Theory Biosci. (2009) 128:227–235
DOI 10.1007/s12064-009-0075-y

ORIGINAL PAPER

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

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Received: 7 June 2009 / Accepted: 25 September 2009 / Published online: 5 November 2009

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*

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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 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 (Cityblock) 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.,

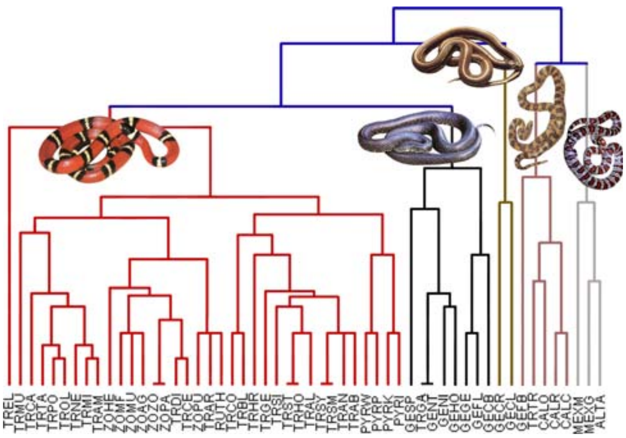

Fig. 1 Phenetic tree of 54 taxa of milk snakes based on color and pattern characters. Manhattan distances and unweighted pair-group average clustering method were applied. The taxa are abbreviated as follows: ALTA—*L.alterna*, CALC—*L.c.calligaster*, CALO—*L.c.occipitolineata,* CALR—*L.c.rhombomaculata*, 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

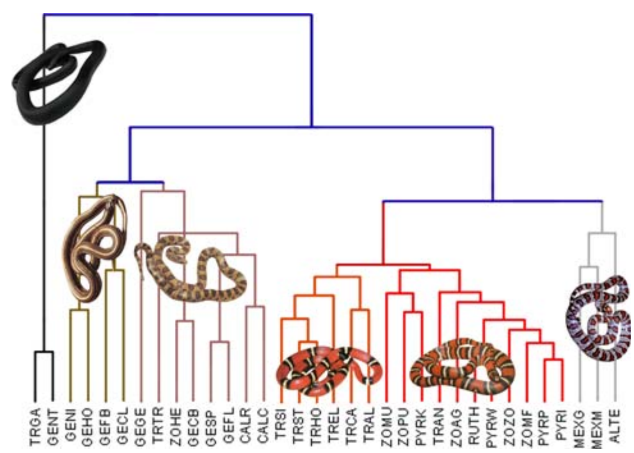

Fig. 2 Phenetic tree of 34 taxa based on preference ranks provided by respondents. The data concerning snakes, heads, and skins were pooled. Manhattan distances and unweighted pair-group average clustering method were applied. The taxa are abbreviated as follows: ALTE—*L.alterna*, CALC—*L.c.calligaster*, 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.

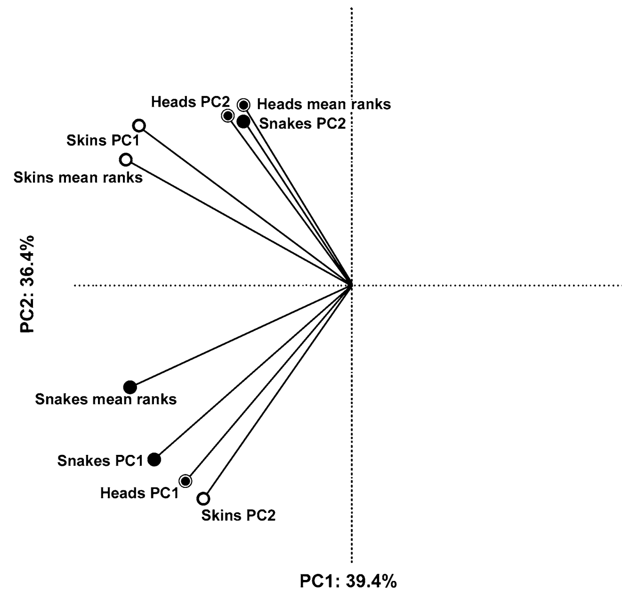

Fig. 3 Relationships between preference ranks, PC1 and PC2 scores computed separately for snakes, heads, and skins datasets. Position of individual variables denotes its loadings revealed by the principal component analysis including all these variables

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.

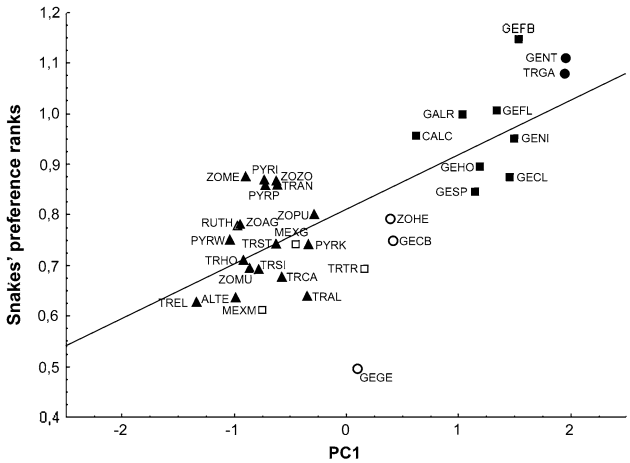

Fig. 4 Relationship between mean ranks computed from snakes dataset and PC1 scores computed from pooled dataset. $r = 0.719$, $P < 0.0001$. For abbreviations of species names see Fig. 2. Color and pattern groups are denoted as follows: *filled circle* uniform black; *filled square* unstriped; *open circle*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

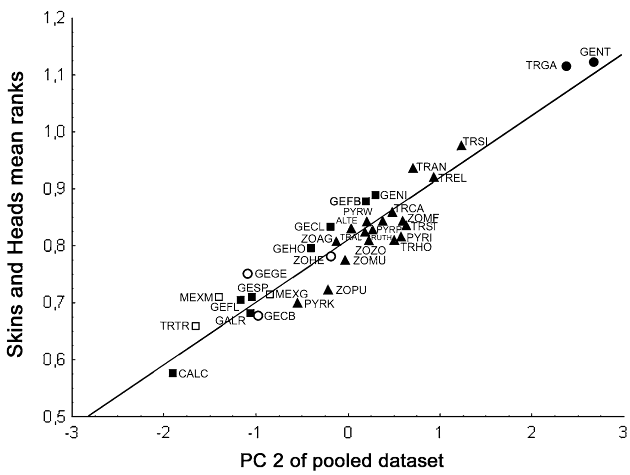

Fig. 5 Relationship between mean ranks computed from combined heads and skins dataset and PC2 scores computed from pooled dataset. $r = 0.951$, $P < 0.0001$. For abbreviations of species names see Fig. 2. Color and pattern groups are denoted as follows: *filled circle* uniform black; *filled square* 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

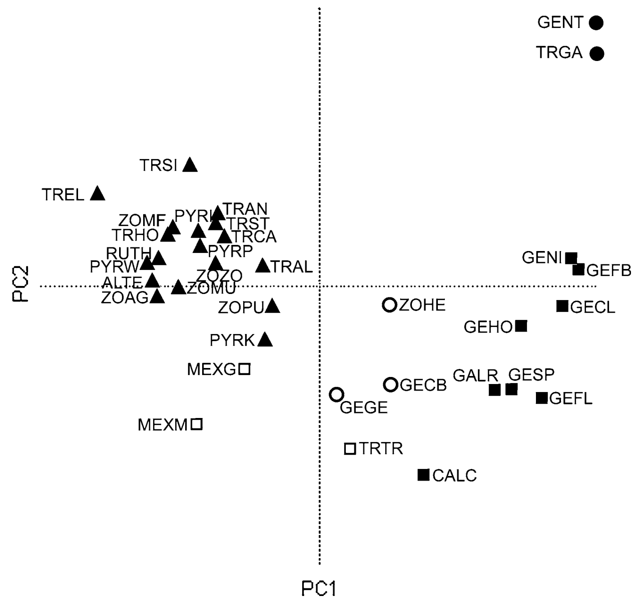

Fig. 6 Plot of studied taxa in space of the first two principal components (PC1 horizontally) computed from pooled dataset. Note that the species most preferred by the respondents are placed on the left bottom part of the plot. For abbreviations of species names see Fig. 2. Color and pattern groups are 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

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.

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.

Acknowledgments The research was supported by Grant Agency of the Academy of Sciences of the Czech Republic project no. IAA 6011410803. Personal costs of J.M. were covered from the grant no.206-05-H012 provided by the Czech Science Foundation. Participation of E.L. was supported by institutional grant no. 0021620828, provided by the Ministry of Education, Youth and Sport of the Czech Republic.

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