful groups of phenotypically similar species. Typical tricolored milk snakes (i.e., *L. pyromelana*, *L. ruthveni*, *L. zonata*, and most *L. triangulum*) form a compact cluster. Next two clusters comprise most *L. getula* that are uniformly dark or bicolor (i.e.,

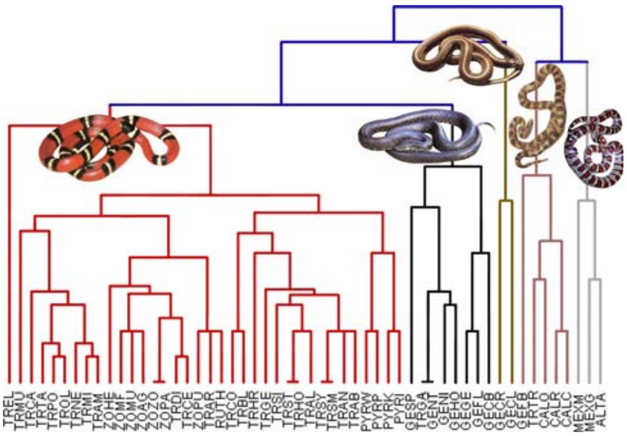

Fig. 1 Phenetic tree of 54 taxa of milk snakes based on color and pattern characters. Manhattan distances and unweighted pair-group average clustering method were applied. The taxa are abbreviated as follows: ALTA—*L.alterna*, CALC—*L.c.calligaster*, CALO—*L.c.occipitolineata,* CALR—*L.c.rhombomaculata*, GECL—*L. getulus californiae* (longitudinal stripes), GECB—*L.g.boylii,* GECR—*L.g.boylii* (brown form), GEFL—*L.g.floridana,* GEFG—*L.g.brooksi,* GEGE—*L.g.getula,* GEHO—*L.g.holbrooki,* GENI—*L.g.niger,* GENT—*L.g.nigrita,* GESP—*L.g.splendida,* MEXM—*L.mexicana,* MEXG—*L.m.greeri,* PYRI—*L.pyromelana infralabialis,* PYRK—*L.p.knoblochi,* PYRP—*L.p.pyromelana,* PYRW—*L.p.woodini,* RUTH—*L.ruthweni,* TRAB—*L.triangulum abnormal,* TRAM—*L.t.amaura,* TRAD—*L.triangulum andesiana,* TRAL—*L.t.annulata,* TRAR—*L.t.arcifera,* TRBL—*L.t.blancahardi,* TRCA—*L.t.campbelli,* TRCE—*L.t.celaenops,* TRCO—*L.t.conanti,* TRDI—*L.t.dixoni,* TREL—*L.t.elapsoides,* TRGA—*L.t.gaigeae,* TRGE—*L.t.gentilis,* TRHO—*L.t.hondurensis,* TRHR—*L.t.hondurensis* (red form), TRMI—*L.t.micropholis,* TRMU—*L.t.multistrata,* TRNE—*L.t.nelsoni,* TROL—*L.t.oligozona,* TRPO—*L.t.polyzona,* TRSI—*L.t.sinaloe*, TRSM—*L.t.smithi,* TRST—*L.t.stuarti,* TRSY—*L.t.syspila,* TRTA—*L.t.taylori,* TRTR—*L.t.triangulum,* ZOAG—*L.zonata agalma,* ZOHE—*L.z.herrerae*, ZOMU—*L.z.multicnta,* ZOMF—*L.z.multifasciata,* ZOPA—*L.z.parvirubra,* ZOPU—*L.z.pulchra,* ZOZO—*L.z.zonata*

with yellow/white pattern of various form as blotches, longitudinal or transversal stripes), and black melanistic form of *L.t.gaigae*. Finally the most distinct is a branch consisting of two clusters characterized by light brown (*L. caligaster, L.g.brooksi, L.t.triangulum*) and gray (*L. mexicana, L. alterna*) background color.

Comparison of objective and cognitive (preference) matrices

We restricted further analyses to selected 34 taxa covering most of color/pattern variation. Next step was to compare objective criteria of studied species with human cognitive classification of the same set of taxa. For this purpose, we compared the above objective matrix based on color and pattern characters with corresponding correlation matrix computed from ranking of individual taxa provided by the respondents (snakes, heads, and skins datasets were pooled). Objective and cognitive matrices fairly corresponded one to another. Mantel test confirmed that correlation between these matrices is significant ($r = 0.537$; 1 000 000 replicates, approximate Mantel $t = 11.46$, P random Z less than observed $Z = 1$).

Phenetic trees constructed from respondents ranking of snakes, heads, and skins

In order to identify classification structure of taxa inherently present in human aesthetic ranking we performed cluster analysis of the 34 taxa. This analysis was based on correlation matrix computed from transformed ranks provided by individual respondents. The resulting trees obtained for pooled snakes, heads, and skins datasets revealed distinct clusters (Fig. 2). Uniform black species (*L.g.nigrita, L.t.gaigae*) were most separated, other unicolored/bicolored species/subspecies (*L. getula, L. caligaster, L.z.herrerae*) and *L.t.triangulum* form the second cluster, and finally the largest group of tricolored species form the main cluster (*L. mexiacana, L. alterna, L. pyromelana*, *L. ruthveni,* remaining subspecies of *L. triangulum* and *L. zonata*). This basal branching pattern remained virtually unchanged when particular analyses of snakes, heads, and skins datasets were carried out and/or the

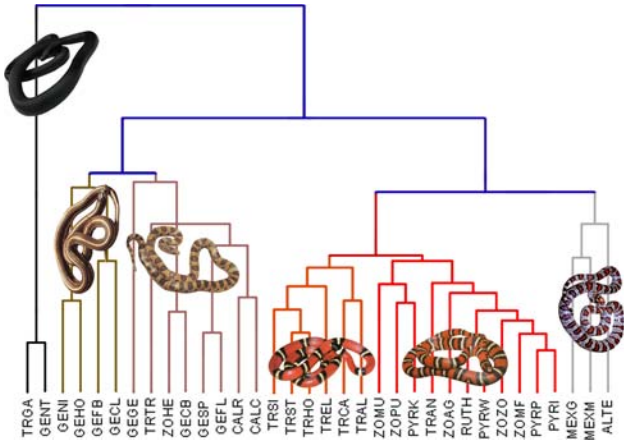

Fig. 2 Phenetic tree of 34 taxa based on preference ranks provided by respondents. The data concerning snakes, heads, and skins were pooled. Manhattan distances and unweighted pair-group average clustering method were applied. The taxa are abbreviated as follows: ALTE—*L.alterna*, CALC—*L.c.calligaster*, CALR—*L.c.rhombomaculata*, GECL—*L. getulus californiae* (longitudinal stripes), GECB—*L.g.boylii,* GEFL—*L.g.floridana,* GEFG—*L.g.brooksi,* GEGE—*L.g.getula,* GEHO—*L.g.holbrooki,* GENI—*L.g.niger,* GENT—*L.g.nigrita,* GESP—*L.g.splendida,* MEXM—*L.mexicana,* MEXG—*L.m.greeri,* PYRI—*L.pyromelana infralabialis,* PYRK—*L.p.knoblochi,* PYRP—*L.p.pyromelana,* PYRW—*L.p.woodini,* RUTH—*L.ruthweni,* TRAD—*L.triangulum andesiana,* TRAL—*L.t.annulata,* TRCA—*L.t.campbelli,* TREL—*L.t.elapsoides,* TRGA—*L.t.gaigeae,* TRHO—*L.t.hondurensis,* TRSI—*L.t.sinaloe,* TRST—*L.t.stuarti,* TRTR—*L.t.triangulum,* ZOAG—*L.zonata agalma,* ZOHE—*L.z.herrerae*, ZOMU—*L.z.multicnta,* ZOMF—*L.z.multifasciata*, ZOPU—*L.z.pulchra*, ZOZO—*L.z.zonata*

clustering methods were altered. Nevertheless, the group of *L. mexicana, L.z.herrerae, L.g.californiae* (transversally stripped), *L.t.triangulum*, and also *L.g.getula* appeared close to the main cluster of tricolored species in snakes' dataset; and *L.p.knoblochi* as well as *L. mexicana* clustered within unicolor/bicolor species according to skins dataset.

First two principal component analysis axes derived from snake, head, and skin rankings are mutually linked

We applied Principal Component Analysis (PCA) as an alternative exploratory statistical method to reveal main gradients in human ranking of milk snakes attractiveness. To explore possible differences between milk snakes seen either as a whole (snake set—simulating view at a distance) or focused on detail (head and skin sets—simulating view on snake from a proximity), we performed separate analyses of these sets. The first two principal component axes (PC1 and PC2) accounted for 29.9 and 12.1% of variation in ranking the snakes. Corresponding values for skins (31.7%, 20.1%) and heads (34.7%, 13.5%) were quite comparable. The percentage of explained variation reflects congruence among the respondents concerning direction of the particular axis. However, even strong agreement among the respondents does not necessarily mean the agreement in polarity of the axis. Respondents may differ in their views which pole of this axis contains species perceived as beautiful (species with low mean rank) and which pole contains species perceived as unattractive (species with high mean rank). The agreement in polarity is easily visible from plot of PCA loadings (not shown).

Next, we correlated PC axes revealed by analyses of partial datasets (snakes, heads, and skins) to assess which of them are mutually linked. PC1 scores of snakes correlated with PC1 scores of heads ($r = 0.75$) and PC2 scores of skins ($r = 0.77$), the latter two being tightly mutually correlated ($r = 0.94$). Thus PC1 of snakes, PC1 of heads, and PC2 of skins represent almost the same axis of variation. However the respondents agreed in polarity of this axis in the PC1 of snakes only. On contrary, in the case of heads and skins the respondents agreed in polarity along the PC2 and PC1 axis, respectively. These two variables were also mutually correlated ($r = 0.59$). Following this agreement in polarity, scores of the first principal axes were closely correlated with mean ranks of particular species in the case of snakes ($r = 0.92$) and skins ($r = 0.98$), while it was second principal component that correlated with mean ranks in heads ($r = 0.59$).

To visualize the above described relationships between PC scores derived from the individual sets and mean ranks we adopted PCA biplot (Fig. 3). It clearly illustrates the presence of two distinct groups of mutually correlated variables. Both groups consist of PC scores belonging to all three data sets. In conclusion, there are two main axes of variability affecting human ranking of milk snakes attractiveness which are shared among all sets.

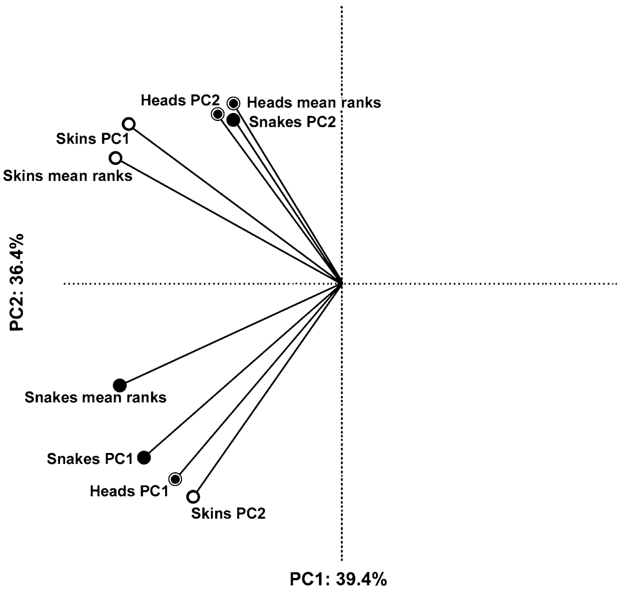

Fig. 3 Relationships between preference ranks, PC1 and PC2 scores computed separately for snakes, heads, and skins datasets. Position of individual variables denotes its loadings revealed by the principal component analysis including all these variables

Therefore, we combined the snakes, heads, and skins sets into the pooled one to assess common variation axes. PC1 accounted for 25.3% and PC2 for 16.2% of total variation in preference ranking. PC1 computed from pooled dataset correlates with the mean rank of the snakes set ($r = 0.72$; Fig. 4), while PC2 is closely associated with the mean ranks of the heads, skins, and its combination ($r = 0.95$, see Fig. 5). The higher the PC scores are, the higher are mean ranks and thus the lower the preference for a particular species is.

Association of the two multivariate axes with selected objective characters of the studied species

In order to interpret these PC axes derived from preference ranks in terms of phenotypic characters of the milk snakes, we performed multiple regressions explaining PC1 and PC2 by the log-transformed number of red (or white/yellow) transversal stripes and four color traits: arcsine-transformed proportions of red, black/dark brown, white/yellow, and gray/light brown on the snake body. The final models selected by backward selection of the variables revealed that variation in PC1 scores can be explained ($R^2 = 82.3\%$) by stripe pattern ($\beta = -0.50$; $P < 0.0001$) and red color ($\beta = -0.48$; $P = 0.0002$), while PC2 ($R^2 = 34.3\%$) by red ($\beta = 0.66$; $P = 0.0019$) and black ($\beta = 0.74$; $P = 0.0006$) colors.

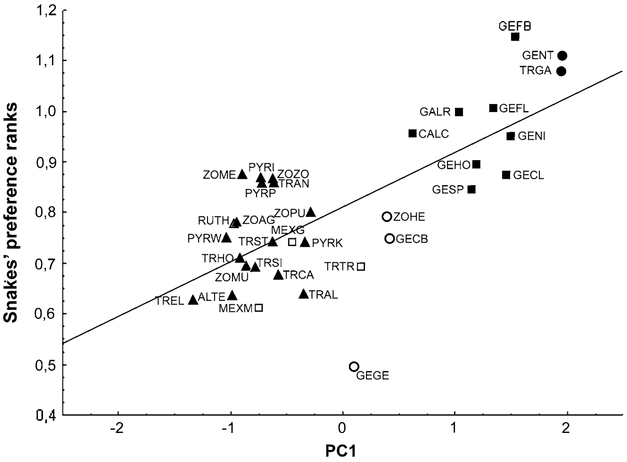

Fig. 4 Relationship between mean ranks computed from snakes dataset and PC1 scores computed from pooled dataset. $r = 0.719$, $P < 0.0001$. For abbreviations of species names see Fig. 2. Color and pattern groups are denoted as follows: *filled circle* uniform black; *filled square* unstriped; *open circle* white/yellow-dark striped; *open square* red-black-gray striped; *filled triangle* aposematic red-black-white/yellow striped

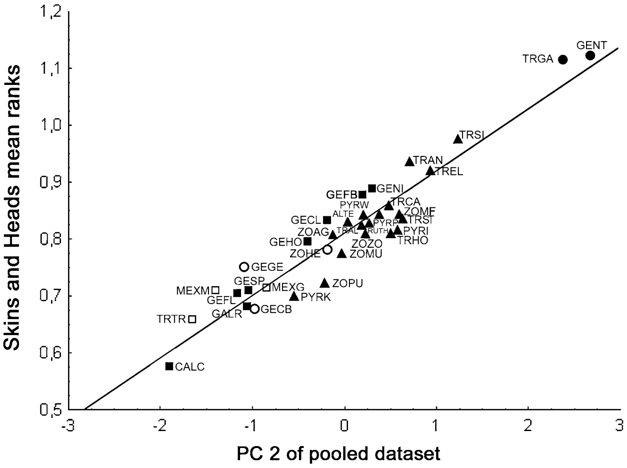

Fig. 5 Relationship between mean ranks computed from combined heads and skins dataset and PC2 scores computed from pooled dataset. $r = 0.951$, $P < 0.0001$. For abbreviations of species names see Fig. 2. Color and pattern groups are denoted as follows: *filled circle* uniform black; *filled square* unstriped; *open circle* white/yellow-dark striped; *open square* red-black-gray striped; *filled triangle* aposematic red-black-white/yellow striped

Alternatively, we added the effect of complex aposematic pattern (defined arbitrarily as simultaneous presence of red, black, and white/yellow transversal stripes) on PC scores. This factor replaced red color in final GLMs both for PC1 ($R^2 = 85.7\%$; stripe pattern: $F = 42.2$; $P < 0.0001$; aposematic: $F = 27.1$; $P < 0.0001$) and PC2 ($R^2 = 49.7\%$; black color: $F = 22.0$; $P < 0.0001$; aposematic: $F = 24.7$; $P < 0.0001$).

Positions of individual species/subspecies on the biplot of the first two principal components calculated from pooled data set are given in Fig. 6. The aposematic forms are characterized by low values of PC1, but high values of PC2. Note that the species most preferred by the respondents are placed on the left bottom part of the plot.

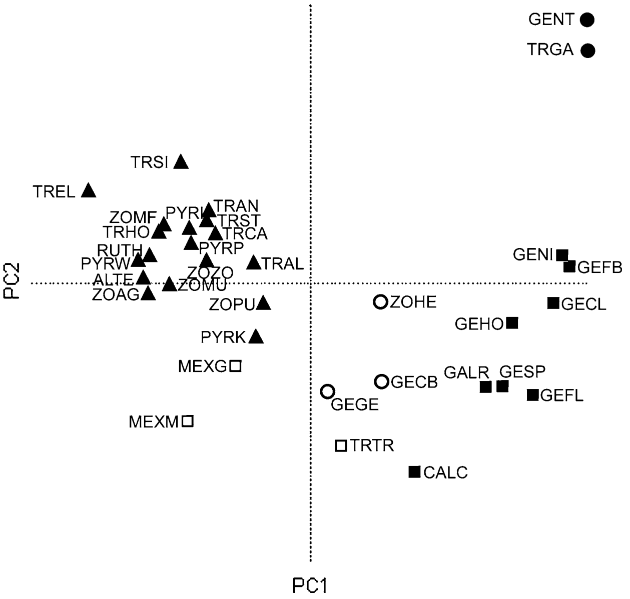

Fig. 6 Plot of studied taxa in space of the first two principal components (PC1 horizontally) computed from pooled dataset. Note that the species most preferred by the respondents are placed on the left bottom part of the plot. For abbreviations of species names see Fig. 2. Color and pattern groups are denoted as follows: *filled circle* uniform black; *filled square* unstriped; *open circle* white/yellow-dark striped; *open square* red-black-gray striped; *filled triangle* aposematic red-black-white/yellow striped

Correlations among respondents' preferences and factors reflecting public or scientific interest

Interestingly, neither ranks means computed from particular sets nor PC scores computed from pooled data are significantly correlated (all $R^2 < 5.3\%$) with following variables reflecting public or scientific interest in individual milk snake taxa: the number of individuals kept in zoos worldwide, the number of articles reported by the Zoological Records, the number of hits reported by Google for the text and pictures searched according to the Latin name (or alternatively according to the Latin or English name).

Discussion

Cognitive categories of milk snakes

Our experiment was primarily designed to assess human ranking of milk snakes only according to the perceived beauty. The respondents were not asked to categorize the pictures of milk snakes into groups, nevertheless, ranking structure allowed us to uncover underlying cognitive categories of studied milk snake taxa. Interestingly, the uniformly black forms (*L.t.gaigeae* and *L.g.nigrita*) were perceived by the respondents as most distinct. The remaining species/subspecies were split into those basically black/brown colored (some with white/yellow stripes) and red banded. The latter group further splits into a small cluster of two species with gray color (*L. mexicana* and *L. alterna*) and the main cluster of regularly red-black-white/yellow-striped forms belonging to *L. triangulum, L. zonata, L. pyromelana*, and *L. ruthveni.* It is the red-black-white/yellow-striped pattern of some *Lampropeltis* that mimics the typical aposematic coral snake pattern. Obviously, the respondents recognized this pattern and placed their bearers together.

The classification structure of taxa reflecting human aesthetic ranking resembles that extracted from a matrix of objectively defined color and pattern characters. It suggests that subjective cognitive categories reflect unconsciously but properly the objective similarities.

This leads to specific questions associated with human color perception and categorization. The opposition of black and white color is the first stage and the concept of red is the second stage of a universal sequence of color names appearance during language evolution according to the pioneering study of Berlin and Kay (1969; cf. Dedrick 2005; Kay 2005; Griffin 2006). Although this study was repeatedly criticized (Saunders and van Brakel 1997; Jameson 2005a, b; Roberson 2005) on methodological grounds as well as because it falsifies the concept of Whorfian linguistic relativism (cf. Whorf 1956), which advocates the cultural determinism, it is of interest that black/light and red colors contribute to the two main multivariate axes. The color variation is however substantially limited within the genus *Lampropeltis* and the above-mentioned colors contribute considerably to the total variation (besides gray and brown).

Rules of human aesthetic ranking

Human unsupervised categorization such as that performed by our respondents should be, for principal reasons, just one- or two-dimensional (Pothos and Chater 2002; Pothos and Close 2008). This conclusion fairly conforms to our results: the responses repeatedly arranged species along two gradients (PC1 and PC2 axes).

Surprisingly, when different sets of pictures depicting alternatively the whole snakes, heads, and mid-body skin were used, the respondents categorized the evaluated forms of milk snakes in a similar manner. Irrespective of the set of pictures, they arranged the forms along two multivariate axes, which were mutually correlated across the sets. Although each of these axes explained a comparable proportion of variance in preference ranking, only one of them was correlated with mean preference rank. The respondents categorized the species along both these axes, but just one of them determined the agreement about what is beautiful and what is ugly. Moreover, the respondents agreed about what is beautiful along one axis (that corresponding to PC1 of pooled data) when evaluating the whole snakes and along the other axis (PC2 of pooled data) when evaluating the snake fragments (head and/or skin). We may speculate that the respondents categorize first and then establish the polarity of the beautiful–ugly axis.

Interpretation of the multivariate axes and perception of aposematic pattern

The components of the aposematic pattern were significantly associated with both main multivariate axes of the human preference ranking. Most relevant in this regard were the proportion of red color as well as the number of stripes in the case of PC1, and proportions of black and red colors in the case of PC2. Surprisingly, these components of aposematic color pattern as well as the aposematic color pattern itself were preferred when the respondents were allowed to evaluate the whole snakes, whereas they were refuted when only heads or skin fragments were the subjects of preference assessment. There are at least three alternative, but not mutually exclusive, hypotheses explaining this observed ambivalent ranking of aposematic patterns. (1) A potentially dangerous aposematic object attracts human attention, but becomes repellent when seen in detail. This seems relevant, as snakes in the photographs may be subjectively perceived as being at a safe distance, while concentration on detail may simulate close confrontation with the animal. (2) The aesthetic appeal of the aposematic pattern may lie in its repetitive nature. These patterns lose their effect when only segments of the snakes are evaluated. (3) Disruptive patterns, which are nearly invisible at longer distance, may be fairly beautiful in detail.

In conclusion, (1) humans showed surprising ability to group milk snake patterns into meaningful clusters and thus perform the process resembling categorization which was extensively studied by psychologists (e.g., Anderson 1991; Malt 1995) and ethnobiologists (e.g., Berlin 1992; Medin and Atran 2004). (2) Obviously, humans recognize coral snake pattern as a coherent category, but (3) its aesthetic value differs according to whether it is evaluated as a whole or in isolated detail. Aposematically colored snakes thus also become a promising model for future studies of human cognition.

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Human responses to live snakes and their photographs: Evaluation of beauty and fear of the king snakes

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ABSTRACT

Animals are ancestrally important stimuli for us and thus, we pay disproportional attention to them over other objects. Some of them, like snakes, attract attention as well as elicit fear reactions. We assessed human aesthetic preferences and fear reaction aroused by 20 forms of king snakes, represented by live snakes and their photographs. There was no correlation between the beauty and fear response exuded by live snakes, which indicates that these are two independent processes. Evaluation of live snakes tightly correlated with the results obtained from photographs in both beauty and fear tasks. Respondents evaluated aposematic (black-and-white/yellow-red striped) and purely black species as the most fear-evoking, which is discussed in an evolutionary framework. Interestingly, irrespective of the actual task, i.e. evaluation of beauty or fear, respondents categorized the species within similar clusters (cognitive categories).

1. Introduction

In general, humans devote increased attention to animal stimuli (New, Cosmides, & Tooby, 2007; Ohman, 2007), and particularly to snakes (Isbell, 2006; LoBue & DeLoache, 2008; Mineka & Ohman, 2002; Ohman, Flykt, & Esteves, 2001; Waters & Lipp, 2008). Isbell (2006) suggested that snakes, especially the constrictors, had been the primary source of predation in early primate evolution. Snakes with a very effective venom delivery system that appeared 60 million years ago in Africa, where humans evolved, represented another selection pressure (Isbell, 2006). According to Bracha (2006), humans have shared a general snake phobia with most simians and such fear of snakes has already been present in the common ancestor. Experimental data support Isbell's and Bracha's theories. Many primates fear snakes and/or exhibit antipredator behavior, e.g. tarsiers (Gursky, 2005, 2006), marmosets (Clara, Tommasi, & Rogers, 2008), macaques (Cook & Mineka, 1989; Coss, McCowan, & Ramakrishnan, 2007; Ramakrishnan, Coss, Schank, Dharawat, & Kim, 2005; Roberts, McComb, & Ruffman, 2008) and humans (Hunt et al., 2006; Ohman, Carlsson, Lundqvist, & Ingvar, 2007; Ohman & Mineka, 2003; Wright, Holborn, & Rezutek, 2002). Learning is an important proximal mechanism of snake fear acquisition (Cook & Mineka, 1989; Gursky, 2006; Mineka, Keir, & Price, 1980). Once the fear is learned, it is not easily overcome.

Öhman and his colleagues (Ohman, Flykt, & Lundqvist, 2000; Ohman & Mineka, 2001) introduced a new theory of an evolved module of fear and fear-learning based on the concept of biological preparedness. Fear module is relatively independent and complex adaptation consisting of behavioral, psycho-physiological and neural system traits that enables a quick problem solving in potentially life-threatening situations without precise recognition of the threat. The module thus helps the organism to react immediately to the threatening stimuli (e.g. predatory animals) and to increase its survival. Ohman and Mineka (2003) considered snakes as a prototype stimulus for evolution of such a fear module in humans.

On the other hand, human attitude toward many non-human animals also involves aesthetic preferences (Thornhill, 1993). Humans are perfectly able to rank pythons and boas according to perceived beauty (Marešová & Frynta, 2008). Surprisingly, this evaluation of snake species is highly congruent across cultures (Frynta et al., in press). Nearly the same rankings were provided by European students and inhabitants of Papua New Guinea (Marešová, Krása, & Frynta, 2009). Moreover, this aesthetic ranking, together with species' body size, explained the conservation efforts devoted to captive breeding of the species (i.e. size of zoo population of the particular species worldwide; Frynta et al., 2009; Marešová & Frynta, 2008).

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Using different image technologies (pictures, photographs, and digitalized images) is necessary for our methods of the animal attractiveness evaluation. However, these methods presume the subject's ability to perceive a high level of correspondence between real animals and their pictorial representations. Similarly, laboratory experiments studying fear reactions to snakes require the understanding of the relationship between a snake stimulus (e.g. a photograph) and the real animal that it represents. Children (DeLoache & LoBue, 2009; LoBue & DeLoache, 2008; Waters & Lipp, 2008) and adults (e.g. Carlsson et al., 2004; Globisch, Hamm, Esteves, & Ohman, 1999; McGlynn, Wheeler, Wilamowska, & Katz, 2008; Miltner, Krieschel, Hecht, Trippe, & Weiss, 2004; Ohman et al., 2001; Ohman & Mineka, 2003; Ohman & Soares, 1994) have to commonly interpret 2D representations (pictures, photos, video stimuli) of 3D objects (live snakes) in studies on the fear reaction to snakes. Non-human primates are usually confronted with dummies of snakes in similar experiments (Emile & Barros, 2009; Prather et al., 2001; Ramakrishnan et al., 2005). Real snake threatening stimuli are used only rarely (Kalin, Shelton, & Davidson, 2004; McGlynn, Moore, Rose, & Lazarte, 1995; Wright et al., 2002), and species are sampled randomly. Also, the number of snake species that have been used as fear eliciting stimuli is low. Developmental studies in humans report that very young children progressively develop an understanding of the correspondence between real objects and their pictures. Newborns presumably (Bower, 1972 but see Dodwell, Muir, & Difranco, 1976) and 4–8 weeks old children certainly (Appel & Campos, 1977; Pipp & Haith, 1977) show behavioral differences when they are exposed to real objects and their two-dimensional representations. Better comprehension of the similarities develops later, between six (Rose, 1977 in Bovet & Vauclair, 2000) and 18 months of age (Ganea, Pickard, & Deloache, 2008). The full understanding of the depicted locations of hidden objects develops afterward, about the age of 30 months (DeLoache & Burns, 1994).

However, some anthropological cross-cultural studies suggest that even adults can experience initial difficulties finding the correct correspondence between objects and their pictorial representations. When adults with minimal contact with pictorial materials in Africa were tested, they recognized the depicted animal objects correctly but with some difficulties. They firstly devoted their attention to particular characters (horns, ears, legs, and tails) and then they recognized the whole animal (Deregowski, 1976; Deregowski, Muldrow, & Muldrow, 1972; for other examples see review Bovet & Vauclair, 2000). According to these studies, both practice with 2D object representations and experience with the real objects seems to be necessary to understand their correspondence.

In our previous experiments, in which we tested human aesthetic preferences over a wide set of animal species (Frynta, Lišková, Bultmann, & Burda, 2010; Frynta et al., 2009; Marešová & Frynta, 2008; Marešová, Landová, & Frynta, 2009), we faced a different problem. The respondents, highly accustomed to use the pictures/photographs, were asked to evaluate the beauty of snakes and other animals represented by their photographs. We assumed that the respondents' visual experience of a photograph/picture was similar to seeing a live animal. It should be noted that even the students of biology were experienced with, or had knowledge of, only a small fraction of the species. This was due to species richness in the examined taxonomic groups and the applied method of random species sampling (Frynta et al., 2009). To validate the usage of pictures and digitalized images, we designed an experiment to compare human ranking of live snakes with the ranking of their photographs. In both instances, we asked the respondents to evaluate both the aesthetic attractiveness of the species (beauty) and the fear that the species evoked. We examined which features of the animal explain human evaluation and we analyzed whether the level of the perceived fear affects human aesthetic preferences to live snakes.

The aims of this paper were: (1) to compare the respondents' assessment of live snakes and their pictorial representations; (2) to examine whether the perceived fear from snakes distorts perception of their beauty; (3) to explore the contribution of the species' physical characteristics and particularly the aposematic (warning) coral snake pattern to both beauty and fear perception; (4) to uncover categorization accompanying the assessment of beauty and fear.

2. Materials and methods

2.1. Stimuli

We selected 20 subspecies/forms of the genus *Lampropeltis* that cover most of the naturally occurring variability in color patterns (Markel, 1994), as well as the perception categories recognized by humans (Marešová, et al., 2009). Eight subspecies/forms exhibited black-and-white/yellow-red striped aposematic coloration. Aposematism is a biological concept introduced by Wallace (1867) and Poulton (1890); it describes the signalization of a defended prey that it is unprofitable (venomous, poisonous and/or dangerous) to its predators, usually by warning coloration (also see Ruxton, Sherratt, & Speed, 2004). Subadult or adult individuals belonging to various subspecies of the genus *Lampropeltis* were gathered from zoos and private breeders. We selected twenty individuals for the experiments, each of them representing a distinct subspecies/color form. They were kept singly in standard conditions, weighed and photographed prior to the experiments. These experimental snakes and/or their color photographs were further used as stimuli. To obtain standardized photographs, we digitally set all the snake bodies on a white background, regardless of their real size. We printed the photos in the format 10 × 15 cm.

2.2. Procedure

Our respondents were undergraduate students of the Faculty of Sciences at the Charles University in Prague, Czech Republic, who agreed to participate in the project. Each subject provided a written consent and additional information about age, sex, attitude toward snakes (very positive, positive, neutral, negative, phobic), and knowledge of the presented species.

Each of the 72 respondents (50 women and 22 men) was exposed to 20 live snakes during the first experimental session. In the second session that was performed after seven days, the same persons were asked to evaluate 20 photographs of the presented snakes. Although no explicit time limit was given, all the respondents performed the tasks within a few minutes.

Live snakes were presented in glass terrariums (600 × 300 × 250 mm), each provided with a white paper covering the floor, water in a transparent dish and a heating cable hidden under the floor. The terrariums were placed on tables (800 mm high) that were arranged in a u-shape manner within an experimental room (60 m^2). Terrariums were presented in a random assemblage and spaced by 300 mm. The respondents had a chance to view all the terrariums/snakes simultaneously from the starting point and were allowed to observe the snakes from close proximity. We asked them: "Please, rank these animals according to their beauty, from the most beautiful snake (rank = 1) to the least beautiful one (rank = 20)". Next (after a short interruption), we asked the respondents to perform another ranking of the same snakes, this time according to perceived fear. The instruction was as follows: "Please, imagine that you are asked to touch the snakes and handle them into another cage. Then rank these snakes from the most fear-evoking (rank = 1) to the most harmless one (rank = 20)".

To evaluate snake photographs, respondents were presented with the photos placed on a table in a random assemblage. We asked them: "Please, pack the photographs in your hand in an order corresponding to the beauty of the depicted snake, 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 20, further referred to as ranks. After a short break (20 min), the respondent was asked to repeat the procedure and rank the same set of photographs according to the perceived fear, from the most "fear-evoking" to the most "harmless" animal.

In the main experiment, the stimuli were rated in a fix order; live snakes first (beauty before fear), followed by the evaluation of pictures one week later. This order of presentation does not favor correlation between the evaluation of live snake stimuli and their pictures. The more difficult task (moving 3D stimuli in a variable position) was tested first to prevent learning of the rating order. However, to control the influence of the presentation order, we performed a control experiment. Additional 81 respondents (28 males, 53 females) ranked beauty and fear of the snakes depicted in photos only. We correlated the ranking of the picture stimuli presented in the first order (this control experiment) with the ranking of the pictures presented after the ranking of the live snakes (main experiment). The ranking of beauty of the picture stimuli in the control experiment highly corresponded to the ranking in the main experiment (quantified by Pearson *r*-squared expressed in percent): $r^2 = 67\%$. Even a better association was revealed in the fear task: $r^2 = 84\%$. Such a strong correspondence of independent sets varying in the order of presentation indicates that the subsequent presentation of picture stimuli in main experiment should not substantially influence the results.

2.3. *Congruence among the respondents and the influence of sex, age, attitude to snakes, experience with them and knowledge of the presented animals*

The agreement among the respondents was quantified by Kendall's coefficient of concordance as implemented in SPSS (Statistical Package for the Social Sciences), version 16.0. The

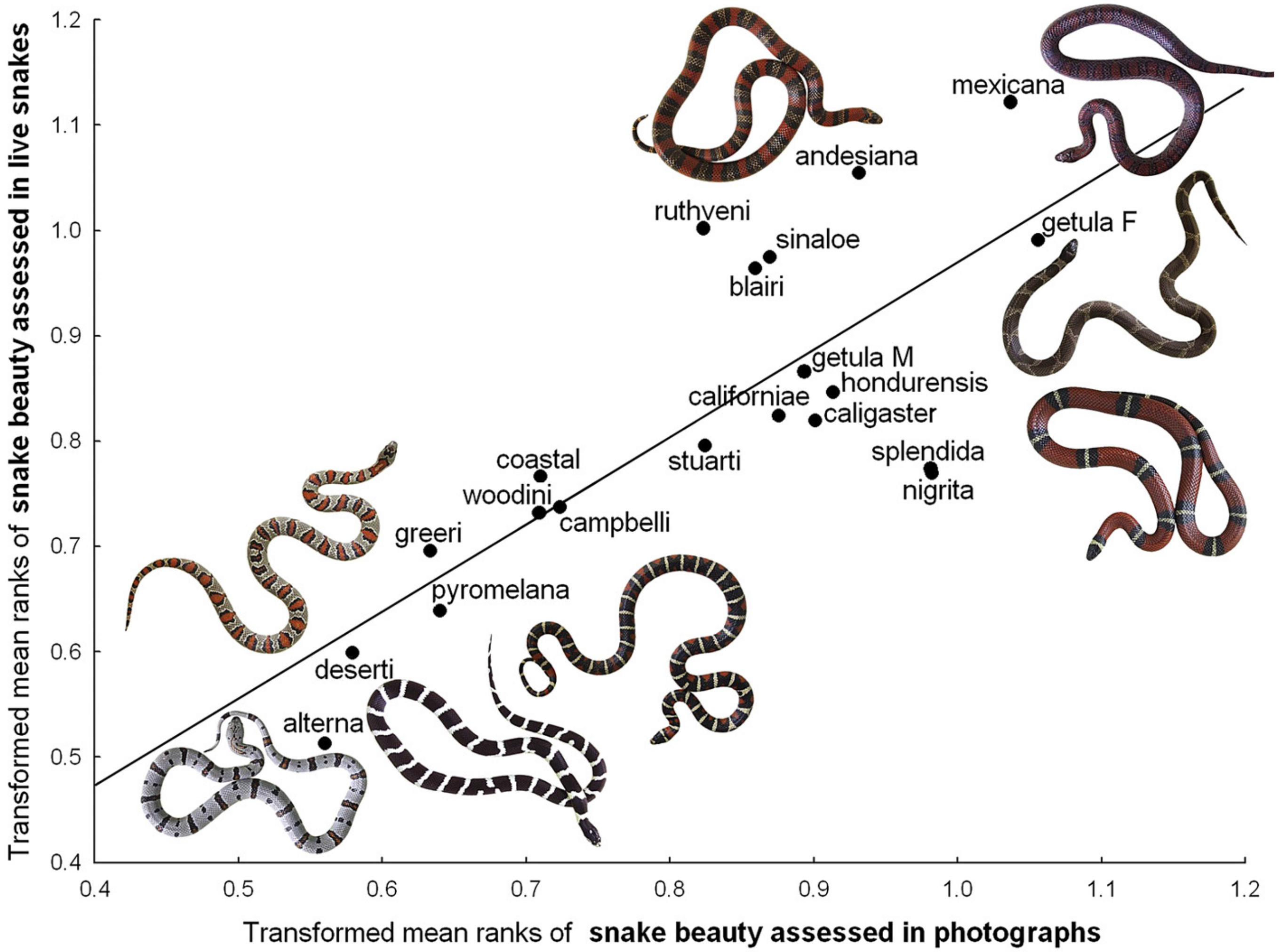

Fig. 1. Relationships between beauty assessed in live snakes and their photos. There is a significant correlation between photo and live snake aesthetic ranking ($r^2 = 0.61$; $r = 0.78$, $p < 0.001$; $y = 0.14 + 0.83^*x$). Note that the species most preferred by the respondents are placed on the left bottom part of the plot. Species with aposematic pattern (tricolor ringed) are equally distributed along the correlation line. The taxa are abbreviated as follows: alterna – *Lampropeltis alterna*, blairi – *L. alterna blairi*, calligaster – *L. c. calligaster*, californiae *L. californiae* (longitudinal stripes), deserti – *L. californiae deserti* (transversal stripes), coastal – *L. californiae coastal* (transversal stripes) getula F– *L. g. getula* (brown patter), getula M– *L. g. getula* (black patter), nigrita – *L. g. nigrita*, splendida – *L. splendida*, mexicana– *L. mexicana*, greeri – *L. m. greeri*, pyromelana – *L. p. pyromelana* (a), woodini – *L. p. woodini* (a), ruthweni – *L. ruthweni* (a), andesiana – *L. triangulum andesiana* (a), campbeli– *L. t. campbelli* (a), hondurensis – *L. t. hondurensis* (a), sinaloe – *L. t. sinaloe* (a), stuarti – *L. t. stuarti* (a); (a) – As aposematic coloration was formally classified red-yellow/white-black ringed color pattern. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ranking of species provided by individual respondents was divided by 20 and square root arcsin transformed to achieve normal distribution. The transformed data were further analyzed by Principal Component Analysis (PCA) to visualize their multivariate structure. Multivariate Hotelling test was used to test the differences between the ranking provided by male and female respondents. No effect of sex was found in any of the four comparisons; beauty of live snakes: $T^2 = 44.86$, $F_{19,52} = 1.75$, $p = 0.056$ (but *Lampropeltis blairi, Lampropeltis triangulum stuarti* and *Lampropeltis woodini* were more preferred by men than women according to results of the partial t tests, $p = 0.025$, 0.017 and 0.020, respectively); beauty of snake photos: $T^2 = 8.81$, $F_{19,52} = 0.34$, $p = 0.993$; fear of live snakes: $T^2 = 32.43$, $F_{19,52} = 1.27$, $p = 0.245$; fear of snake photos: $T^2 = 29.90$, $F_{19,52} = 1.17$, $p = 0.318$. These results allowed us to pool the rankings provided by the respondents of both sexes in further analyses.

Next, we constructed a complete model that included sex and additional information that the respondents provided (age, attitude to, and experience with, snakes, and knowledge of the tested species). MANOVAs (Multivariate Analysis of Variance) performed separately for each task (beauty and fear in pictures and live animals) revealed a single significant effect of the attitude to snakes on the ranking of beauty in photos ($F = 1.65$; $p = 0.004$). The respondents with positive attitudes to snakes more preferred *Lampropeltis alterna* and aposematic snakes (*Lampropeltis ruthveni, Lampropeltis triangulum sinaloe*, *L. t. stuarti, L. woodini*) than the respondents with negative attitudes to snakes, who liked better black *Lampropeltis nigrita* and black-and-white *Lampropeltis getula* and *Lampropeltis splendida*.

2.4. Further statistical tests

Means of the transformed ranks for each analyzed snake and/or photograph were used as measures of the perceived beauty and fear. These variables were further analyzed by the least square linear regression (Pearson r-squared) and multiple regressions. We also performed GLMs, in which characters assessed in the experimental snakes, i.e. log-transformed body weight (in grams), the presence of black, red and white/yellow colors and the regular striping pattern, were adopted as explanatory variables.

Correlation matrices of the transformed rankings of the species (performed by individual respondents) were further treated by Cluster Analysis (CA) to reveal species grouping that underlay all respondents' rankings. We performed most calculations in Statistica 6.0. (StatSoft, 2001).

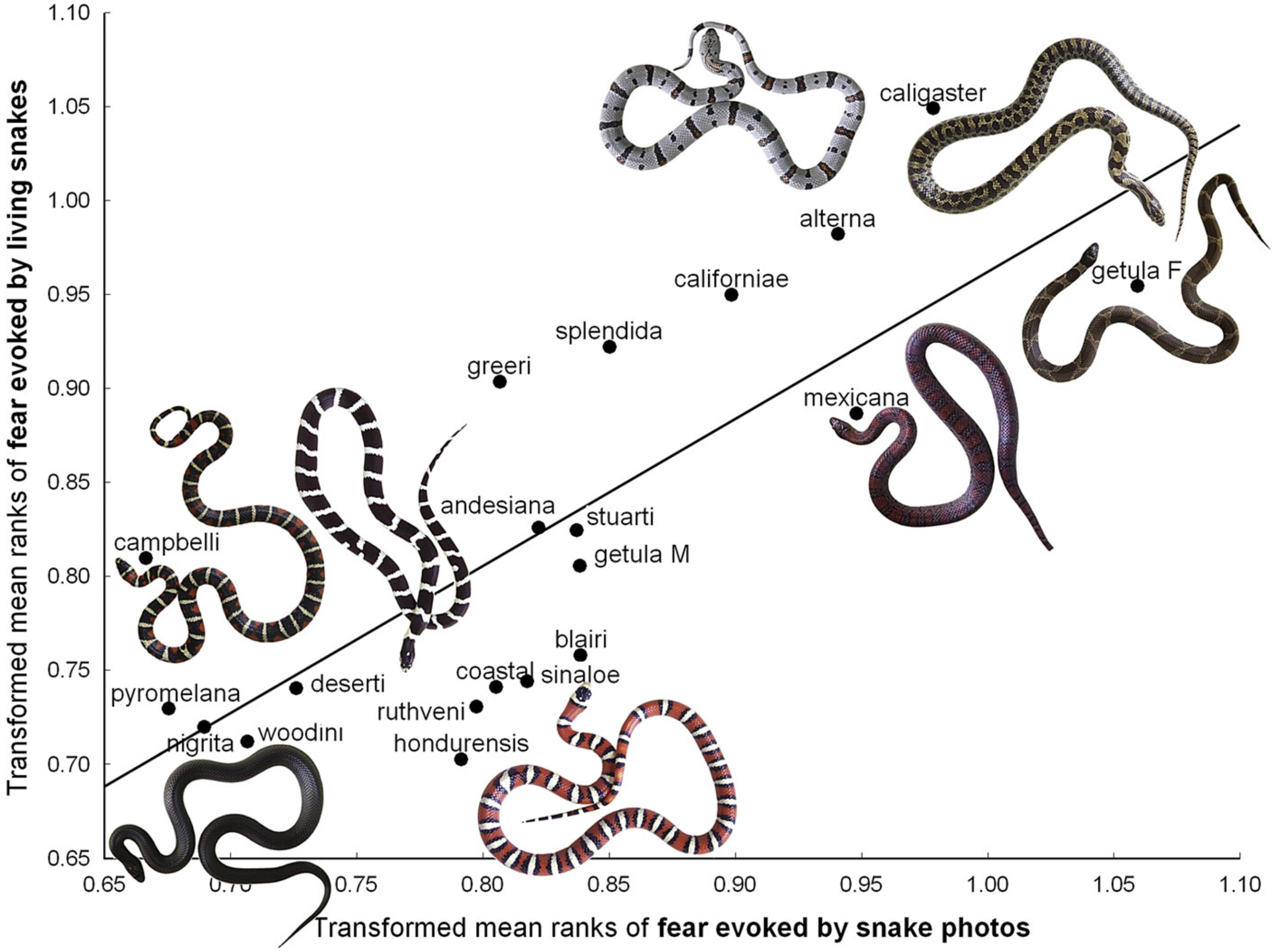

Fig. 2. Relationship between fear assessed by ranking live snakes and their photos. There is significant correlation between photo and live snake fear evaluation ($r^2 = 0.60$; $r = 0.78$, $p < 0.001$; $y = 0.18 + 0.78^*x$). Note that the species perceived by the respondents as most dangerous are placed on the left bottom part of the plot. Species with aposematic pattern (tricolor ringed) were repeatedly perceived as dangerous. For abbreviations of species names see Fig. 1.

3. Results

3.1. Congruence among the respondents

The Kendall concordance coefficient expresses the simultaneous association (relatedness) between several sets of rankings and it is usually used to assess inter-judge reliability (Statistica 6.0). Here, in order to quantify the agreement among respondents, we computed Kendall's coefficient of concordance (W; $df = 19$) separately for each combination of stimulus and question. The respondents agreed in the decisions regarding snake beauty (live snakes: $W = 0.196$, $p < 0.001$; photos: $W = 0.183$, $p < 0.001$). This level of agreement is common in beauty tasks with photos in other taxonomic groups (parrots, Frynta et al., 2010) or different ethnics (Papua New Guinea, Marešová et al., 2009). In contrast, the agreement in the fear perception was less apparent (live snakes: $W = 0.084$; photos: $W = 0.083$), although still statistically significant (both p's < 0.001).

In the case of the beauty assessments, the transformed mean ranks of both live snakes and photos highly corresponded to the first multivariate axes (PC1) extracted from the original data sets: $r^2 = 97.0\%$ and 79.8%, respectively. Thus, we further treated the transformed mean ranks as an intuitive and easily interpretable measure of the perceived snake beauty. Correlations between the transformed mean ranks and multivariate axes were less apparent in the case of fear aroused by live snakes (PC1: $r^2 = 56.0\%$) and corresponding photos (PC2: $r^2 = 53.5\%$). In the case of the other principal axes (PC2 in live snakes and PC1 in photos), respondents ranked the species along the shared axis, but they differed in the orientation of the fear scale (i.e. which pole contain species most evoking fear). Thus, mean ranks of fear (henceforth referred to as the measures of perceived fear), reflecting only those components of variation in the ranking that share both the gradient and its orientation, are still applicable in this particular case.

3.2. Relationships between perceived beauty and fear in live snakes and photos

Next, we performed mutual correlations of the four variables, i.e. the beauty and fear measures obtained from the experiment with live snakes and photos. The perceived beauty of live snakes tightly correlated with the beauty of the depicted ones and explained a considerable portion of variance: $r^2 = 61.3\%$ (Fig. 1). The same correspondence was revealed in the fear task: $r^2 = 60.3\%$ (Fig. 2). In contrast, there was hardly any relationship between the perception of beauty and fear. Measures of beauty and fear obtained in the experiment with live snakes have remained completely uncorrelated ($r^2 = 0.1\%$, $p = 0.92$), and the corresponding values from the experiment with photos were correlated only loosely ($r^2 = 20.4\%$, $p = 0.046$).

Stepwise multiple regression confirmed that the beauty perception of live snakes can only be explained by the beauty assessed using their photographs ($r^2 = 61.3\%$, $F_{(1,18)} = 28.5$, $p < 0.001$), but not by the measures of fear or body size. Similar analysis performed with the measures of the fear of live snakes ($r^2 = 81.5\%$, $F_{(2,17)} = 37.4$, $p < 0.001$) showed that this variable can be predicted from the fear assessed by ranking the snake photos ($\beta = 0.90$, $p = 0.002$) and from the body weight of the evaluated snakes ($\beta = 0.90$, $p < 0.001$).

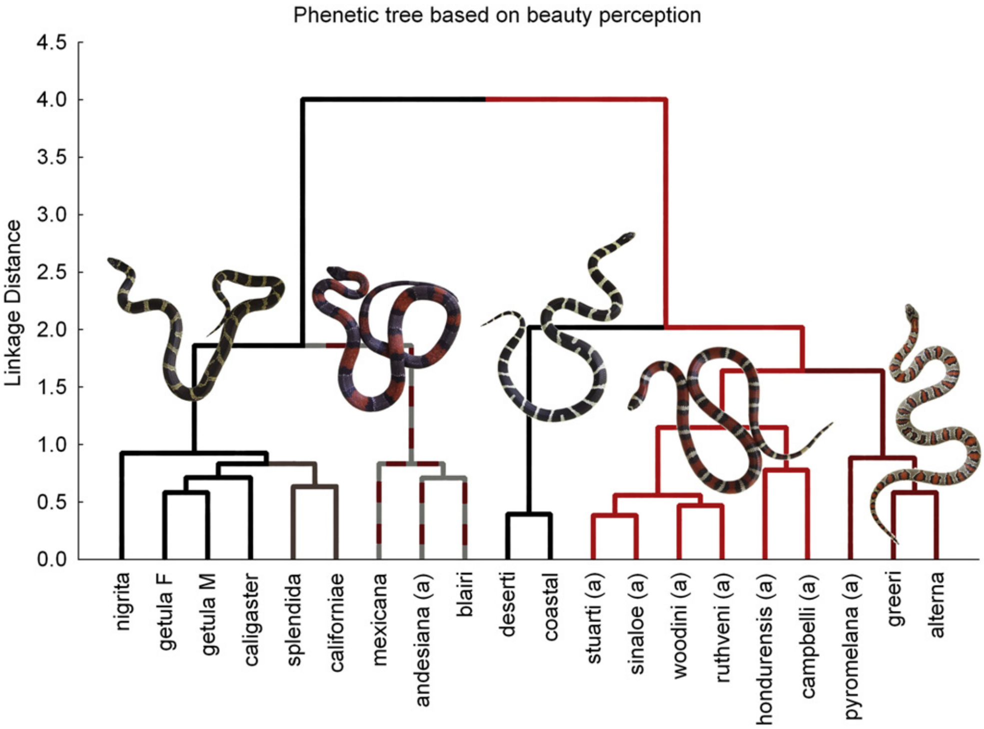

Fig. 3. In order to reveal beauty categories inherently present in respondent's evaluation of our set of king snakes we constructed phenetic tree based on matrices of correlations among the rankings of 20 studied snakes. Ward's clustering method was applied. The aposematic species clustered together, only *L. triangulum andesiana* that was very dark individual clustered with non-aposematics. Black and white ringed forms (*L. californiae deserti, L. californiae coastal)* and those with big portion of red color (*L. alterna, L. mexicana greeri*) clustered together with aposematics. Remaining darkly colored species (sometimes with sporadically red, e.g. *L. mexicana, L. alterna blairi*) form another cluster. As aposematics were formally classified those forms possessing red-yellow/white-black ringed color pattern (a). For abbreviations of species names see Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. *Explanation of perceived beauty and fear by visceral traits (physical characteristics) of snake stimuli*

In order to find the factors underlying human responses to live snakes, we performed GLMs in which beauty or fear was given as dependent variable. The body weight of the snake, presence of red, black and white/yellow colors and striping pattern were used as factors. The final reduced model for beauty perception (GLM: $r^2 = 68.9\%$, $F_{(3,16)} = 11.81$, $p < 0.001$) included the body weight ($\beta = 0.71$, $F = 24.3$, $p < 0.001$), and red ($\beta = 0.45$, $F = 8.51$, $p = 0.01$) and black ($\beta = -0.41$, $F = 7.59$, $p = 0.014$) colors. The perceived fear (GLM: $r^2 = 56.8\%$, $F_{(2,17)} = 11.17$, $p < 0.001$) increased with the body weight ($\beta = -0.37$, $F = 5.12$, $p = 0.037$) and the proportion of the black color ($\beta = -0.72$, $F = 20.01$, $p < 0.001$).

3.4. *Phenetic trees based on fear or beauty rankings – categorization of the species*

In order to reveal categories inherently present in the respondent's evaluation of our set of king snakes, we computed matrices of correlations among the rankings of 20 studied snakes, separately for the data reflecting the perceived beauty and fear. These two matrices fairly corresponded one to another ($r = 0.89$). Mantel test confirmed that this correlation between the matrices was significant (1,000,000 replicates, $t = 11.91$, p random $z <$ observed $z = 1.00$). Next, we employed cluster analysis and constructed a phenetic tree from each of these correlation matrices (Figs. 3 and 4) to reveal the categorization processes underlying beauty and fear rankings. Basal branching clearly separated tricolored species (including red stripes and/or spots) from bicolor (black/brown with yellow/white stripes or spots) and unicolor (black/brown) ones.

4. Discussion

Our results proved that the respondents' little direct experience with the presented species did not result in difficulties when they were to rank live snakes and their photographs according to the perceived beauty or fear. The unexplained portion of variability in ranking may arise not only from inter-individual differences but also from random factors such as the respondents' mood, immediate vigilance of the snake in the terrarium, or mistakes that may occur during the ranking of 20 simultaneously presented snakes/photographs. We found the usage of pictorial stimuli appropriate and comparably relevant as the use of live animals.

The high congruence in beauty perception may be partly explained not only by shared aesthetic preferences for colors (Crozier, 1999), symmetry (Enquist & Johnstone, 1997) and repetitive patterns (Kenward, Wachtmeister, Ghirlanda, & Enquist, 2004), but also by more delicate features like animal body shapes (Halberstadt & Rhodes, 2000, 2003). However, the role of warning coloration in human aesthetic and fear perception is worth further interest. Many species of relatively harmless king snakes (genus *Lampropeltis*) are Batesian mimics (Bates, 1981) of the genus *Micrurus* (Elapidae). Visual similarity to these deadly poisonous

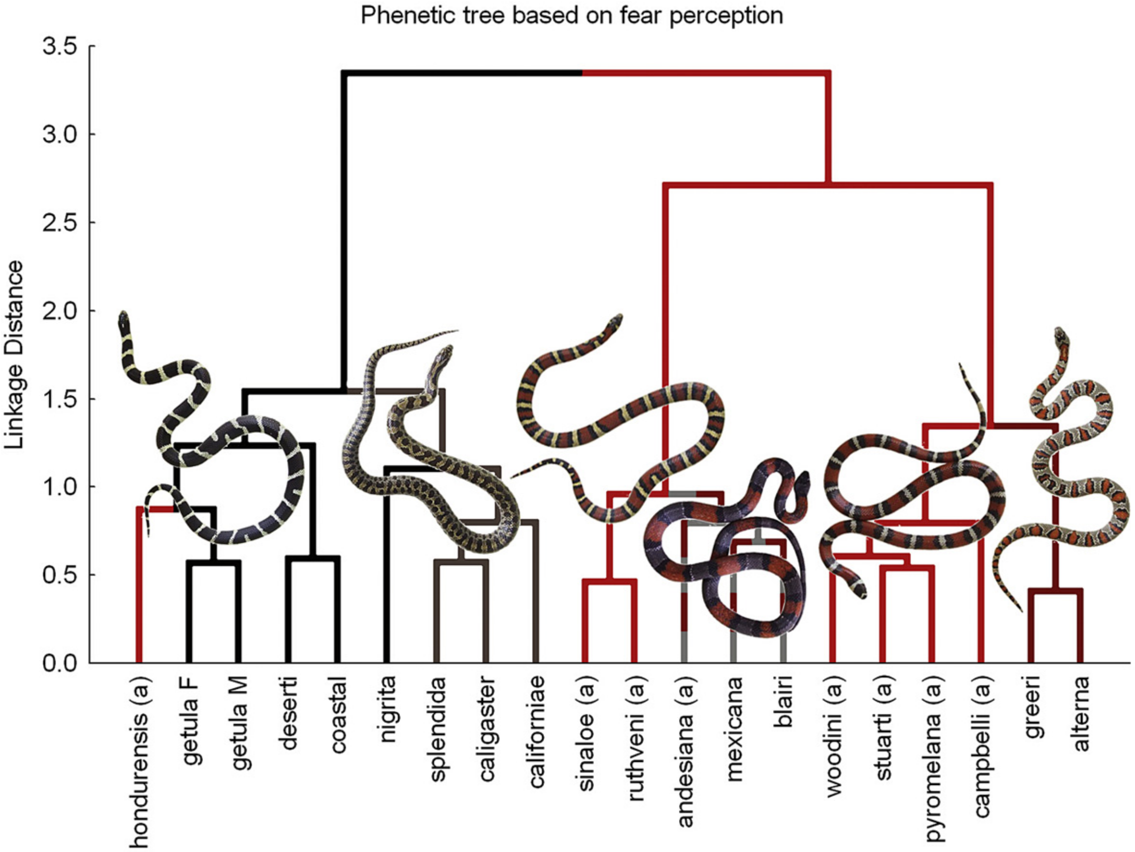

Fig. 4. Phenetic tree based on fear rankings. In order to reveal fear categories inherently present in respondent's evaluation of our set of king snakes, we computed matrices of correlations among fear ranking of 20 studied snakes. Ward's clustering method was applied. The aposematic species clustered together with the exception of *L. t. hondurensis* – It was the biggest individual. With aposematics now clustered all remaining species possessing red color. The "non-aposematics" split in two clusters: forms with ringed and disruptive or plain pattern. As aposematics were formally classified those forms possessing red-yellow/white-black ringed color pattern (a). For abbreviations of species names see Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

snakes helps them to deceive visually oriented predators, mostly birds of prey, and therefore avoid predation pressure (Brodie & Brodie, 2004). Eight forms of king snakes presented in this study possess aposematic red-yellow/white-black ringed color pattern. Some of these species were perceived as very attractive (e.g. *Lampropeltis pyromelana pyromelana*) and some as unattractive (e.g. *Lampropeltis triangulum andesiana* or *Lampropeltis hondurensis*). Rather than classical aposematic pattern, humans preferred slim forms of king snakes with highly contrasting coloration, while big and dark forms with disruptive or plain pattern appeared unattractive. The most attractive species *L. alterna* (Fig. 5a) was greyish blue with black and red stripes, the only form exhibiting blue shade. This is in congruence with studies of color preferences, in which humans (McManus, Jones, & Cottrell, 1981) as well as rhesus monkeys (Humphrey, 1972; Saghal, Pratt, & Iverson, 1975 cited in McManus et al., 1981) favored blue color.

Aposematic (tricolor ringed) and purely black species evoked the most fear (Figs. 2 and 5b,c). Also, bigger species were perceived as more dangerous than smaller ones. It is well known that avian predators of snakes living in sympatry (together) with coral snakes, but not those living in allopatry (different ranges), have evolved innate avoidance of these dangerous animals (Smith, 1975, 1977, 1980). Humans probably encountered coral snakes, that occur exclusively in the New World range, about 13 thousand years ago (Erlandson, Moss, & Des Lauriers, 2008), when the first people colonized America. Nevertheless, European participants had no direct co-evolutionary experience with coral snakes. Instead, our fear of aposematic coral snake pattern may be explained by the universal perception of the warning black-and-white/yellow-red striped pattern signal that we share with other animals. This hypothesis is widely accepted in a number of studies focused on the detection of aposematics by humans (Bohlin, Tullberg, & Merilaita, 2008; Sandre, Tammaru, & Mand, 2007; Tullberg, Gamberale-Stille, Bohlin, & Merilaita, 2008), or on the simulating evolution of the aposematic pattern (Beatty, Beirinckx, & Sherratt, 2004; Hagman, Forsman, & Wainwright, 2003). On the other hand, humans can acquire fear indirectly through social learning, without personal experience of the aversive event. There are similar neural mechanisms engaged in this process as during fear conditioning (Olsson, Nearing, & Phelps, 2007). The indirect experience such as various forms of education is an alternative explanation for the fear of aposematic snake species.

In our previous paper (Marešová et al., 2009), we examined the rules commonly used by respondents in the ranking of king snake attractiveness. The respondents spontaneously classified the attractiveness of the species according to two dimensions. However, the data revealed several distinct clusters of species instead of a continuous gradient. This process resembled an unsupervised categorization (Pothos & Chater, 2002; Pothos & Close, 2008). The structure of present data also uncovered the underlying cognitive categories of the studied king snake taxa, both in beauty and fear tasks. There were two main clusters of species: (1) tricolor species (including red stripes and/or spots) and (2) bicolor (black/brown with yellow/white stripes or spots) and unicolor (black/brown) ones. Interestingly, the species clustered in a similar way irrespective of the actual task, i.e. whether the beauty or fear had been assessed (see Figs. 3 and 4).

The respondents showed no trouble to evaluate the beauty of the presented king snakes whereas they were less confident when assessing the fear, which is reflected by lower congruence. This might have contributed to the loose correlation between perceived beauty and fear in the case of photographs. On the other hand, the measures of beauty and fear exuded by live snakes remained clearly uncorrelated. The measures of the perceived fear obtained from

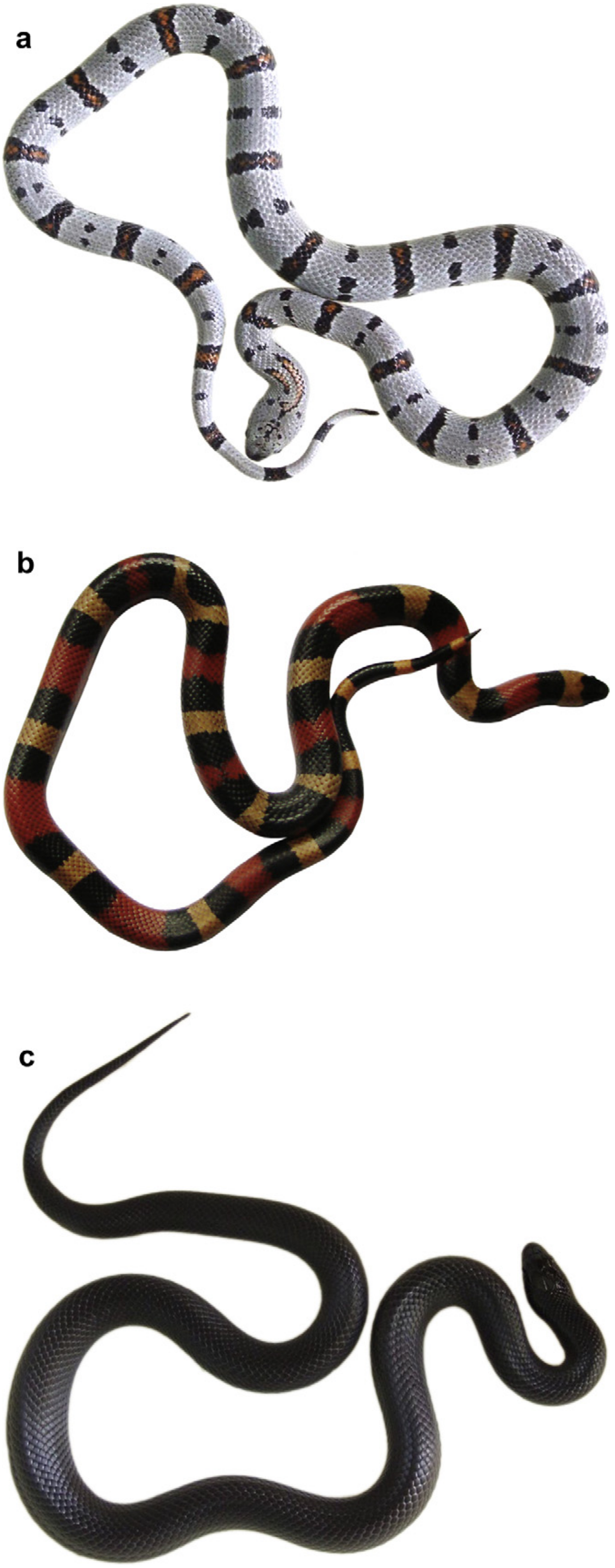

Fig. 5. The most preferred form *Lampropeltis alterna* posseses greyish blue background color (a). Humans prefer blue color (McManus et al., 1981) and also animals that posses blue color (Frynta et al., 2009). The most fear evoked *Lampropeltis triangulum cambelli* (b) and *Lampropeltis nigrita* (c). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

photographs highly corresponded to those of live animals. The species can be assessed as beautiful and fearful at the same time.

In conclusion, the perception of beauty and fear of the snakes appeared to be two independent processes. Despite that, humans grouped the species to similar cognitive categories. This phenomenon may be interpreted by a need for simple explicit categorization rules that help us to deal with new situations promptly. Although our participants do not have relevant evolutionary experience with deadly coral snakes and their aposematic pattern, the respondents recognized this pattern as a fear-evoking signal.

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Appendix. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.jenvp.2011.10.005.

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ANALYSIS

Noah's Ark is full of common species attractive to humans: The case of boid snakes in zoos

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ABSTRACT

As the fate of endangered species may largely depend on human decisions, we analyzed the effect of species attractiveness to humans on conservation efforts devoted to captive breeding. Our respondents were asked to rank photographs of 56 species of boas and pythons according to perceived attractiveness. Surprisingly, attractiveness, body size and, marginally, also taxonomic uniqueness of the species were the only significant predictors of the size of zoo population. On the other hand, variables putatively associated with species rarity (inclusion in the Red List or protection by international law, geographic range size, and commercial price) had no effect. The range size was, however, positively correlated with attractiveness. As the perceived attractiveness affects at least some components of the conservation effort, it should not be further neglected but should be routinely included into conservation reasoning.

1. Introduction

Human attention no longer poses such an obvious threat to vertebrate populations as it did in the past. Although conspicuous forms do suffer more than others from hunting, this fact is outweighed by increased conservation effort. As a result, the proportion of conspicuous forms among threatened species gradually decreases, e.g. the typical threatened bird used to be a large one suffering from hunting while now it is a small bird suffering from loss of habitat (Bennett and Owens, 2002). Furthermore, endangered species now compete with one another for financial and political support of "in situ" as well as "ex situ" projects. The winners tend to be species that satisfy human aesthetic and emotional requirements, rather than those most vulnerable. It is perceived attractiveness to humans (Gunnthorsdottir, 2001), physical size (Metrick and Weitzman, 1998), the degree to which a particular species is considered "a higher form of life" (Metrick and Weitzman, 1996) and resemblance to humans (Samples et al., 1986), that increase support for efforts to save a given species.

Although perceived attractiveness 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. Quantitative studies carried out on a finer taxonomic scale are therefore needed.

A suitable group of animals for such a study are boas and pythons. They can be bred in captivity and are frequently kept in zoos. They also vary considerably in pattern, color and size. Moreover, this group includes species that are very rare as well as those that are common and the conservation value of captive populations therefore differs a great deal.

Hunting to obtain skins and to supply pythons and boas to the pet trade is presently reduced (Murphy and Henderson, 1997). Skin hunting is restricted by the Convention on International Trade in Endangered Species of Wild Flora and

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Fauna (CITES) while the pet market is sufficiently supplied by captive breeding. Wild populations, however, are threatened nowadays primarily by the loss of their habitat and by expanding human population. In the case of several forms, which are rare or even restricted to a particular island, captive breeding guaranteed by zoos becomes crucial to their fate.

The aim of this study was (1) to assess human aesthetic preferences within a representative sample of living species of boas and pythons; (2) to evaluate the extent to which such preference as well as body size of the species explain the number of individuals of a given species kept in zoos worldwide; and (3) to assess also whether this number can be explained by factors reflecting the conservation value of the captive population, i.e. taxonomic uniqueness, present geographic distribution, listing in the categories of The World Conservation Union (IUCN) and CITES Appendices and market availability, here substituted by commercial price.

2. Materials and methods

We collected 56 photographs of boas and pythons each depicting a typical individual of its species. The snakes were digitally photographed in a moderately packed position to cover the whole body of the animal. In case of rare species, photos adopted from the book (Walls, 1998a,b) supplemented original ones. We digitally set all the snake bodies on black background regardless of their real size and printed in the format 10 × 15 cm. As the number of tested species was too high to be scored altogether, we split them into two comparable sets (I and II), each consisting of 32 photographs (the same 8 photos repeated in both sets as a control).

Our respondents were undergraduate students of Charles University (Faculty of Natural Sciences), who agreed to participate in the project. Each person was exposed to one set, i.e. 32 photographs, placed on a table in a random assemblage. Then we asked her or him: “Please, pack the photographs in an order corresponding to the beauty of the depicted snake 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 32, further referred to as ranks. Each subject provided a written consent and additional information about age, sex, attitude toward snakes (positive, neutral, negative, phobic), experience with snakes and other pets, and knowledge of the presented species. Although no explicit time limit was given, all the respondents performed the task within a few minutes.

Set I and set II were evaluated by 62 (40 women and 20 men) and 56 (45 women and 11) respondents, respectively. The ranking of species provided by individual respondents was analyzed by Principal Component Analysis (PCA) to visualize the multivariate structure of our data sets. The first principal component accounted for 43.2% and 45.9% of variation in set I and set II, respectively. As it closely correlated with the mean rank of the species (in both sets $r_S = 0.99$, $P < 0.001$), we adopted the latter variable as a measure of human preference in further analyses (referred to as preference). Next we compared the ranks of control species in sets I and II, found high correlation of the means ($r = 0.98$, $P < 0.001$) and pooled the mean ranks from sets I and II.

As the sexes were unequally represented among respondents, it was necessary to test sex differences prior to further analyses. For this purpose we increased the number of male respondents of set I up to 35 and randomly selected a corresponding number of female respondents, who had evaluated the same set. Multivariate Hotelling's t-test revealed no significant effect of sex on the ranking of species ($F = 1.40$; $P = 0.160$).

We carried out an additional experiment to test the effect of snake within-species variation and/or the posture on the photograph. The respondents ($n = 25$) were asked to rank 30 photographs (selected from those used in the main experiment) and after 24–48 h retested with a different set of photographs, in which each species from the previous set was represented by another individual exhibiting an apparently different position. A different 25 respondents were asked to rank the same set of photographs two times (controls). The resulting ranking of the species remained nearly unchanged by these procedures ($r_S = 0.97$ in both sets).

We included in our analyses 52 species and 4 subspecies, the remaining taxa were either omitted (rare species missing in captivity) or pooled with their closest relatives of similar appearance, i.e. *Python natalensis* Smith, 1833 with *Python sebae* (Gmelin, 1789) and *Python curtus* Schlegel, 1872 with *Python breitensteini* Steindachner, 1881. The numbers of individuals kept in zoos in the years 2004, 2005 and 2006 were obtained from the International Species Information System online database (www.isis.org) covering almost 650 zoos and aquariums worldwide. Corresponding data from the years 1988, 1994 and 2000 were adopted from printed reports (Anonymous, 1989, 1995, 2001). Equitability of the species composition in each studied year was characterized by a standard index J' (Pielou, 1966). Individuals not assigned to subspecies or those of subspecies not recognized in our analyses were considered as belonging to the subspecies most represented in zoos. The distribution range and adult body length of studied species were adopted from literary sources (Walls, 1998a,b). We coded the size of the distribution range on semi-quantitative (ordinal) five-graded scale (1 = island endemic, 2 = large island or archipelago endemic, 3 = limited mainland distribution, 4 = extended mainland, 5 = continent wide). Conservation status was expressed by inclusion of the species either in CITES I Appendix or in any of IUCN categories (0 = not included, 1 = included). Taxonomic uniqueness was implied as the number of living species in the genus. We recorded offering prices of the studied species in two prominent European markets in Houten (Netherlands) and Hamm (Germany) held in 2005 and 2006. The mean price of an adult male was referred as the commercial price in further analyses. In case that the price of male was not available, we calculated it from the mean price of a female, subadult or juvenile multiplied by corresponding coefficient (1.047, 1.367 and 1.316, respectively). This was computed across species by pairwise comparison of particular age category and adult male price.

The variables showing lognormal distribution (number of individuals kept in zoos, body length, taxonomic uniqueness and commercial price) were transformed by natural logarithm prior to the analyses. We performed most calculations in Statistica 6.0. (StatSoft., 2001), independent contrasts were based on a phylogenetic tree compiled from literature (Tolson,

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Fig. 1 – An example of perceived by humans as well favored — the Brasilian rainbow boa (*Epicrates cenchria cenchria*) the champion of our respondents.

1987; Underwood and Stimson, 1990; Austin, 2000; Keogh et al., 2001; Vences and Glaw, 2003; Burbrink, 2004; Rawlings et al., 2004) and computed in Compare version 4.4. (Martins, 2001).

3. Results

Resulting ranks varied considerably among tested species, the most preferred species were *Epicrates c. cenchria* (Fig. 1), *Python regius*, *Python molurus bivittatus*, *Python brongesmai*, and *Corallus caninus*, while the least preferred were *E. gracilis*, *Epicrates inornatus* (Fig. 2), *Liasis olivaceus*, *Eryx johnii* and *C. annulatus* (see <<<Appendix S1).

The results of the General Linear Models (GLM) revealed that the number of individuals kept in zoos in the year 2006 was affected by preference ($F_{1,49}=8.73$; $P<0.005$), body length of the species ($F_{1,49}=11.05$; $P<0.002$) and number of living species in the genus ($F_{1,49}=4.15$; $P<0.05$). We found no significant effects of the conservation status, present range size and commercial price. As only three continuous variables significantly contributed to the dependent variable, multiple regression was adopted for the construction of final reduced model ($R^2=0.45$; $F_{3,52}=14.23$; $P<0.001$). The results confirmed that the number of individuals kept in zoos in the year 2006, increased with preference ($\beta=-0.39$; $P<0.001$; Fig. 3), body length ($\beta=0.39$; $P<0.001$) and also marginally with taxonomic uniqueness ($\beta=-0.21$; $P<0.05$). When we applied independent contrasts instead of original variables to remove possible effect of shared ancestry violating the assumption of independence among species data (the procedure allows to avoid false correlations resulting from possible hidden effects of phylogeny; for rationale of phylogenetically informed comparisons see Harvey and Pagel, 1991; Garland et al., 1992), only the relationship between the number of individuals kept in zoos and preference remained highly significant ($\beta=-0.42$, $P<0.005$). The effect of body length disappeared due to considerable phylogenetic component of this variable.

Fig. 2 – An example of species perceived by humans as graceless — the Puerto Rican boa (*Epicrates inornatus*).

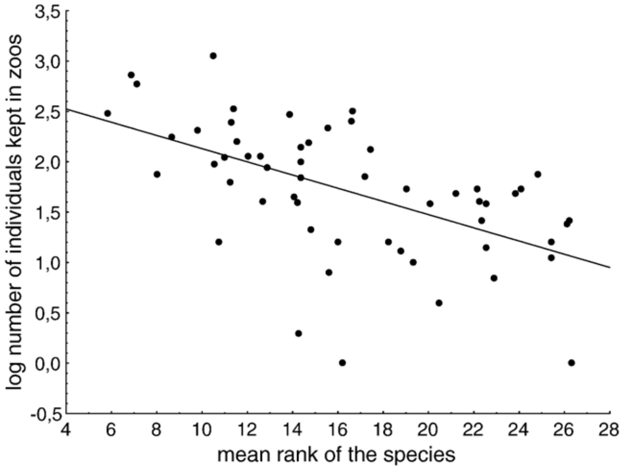

Fig. 3 – Scatter plot of mean rank of the species (referred also as preference) and number of individuals kept in zoos in the year 2006.

Next we substituted the number of individuals kept in zoos in the year 2006 by corresponding data from previous years. The multiple regression was repeated to describe possible changes of the explanatory power of preference and body length in the course of last two decades. These two variables explained 31.3, 43.7, 47.0, 45.9, and 46.0% of variation in the years 1988, 1994, 2000, 2004, and 2005, respectively. It should be noted here that during the studied period the number of boas and pythons kept in zoos increased rapidly but it was accompanied by only a mild raise of species number and even a slight decrease of species equitability (Table 1).

Table 1 – The species composition of pythons and boas kept in zoos since 1988

	1988	1994	2000	2004	2005	2006
Number of species	43	54	56	56	55	54
J' (species equitability)	0.87	0.85	0.84	0.83	0.82	0.83
Number of individuals	1313	4649	5354	6341	6801	7070

The index J' (Pielou, 1966) ranges from 0 to 1, the higher value, the more balanced species composition is.

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4. Discussion

We were surprised that endangered species are not overrepresented in zoo collections. Except taxonomic uniqueness, no variable putatively associated with endangerment (CITES/IUCN, range size and commercial price) affected the number of individuals kept in zoos. This fact cannot be explained by difficulty of obtaining rare species. Commercial prices of nearly all boid snakes are low and obviously, would not prevent zoos from obtaining them.

Factors apparently dealing with attractiveness to humans, i.e. preference (see above) and body length, were the best predictors of representation of a particular species in zoo collections, moreover, this relationship was unexpectedly close. It may lead to the conclusion that Noah's Ark is full of numerous repeats of a few attractive species. Only three species, *Boa constrictor constrictor* Linnaeus, 1758, *P. regius* (Shaw, 1802) and *P. molurus bivittatus* Kuhl, 1820, are represented by more than 500 individuals! All of these are common continental species possessing extensive distribution ranges. As the total number of pythons and boas of all kinds kept in zoos is limited, the captive populations of really endangered species fall far below the limit required for viability. The pressure of public attendance hereby often outweighs conservation concerns.

Although these results may be viewed as alarming, they have close parallels in other conservation activities. There is more public support for saving species resembling humans (Samples et al., 1986), species perceived as attractive and those larger in size (Gunnthorsdottir, 2001). Sometimes, human willingness to protect a species may even correlate negatively with the degree of endangerment. Metrick and Weitzman (1998) reported this phenomenon in public comments to changes in the Red List. Not only willingness to protect but also resources are allocated to species conservation in accord with human attitudes rather than conservation needs. Funding decisions by FWS are not related to species' recovery priority rank (Simon et al., 1995). U.S. federal government 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 a species is considered to be a "higher form of life", than on "scientific" ones, i.e. "degree of endangerment" and "taxonomic uniqueness" (Metrick and Weitzman, 1996). "Incredibly, a 10% increase in body length is accompanied by an 8.6% raise in funding (Metrick and Weitzman, 1998)."

The International Species Information System database seems to be the only available representative source of worldwide data. It may be argued that the database does not cover all snake keepers because some local zoos as well as private breeders are not included. Large zoos are, however, the most important as they attract the attention of the general public and the media, and consequently help the species to gain additional support. The number of individuals kept in zoos provides therefore a good estimate of the conservation effort.

There was considerable agreement among respondents, which enabled us to use a single preference scale. Nevertheless, our respondents come from one cultural area while zoo data are covered worldwide. Although we are conscious 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 analysis also revealed unexpected correlation between preference and range size, which remains close even when the phylogenetic component of variation is removed. Typically, continental species are considered the most attractive, while island endemics are inconspicuous. We can speculate that aposematic coloration, perceived attractive by humans, is more frequent in continental forms as a result of higher predation pressure.

Results of this study present further evidence that conservation efforts are biased in favour of "attractive" species. We can imagine a selective extinction of "unattractive" species as an anthropogenous macroevolutionary process forming the fauna of the future. Therefore, studies of species attractiveness should be incorporated into conservation reasoning.

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Appendix S1.
Studied species, number of individuals kept in zoos in the year 2006, and mean rank of the species (preference)

Species	Number of individuals kept in zoos	Mean rank of the species
Epicrates cenchria cenchria	306	5.8
Python regius	722	6.9
Python molurus bivittatus	598	7.1
Python brongesmai	75	8.0
Corallus caninus	175	8.7
Eunectes murinus	203	9.8
Boa constrictor constrictor	1114	10.5
Python sebae & natalensis	95	10.5
Eryx conicus	16	10.7
Corallus hortulanus	112	11.0
Python molurus molurus	63	11.2
Python reticulatus	248	11.2
Chondropython viridis	336	11.4
Eunectes notaeus	157	11.5
Python curtus & breitensteini	114	12.0
Acrantophis madagascariensis	114	12.6
Antaresia childreni	40	12.7
Boa constrictor imperator	87	12.9
Acrantophis dumerili	295	13.9
Python anchietae	45	14.1
Morelia boeleni	39	14.2
Epicrates fordi	2	14.3
Lichanura trivirgata	141	14.3

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Appendix S1 (*continued*)

Species	Number of individuals kept in zoos	Mean rank of the species
Aspidites ramsayi	70	14.4
Epicrates subflavus	99	14.4
Eryx colubrinus	153	14.7
Boa constrictor occidentalis	21	14.8
Epicrates angulifer	216	15.5
Candoia aspera	8	15.6
Eryx miliaris	16	16.0
Eryx muelleri	1	16.2
Morelia spilota	250	16.6
Sanzinia madagascariensis	320	16.6
Aspidites melanocphalus	72	17.2
Epicrates cenchria maurus	133	17.4
Liasis fuscus	16	18.3
Charina bottae	13	18.8
Antaresia maculosa	53	19.1
Eryx tataricus	10	19.3
Liasis boa	38	20.1
Eryx jaculus	4	20.5
Liasis albertisi	48	21.2
Corallus ruschenbergeri	53	22.2
Morelia amethistina	40	22.4
Python timorensis	26	22.3
Epicrates striatus	38	22.5
Calabaria reinhardti	14	22.6
Candoia bibroni	7	22.9
Liasis savuensis	49	23.8
Candoia carinata	54	24.1
Liasis mackloti	75	24.8
Corallus annulatus	16	25.4
Eryx johnii	11	25.4
Liasis olivaceus	24	26.1
Epicrates inornatus	26	26.2
Epicrates gracilis	1	26.3

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Are Animals in Zoos Rather Conspicuous than Endangered?

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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.

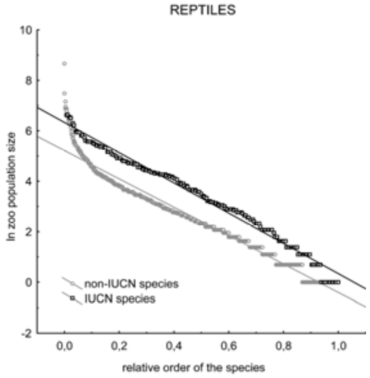


Figure 1. Size distribution of worldwide zoo populations of reptiles: a comparison of endangered species (IUCN category NT-nearly threatened or higher) with the remaining ones (non-IUCN). ln population size = log transformed number of individuals of a given species kept in zoos worldwide. Population 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.

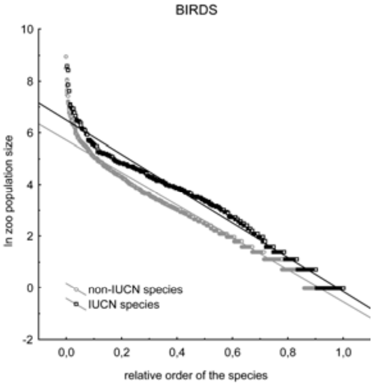


Figure 2. Size distribution of zoo populations of birds: a comparison of endangered species (IUCN category NT-nearly threatened or higher) with the remaining ones (non-IUCN). ln population size = log transformed number of individuals of a given species kept in zoos worldwide. Population sizes are sorted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

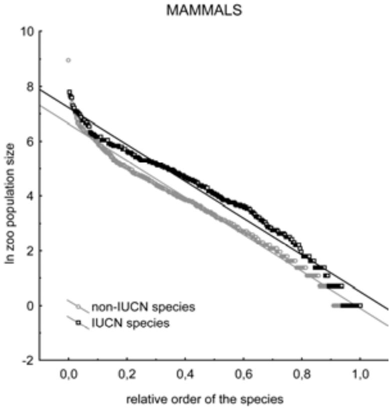


Figure 3. Size distribution of zoo populations of mammals: a comparison of endangered species (IUCN category NT-nearly threatened or higher) with the remaining ones (non-IUCN). ln population size = log transformed number of individuals of a given species kept in zoos worldwide. Population sizes are sorted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

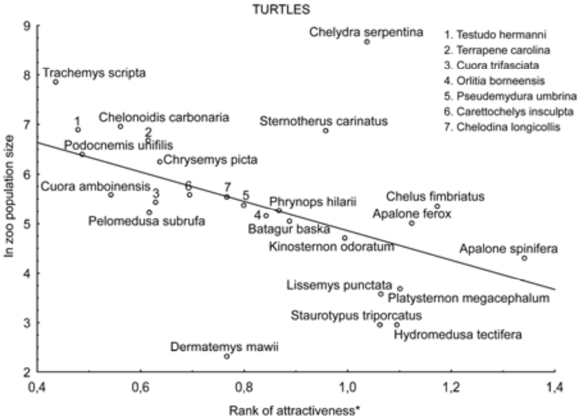
Pythons and Boas

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.

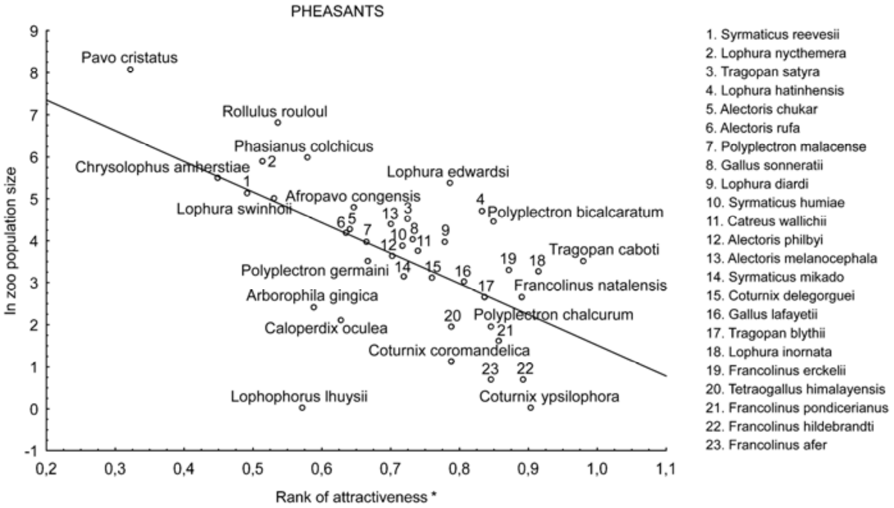
Figure 4. Relationship between size of zoo populations and human preferences in turtles (Testudines). Rank of attractiveness = mean square-root arcsin transformed rank. ln zoo population size = log transformed number of individuals of a given species kept in zoos worldwide. R2 = 24.2%, P = 0.0107, y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

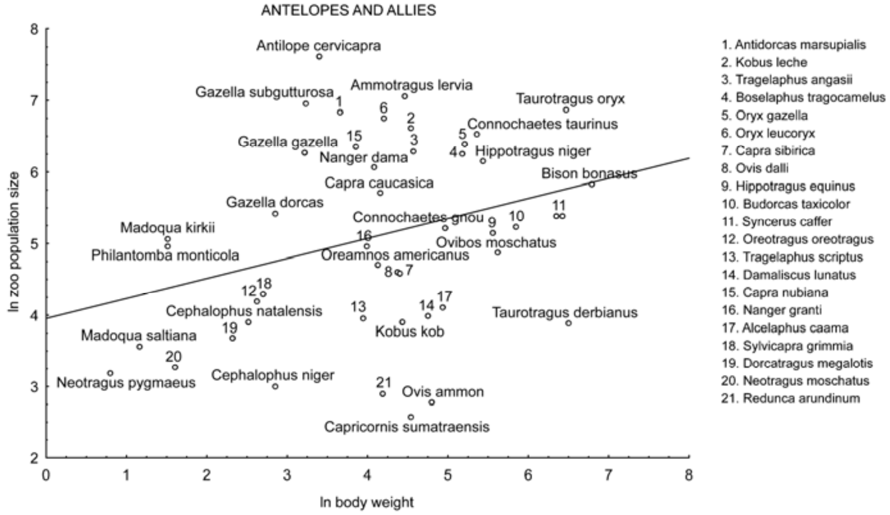


Figure 6. Relationship between size of zoo populations and body size in antelopes and allies (Bovidae). ln zoo population size = log transformed number of individuals of a given species kept in zoos worldwide. R2 = 10.3%, P = 0.0261, y = 3.91 * x +0.29.

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).

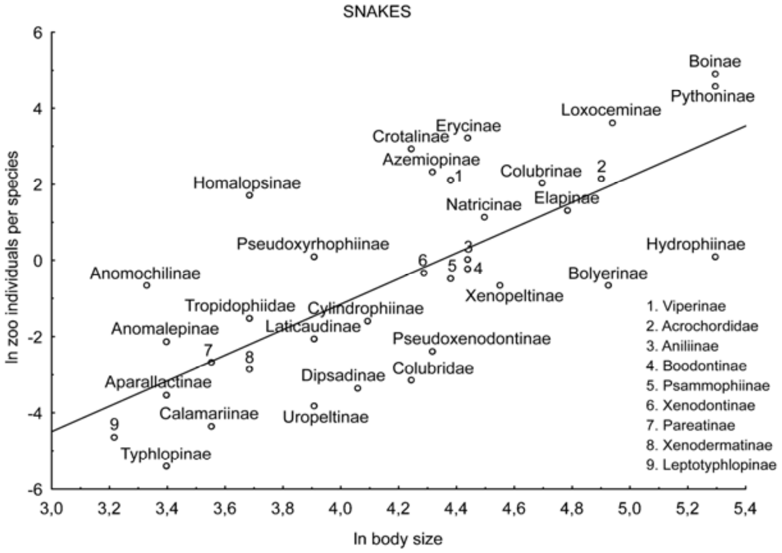
In accord with expectations, body size was the best predictor of the number of individuals per species. Its effect was positive in ten out of eleven analyzed groups (except turtles); nine of these effects were significant ($P<0.05$) and one (group of “basal mammals”) approached significance ($P<0.1$). 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

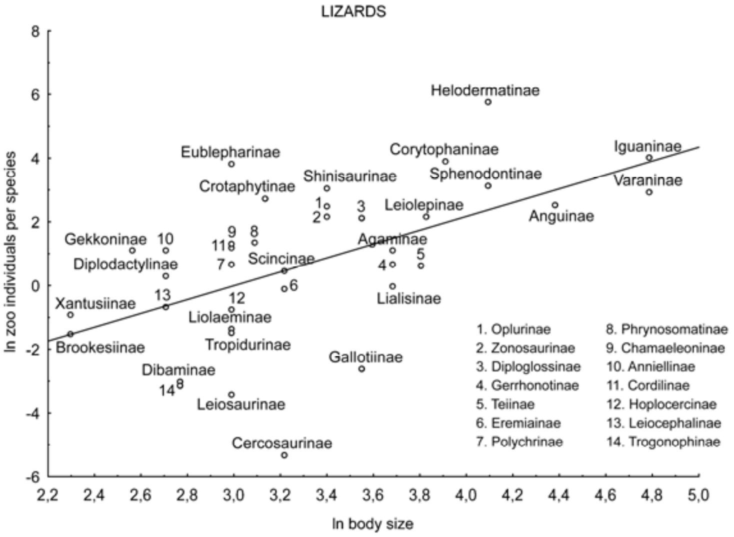
Table 3. (Continued).

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).

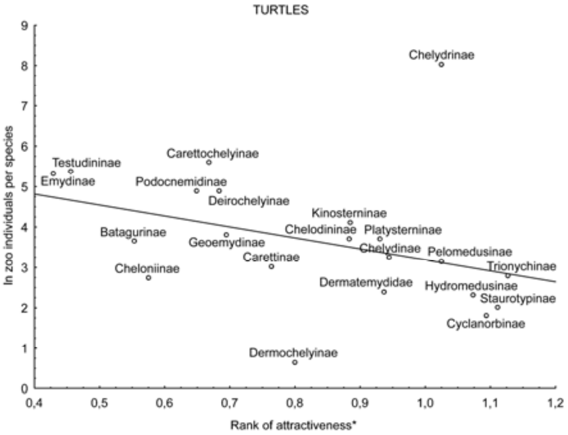
Figure 7. Relationship between size of zoo populations per species and body size in snakes. Ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed 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.

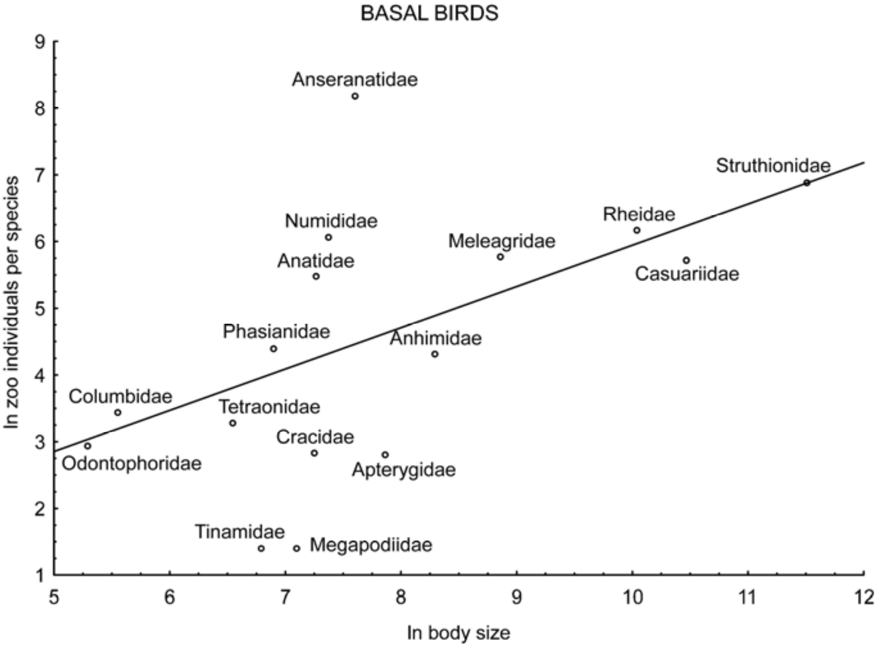
Human preference contributed less apparently to the models explaining the number of individuals per species. Interestingly enough, the effects of ranking were always negative, i.e., the higher the human preference, the better the representation of the given family/subfamily in zoos. However, this factor 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.

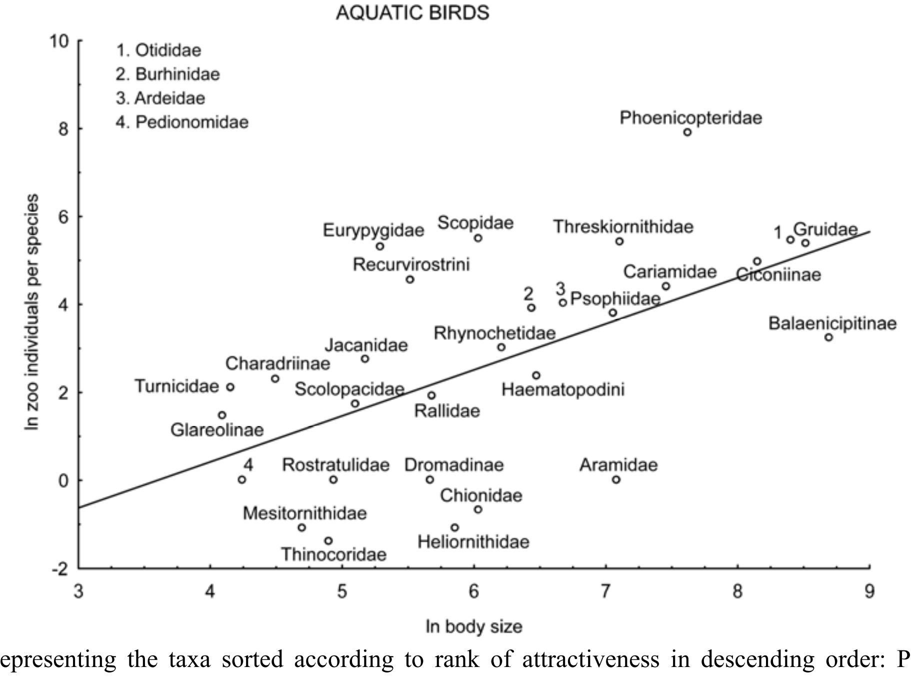
Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Clemmys guttata (Emydinae), Astrochelys yniphora (Testudininae), Malayemys subrijuga (Batagurinae), Chelonia mydas (Cheloniinae), Podocnemis erythrocephala (Podocnemidinae), Carettochelys insculpta (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.



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).

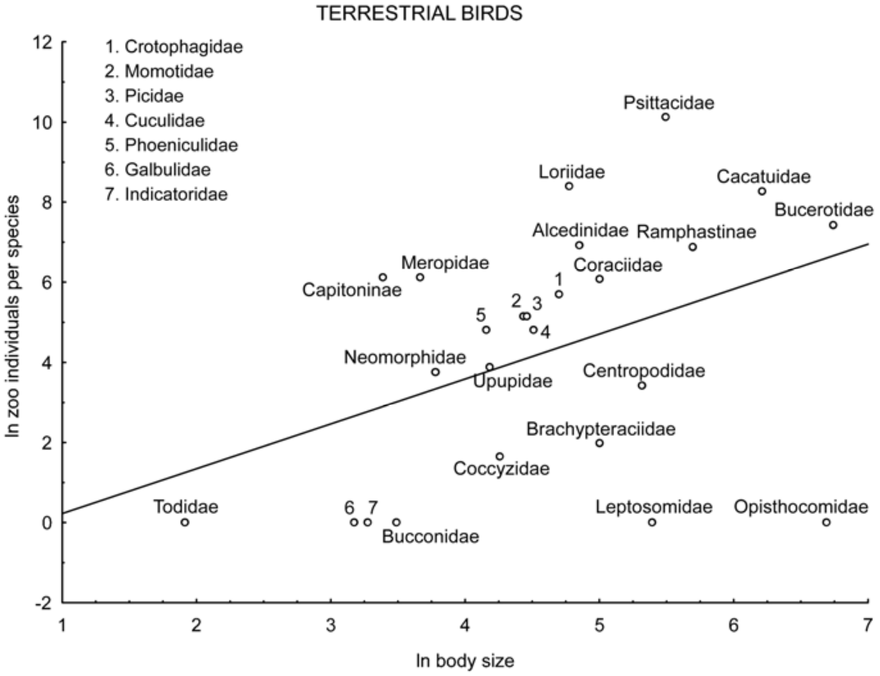
Figure 10. Relationship between size of zoo populations per species and body size in basal birds. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed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



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

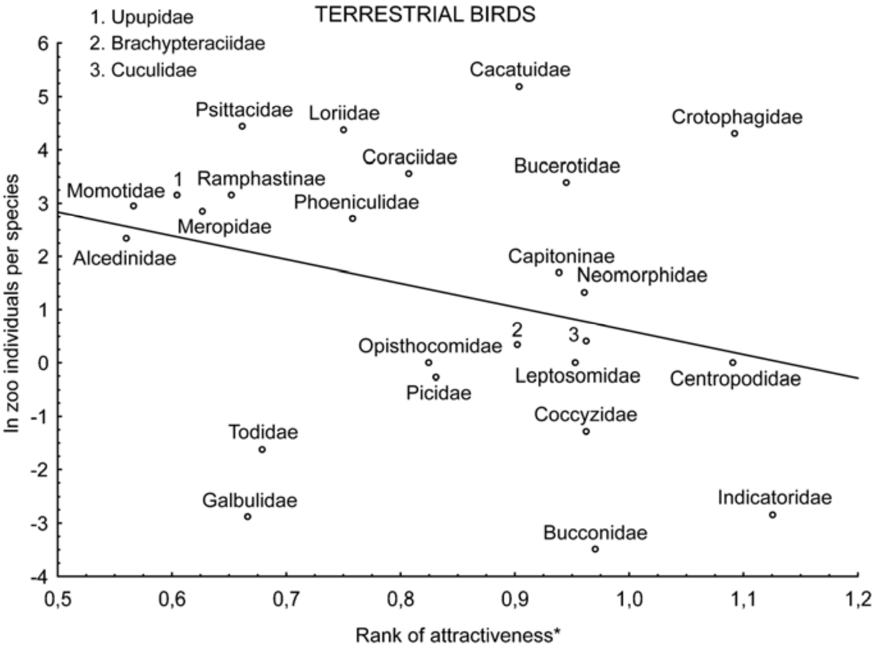
(Scopidae), Glareola ocularis (Glareolinae), Tringa incana (Scolopacidae), Psophia leucoptera (Psophiidae), Heliopais personata (Heliornithidae), Pedionomus torquatus (Pedionomidae), Burhinus recurvirostris (Burhinidae), Haematopus moquini (Haematopodini), Monias benschi (Mesitornithidae), Thinocorus 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).

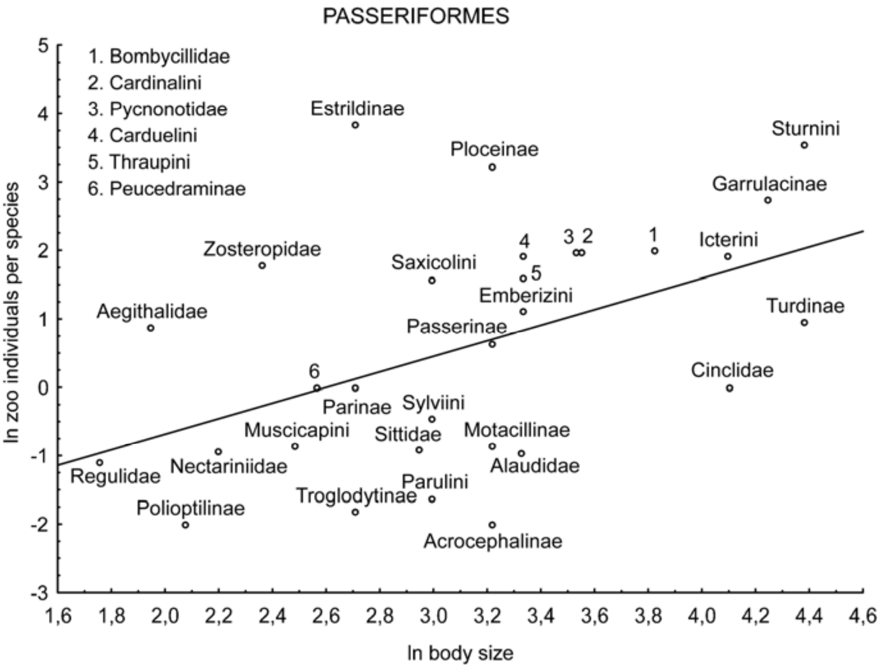
Figure 12. Relationship between size of zoo populations per species and body size in terrestrial birds. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = 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.

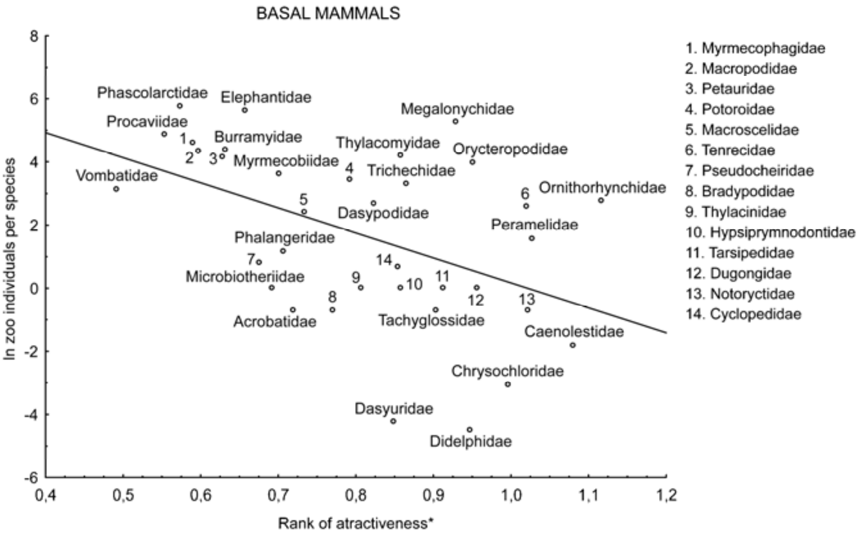
Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Alcedo cyanopecta, Halcyon smyrnensis, Megaceryle alcyon (Alcedinidae); Momotus mexicanus (Momotidae); Upupa epops (Upupidae); Merops boehmi (Meropidae); Aulacorhynchus prasinus (Ramphastinae); Ara 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).

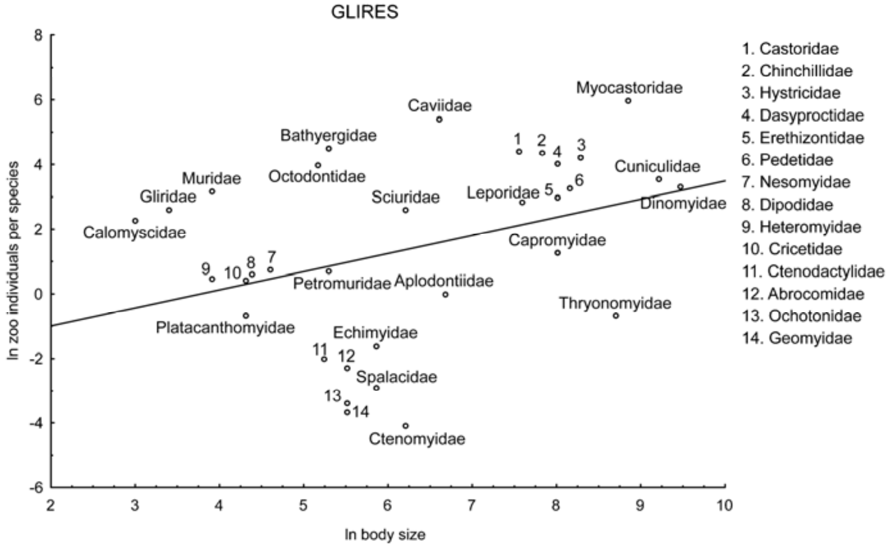
Figure 14. Relationship between size of zoo populations per species and body size in passerines. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed 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.

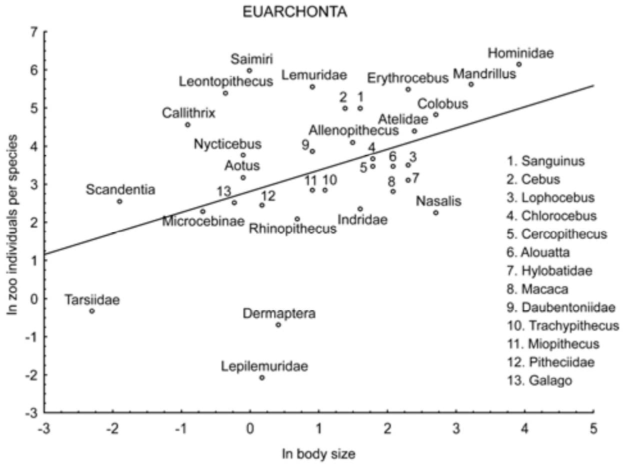
Specimen species representing the taxa sorted according to rank of attractiveness in descending order: Vombatus ursinus (Vombatidae), Dendrohyrax arboreus (Procaviidae), Phascolarctos cinereus (Phascolarctidae), Tamandua mexicana (Myrmecophagidae), Petrogale xanthopus (Macropodidae), Petaurus norfolcensis (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).

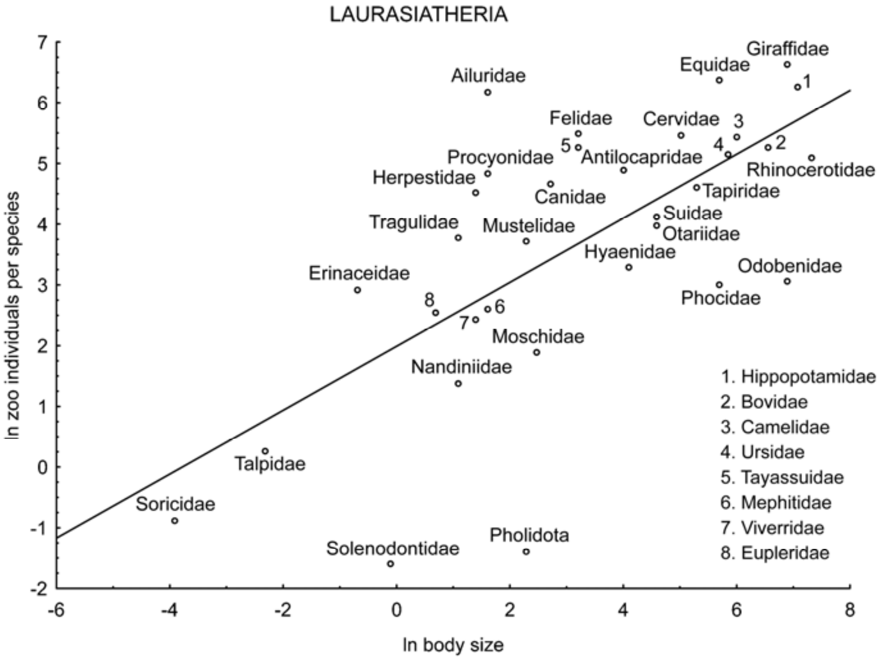
Figure 16. Relationship between size of zoo populations per species and body size in Glires. ln zoo individuals per species = log-transformed number of individuals belonging to a given family/subfamily kept in zoos worldwide per the total number of living species in this group. ln body size = log-transformed 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) 2. Coral Earth Snake *Geophis semidoliatus* (Dipsadinae) 3. Coral Cylinder Snakes *Anilius scytale* (Aniliinae)	35. Brongersma's Worm Snake *Typhlops brongersmianus* (Typhlopinae) 34. Beu's Dawn Blind Snake *Liotyphlops beui* (Anomalepinae) 33. Western Threadsnake *Leptotyphlops humilis* (Leptotyphlopinae)
Lizards	1. Coarse Chameleon *Chamaeleo rudis* (Chamaeleoninae) 2. Anzamala Madagascar Swift *Oplurus fierinensis* (Oplurinae) 3. Tschudi's Pacific Iguana *Microlophus thoracicus* (Tropidurinae)	37. California legless lizard *Anniella pulchra* (Anniellinae) 36. Blind Lizard *Dibamus bogadeki* (Dibaminae) 35. Exmouth Worm-lizard *Aprasia rostrata* (Lialisinae or Pygopodinae)
Turtles	1. Spotted Turtle *Clemmys guttata* (Emydinae) 2. Madagascan Tortoise *Astrochelys yniphora* (Testudininae) 3. Snail-eating Turtle *Malayemys subtrijuga* (Batagurinae)	21. Florida Softshell Turtle *Apalone ferox* (Trionychinae) 20. Mexican Giant Musk Turtle *Staurotypus triporcatus* (Staurotypinae) 19. Indian Soft-shelled Turtle *Lissemys punctata* (Cyclanorbinae)
Basal birds	1.Brown Kiwi *Apteryx australis* (Apterigidae) 2. Stephan's Dove *Chalcophaps stephani* (Columbidae) 3. Hazel Grouse	16. Micronesian Scrubfowl *Megapodius laperouse* (Megapodiidae) 15. Wild Turkey *Meleagris gallopavo* (Meleagridae) 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.

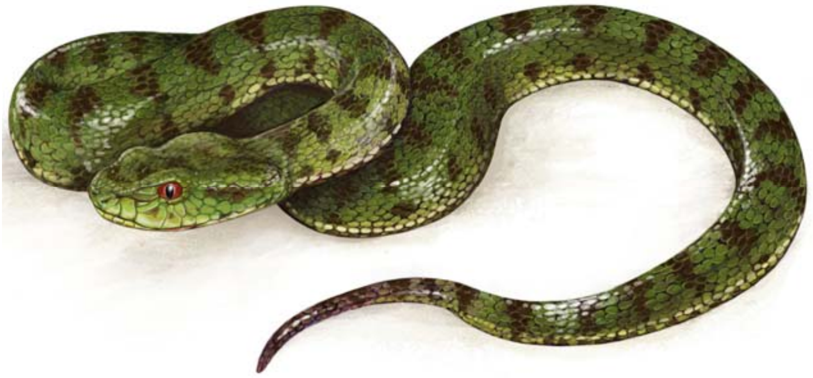


Figure 19. Examples of most preferred species within particular higher taxa according to our respondents. Philippine Pitviper (*Parias flavomaculatus*); Lizards: Crotalinae. Original painting by Silvie Lišková.

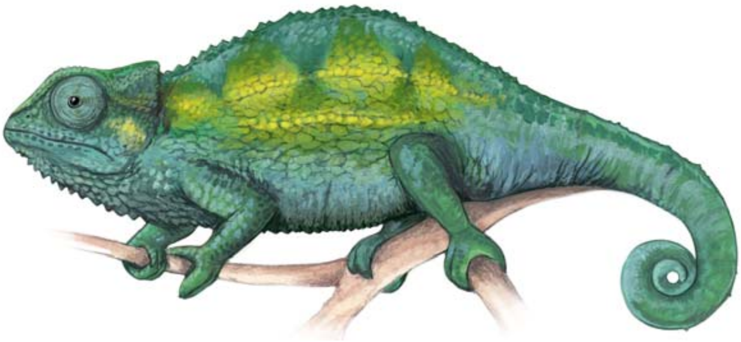


Figure 20. Examples of most preferred species within particular higher taxa according to our respondents. Coarse Chameleon (Chamaeleo rudis); Lizards: Chamaeleoninae. Original painting by Silvie Lišková.

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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Conclusions

The main conclusions of the thesis are**:**

- Human perception of animal (or at least snake) beauty is consistent across distant cultures.
- Our aesthetic requirements (whether expressed as preference or body size of the species) determine conservation effort devoted to captive breeding.
- Zoo collections are clearly biased in favour of some taxonomic groups and the species are kept in very low numbers.
- The aesthetic preference to snake species is similar in adults and pre-school children.
- Evaluation of both the attractiveness and fear of animal species is a two-dimensional process accompanied by an unsupervised categorization. The categorization probably happens before the respondents decide about the beautiful-ugly axis.
- Perceived beauty and fear are two independent emotions that are not mutually correlated.
- Respondents rank photographs in the same order as live animals; photographs are valid substitutes.
- Aposematic pattern is recognized, and feared in the case that a whole animal is viewed.
- Attractiveness of an animal generally increases with certain body traits and bright colours and the factors determining the preference differ among higher taxa.

I believe that the thesis has opened up new research possibilities. The included papers bring novel information about human aesthetic preferences to other kinds, their nature, cross-cultural validity and their implications in conservation. Although it was uneasy to start publishing an unusual topic, the papers were eventually accepted in journals in fields of ethology, human ecology or environmental economy and psychology. I can see the topic further expand, especially in its cognitive, adaptive and conservation aspects.

Appendix

Prohlašuji, že podíl předkladatelky dizertační práce Jany Marešové, na rukopisu a publikacích, jichž jsem spoluautorem, není menší, než odpovídá pořadí a počtu spoluautorů.

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