Just beautiful?! What determines butterfly species for nature conservation

Jan Christian Habel1 · Martin M. Gossner2,3 · Thomas Schmitt4,5,6

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Abstract
Prioritization is crucial in nature conservation, as land and financial resources are limited. Selection procedures must follow objective criteria, and not primarily subjective aspects, such as charisma. In this study, we assessed the level of charisma for all European butterflies. Based on these data, we analysed the charisma values of the species listed on the annexes of the EU Habitats Directive and of the species being of conservation priority according to criteria derived by three objective criteria: Species ecological specialization, distribution, and threat. The mean level of charisma was higher for species of the EU Habitats Directive than for species of conservation priority and for not-listed species. Five of the twenty most charismatic species were also listed on the EU Habitats Directive, but none occurred on the list of species being of conservation priority. A trait space analysis revealed remarkable differences between the different species assortments: The species listed on the EU Habitats Directive covered a large trait space and included many species with high charismatic value, but low ecological and biogeographical relevance, while species of high conservation priority covered a restricted trait space and did not overlap with charismatic species. According to our findings, the selection of species for nature conservation still follows a mix of being aesthetic combined with some ecological criteria.

Keywords Butterflies · Biodiversity conservation · Prioritizing · Charismatic species · Endangered species · Specialist species · EU Habitat Directive

Introduction
Prioritization is a main task in nature conservation, as land for conservation is scarce and financial resources are limited (Arponen 2012; Hill et al. 2016; Essens et al. 2017). Thus, prioritization includes all spatial scales: Ecotones across the globe (Myers et al. 2000), single ecosystems, communities, particular species and populations (Hill et al. 2016). Various tools have been developed to identify the most threatened and rarest ecosystems or
which of them are characterized by extraordinarily high species richness or particularity in
their species composition (Arponen 2012; Gauthier et al. 2013). Similarly, at the species
level, many strategies focus on the conservation of the most endangered ones, species with
geographically restricted distributions, and on species which are most sensitive to environ-
mental changes (Simberloff 1998; Peterson et al. 2010). At the population level, conserva-
tion strategies frequently focus on the preservation of relict populations or on groups being
characterized by unique genetic structures (Hampe and Petit 2005; Habel et al. 2011).

However, the applied selection procedures to identify the most appropriate ecosys-
tems, species, or populations only rarely follow objective selection criteria (Cardoso 2012;
Hochkirch et al. 2013a). Consequently, most organisms selected for the purpose of nature
conservation are large and charismatic species, mostly vertebrates or vascular plants (Stork
and Habel 2014, with references therein), but also incorporate beautiful invertebrates, such
as colourful butterflies (Barua et al. 2012). Thus, the level of beauty of species strongly
impacts the selection of taxa for nature conservation (Barua et al. 2012). However, char-
ismatic species are of key relevance to sell nature conservation to politics and the pub-
lic (Landová et al. 2018). Studies have shown that charismatic species positively influ-
ence attitudes towards nature conservation, increase awareness, and thus the acceptance
of conservation action (Ducarme et al. 2013; Brambilla et al. 2013) and financial support
(Bowen-Jones and Entwistle 2002; Home et al. 2009). Consequently, flagship, indicator
and umbrella species are often taxa, which are extraordinary beautiful (Leader-Williams
and Dublin 2000). This fact is also supported by the success story of the flag-ship-species-
concept in nature conservation (Heywood 1995; Simberloff 1998; Barua et al. 2012). With-
out denying the importance of individual species as flagships in nature conservation, we
are convinced that nature conservation should mainly follow ecological evidence (Pullin
and Knight 2003; Harrison et al. 2008). However, it is still rarely studied, to which degree
different approaches of selecting priority species in nature conservation are influenced by
objective ecological criteria or by the level of beauty (Macdonald et al. 2017).

We assume that objective ecological criteria make nature conservation most efficient
and transparent (see also Harrison et al. 2008). Therefore, in a previous study on the prior-
itization to conserve butterflies, Habel et al. (2019) presented a selection protocol based on
three criteria: 1. Distribution of species (range restricted species, endemism), 2. Ecologi-
cal specialisation (species demanding specific ecological requirements), and 3. Level of
endangerment (according the IUCN Red List). This study showed that selection of species
for nature conservation based on these three criteria do not agree with the species listed
on the annexes of the EU Habitats Directive for the group of butterflies. In the study pre-
sented here, we therefore assessed the level of charisma for all 404 European butterfly spe-
cies (except some species restricted to the Macaronesian islands, due to biogeographical
reasons) based on wing characters. The most charismatic species (CS hereafter) identified
according to our scoring were then compared with (1) the species listed on the annexes of
the EU Habitat Directive (HD hereafter), (2) the species identified as species of conserva-
tion priority (SCP hereafter) according to the criteria defined in Habel et al. (2019), and
(3) all remaining species not included in any of the three groups mentioned above (i.e. not
considered, NC hereafter). We hypothesize that (1) species of all four groups (CS, HD,
SCP, NC) differ in their trait space with species of HD having a higher and SCP a mostly
similar charismatic value than not classified species, and that (2) HD species cover a larger
trait space than SCP because HD species include charismatic species as well as species
with high ecological relevance, but underrepresent species of high geographic relevance, as
well as the truly threatened species. In addition, we asked citizens to rank the beauty of all
CS, HD and SCP species to test whether our own scoring based on simple wing characters
reflects the perception of beauty by the society. We finally discuss how these results should influence future prioritization of species for nature conservation.

**Material and methods**

**Data set**

We used 404 butterfly species, which are recorded from the 27 member states of the European Union (according to the 2010 revision of the Taxonomy Commission of Butterfly Conservation, Wiemers et al. 2018, modified). We excluded all species that in the EU are restricted to the Macaronesian Islands because they represent a separate entity most closely related to North Africa; Schmitt 2020), species that became extinct in Europe prior to World War II, as well as temporary vagrants, and those that are not constantly established. For controversially discussed species complexes and sister species, we only considered the oldest species name (Kudrna et al. 2015).

We classified all remaining European butterfly species into (1) Species that are listed in the annexes of the EU Habitat Directive (HD) (European Union 1992), (2) Species which are of conservation priority (SCP) based on criteria related to ecological specialization, distribution patterns, and the level of threat (see Habel et al. 2019), (3) Charismatic species (CS) (classification described below), and (4) All other species not selected by one of these approaches (NC). Species of conservation priority (SCP) were identified based on their geographical distribution, level of threat, and ecological specialization (the latter composed of assessing larval food plant specialisation, habitat specialisation of imagoes, dispersal behaviour of imagoes); thus, species with restricted distributions, high degree of ecological specialization, and/or high level of threat were ranked as SCP in an iterative process (cf. Habel et al. 2019). A list of all species with respective classification is given in electronic Appendix 1.

**Classification of charismatic species (CS)**

The term charisma first appeared in conservation literature as a specific trait in flagship species identification (Heywood 1995). Quantifications of the level of charisma have been performed already in previous studies. For example, Bricchetti and Gariboldi (1997) created an “anthropogenic value index” (based on bibliographic references), and Macdonald and colleagues (2017) calculated appeal scores for mammals across the globe using morphological characteristics and rarity (see also Courchamp et al. 2006; Macdonald et al. 2015). For our study, we used four morphological wing characteristics, that are known to be of particular relevance when it comes to the general beauty of a butterfly, i.e. being big, colourful, shiny or with conspicuous wing shape features (see Farroni et al. 2005; Manesi et al. 2015; Lopez-Collado et al. 2016), and thus are assumed to foster environmental concern and environment-friendly attitudes (Root-Bernstein et al. 2013; Tam et al. 2013; Ahn et al. 2014): (A) average size of forewing (> 40 mm: 2 points; > 30 mm: 1 point; ≤ 30 mm: 0 points); (B) colour of upper wing side (three or more contrasting colours: 2 points; similar, but one of these colours not conspicuous or two contrasting colours: 1 point; all others: 0 points); (C) shiny upper wing side (conspicuously shiny: 2 points; shiny, but not conspicuous: 1 point; not shiny: 0 points), and (D) shape of wings (with long tails or conspicuously curved margin: 2 points; similar, but not conspicuous: 1 point; no specific appendices
or shape: 0 points). Previous studies showed that these selected factors particularly attract attention and can enhance prosocial behaviour among people (Manesi et al. 2015; Lopez-Collado et al. 2016). We summed the values of all four wing traits and defined species with three or more points as charismatic species. Note that we have not weighted the respective characteristics here as each applied weighting of the four characteristics also might be biased by personal preferences and opinions and thus might not be objectively justifiable, we argue that an equal contribution of all four characteristics might be the most appropriate way here. The obtained scoring of charisma of each butterfly species is given in electronic Appendix 2.

In order to validate our method of estimating the charisma of the European butterfly species based on the four wing characters by the perception of citizens, we conducted an additional enquiry containing all species belonging to CS, HD or SCP. We prepared insect boxes (40 cm x 30 cm), each of them containing 16 equally sized unit trays. Individuals of each of the 94 taxa were pinned in the middle of each unit tray. These butterflies were provided to 34 citizens (all non-lepidopterologists). Each participant completed one questionnaire to classify the level of charisma of each butterfly species with values ranging from 1 (not charismatic) to 4 (highly charismatic). For each butterfly species, we calculated the median charisma rank given by all citizens. These data were regressed against the charisma values obtained by wing characters. Obtained data are provided in electronic Appendix 2.

**Statistics**

To test for significant differences in median charismatic values (morphological characters) between the four classifications (CS, HD, SCP, NC), we used an Ordinal logistic regression, i.e. Cumulative Link Mixed Model fitted with the Laplace approximation (clmm and Anova function (type II), packages “ordinal” (Christensen 2019), “car” (Fox & Weisberg 2019), “RVAideMemoire” (Hervé 2021)) with the classification as predictor, the charismatic value as response and the species identity as random factor. For post-hoc comparisons between classifications we used Tukey-adjusted comparisons (lsmeans and cld function, packages “multcompView” (Graves et al. 2019), “emmeans” (Lenth 2021)). To test for significant differences in median charismatic values (questionnaire) between the three classifications (CS, HD, SCP), we used a linear mixed effects model fit by REML (lmer and anova function (type II) with Satterthwaite’s method, packages “lmerTest” (Kuznetsova et al. 2017)) with the classification as predictor, the charismatic value as response and the species identity as random factor. For post-hoc comparisons between classifications we used Tukey-contrasts (glht function, package “multcomp” (Hothorn et al. 2008)). We plotted the probabilities of charismatic values for each of the four classifications (CS, HD, SCP, NC) based on either the ordinal-response or the linear model using the emmeans function in the “lsmeans” package (Lenth 2016).

To compare species specific trait spaces covered by the four groups of species defined above, we conducted an ordination analysis. First, we used the Gower dissimilarity coefficient (Gower 1971) with Podani’s (1999) extension to ordinal variables to create a distance matrix from our trait data (gowdis function in the FD package; Laliberté and Legendre 2010; Laliberté et al. 2014). We used: Proportion of total distribution within EU (binary: < 50%/≥ 50%), endemcity (binary: <35,000 km²/≥35,000 km²), threat (ordinal: 0=LC (Least Concern), 1=NT (Near Threatened), 2=VU (Vulnerable), 3=EN (Endangered), 4=CR (Critically Endangered)), larval hostplant specialisation (ordinal: 0=polyphagous, 1=oligophagous, 2=monophagous), habitat specialisation (ordinal: 0=generalist, 1=intermediate;
2 = specialist), dispersal behaviour (ordinal: 0 = sedentary, 1 = dispersive, 2 = migratory), and the additive values of the four wing characteristics (continuous: size, ordinal: colour, shininess, shape). Second, we performed a non-metric multidimensional scaling (two axes) on the Gower distance matrix using the metaMDS function in the vegan package (Oksanen et al. 2016). We tested for differences between groups in trait space using PERMANOVA (adonis function, 1000 permutations). For illustration, traits were plotted post-hoc using the envfit function with 1000 permutations. All analyses were conducted in R 3.5.1 (R Core Team 2018). An overview of all parameters used and of all species-specific classifications is given in electronic Appendix 2.

**Results**

The charismatic value assessed by four wing characters for all 404 butterfly species differed significantly between the four classifications (Cumulative Link Mixed Model: \( \chi^2 = -119.69, p < 0.001 \)). The charismatic value was higher for CS than for HD (\( z \)-ratio = 7.094, \( p < 0.0001 \)), NC (\( z \)-ratio = 3.855, \( p < 0.0001 \)) and SCP (\( z \)-ratio = 8.747, \( p < 0.0001 \)), higher for HD than for NC (\( z \)-ratio = 3.435, \( p < 0.01 \)) and SCP (\( z \)-ratio = 3.182, \( p < 0.01 \)), but did not differ between NC and SCP (\( z \)-ratio = 1.143, \( p < 0.6629 \)) (Tukey-adjusted comparisons) (Fig. 1).

The enquiry on being a charismatic butterfly species yielded median scorings of the subset of 94 species (i.e. all CS, HD and SCP taxa) of 2.5 (25%: 1.73/75%: 3.09), i.e. the majority of species were assessed as little to medium attractive. In line with the results presented above, the citizens in the enquiry (Linear mixed effects model: \( F_{3,73.64} = 22.82, p < 0.001 \)) ranked CS (\( n = 20 \)) higher than HD (\( N = 32 \)) (\( z = 4.269, p < 0.001 \)) and SCP (\( n = 48 \)) (\( z = 8.098, p < 0.001 \)), and HD higher than SCP (\( z = 4.670, p < 0.001 \)) (Fig. 1). For the subset of species for which the questionnaire was conducted, the charismatic values of the two methods applied correlated strongly (Spearman’s rank correlation: \( \rho = 0.691, p < 0.001 \)) (Fig. 1).

The ordination analysis showed that species selected by the three approaches occupy different trait spaces (Fig. 2, ANOSIM \( F_{3,409} = 56.238, R^2 = 0.29, p < 0.0001 \); stress value: 0.13). The most important discriminating factor was endemism \( (R^2 = 0.761, p < 0.001) \), followed by dispersal \( (R^2 = 0.629, p < 0.001) \), habitat specialization \( (R^2 = 0.613, p < 0.001) \) and geographic distribution \( (R^2 = 0.422, p < 0.001) \). Hostplant specialization \( (R^2 = 0.300, p < 0.001) \), wing size \( (R^2 = 0.231, p < 0.001) \), wing shape \( (R^2 = 0.215, p < 0.001) \), threat \( (R^2 = 0.196, p < 0.001) \), colour \( (R^2 = 0.190, p < 0.001) \) and shininess \( (R^2 = 0.027, p < 0.01) \) explained much less. CS and SCP each occupied comparatively small areas in the trait space, which were largely located at different ends. CS were mainly characterised by wing traits and a high dispersal ability, SCP by a distribution mainly in the EU and by endemism. The HD species as well as the species not classified in any of the three groups were widely distributed over the whole trait space, but the distribution of the HD species was even wider than that of the not-classified species.

**Discussion**

Our results show that the mean level of charisma is higher for species of the EU Habitats Directive than for species of conservation priority and for not-listed species. Five of the twenty most charismatic species are also listed on the EU Habitats Directive, but none occurred on the list of species being of conservation priority. A trait space analysis show that species listed on the EU Habitats Directive cover a comparatively large trait space and
include many species with high charismatic value, but low ecological and biogeographical relevance, while species of high conservation priority cover a much more restricted trait space and do not overlap with the trait space covered by charismatic species. In the following, we discuss these main results linked to our main hypotheses in more detail.

Our first hypothesis states that species of all four groups (CS, HD, SCP, NC) differ in their trait space, with species of HD having a higher and SCP a mostly similar charismatic value than not-classified species. This is strongly supported by our data and further corroborated by our citizen enquiry ranking the beauty of the HD species intermediate between the CS solely chosen for their charismatic wing characters and the SCP that were selected by rather objective, conservation relevant traits and not by their beauty (Habel et al. 2019).

Our findings thus underline that the selection of the species included in the annexes of the EU Habitats Directive in parts follows subjective perceptions such as charisma and beauty (see also Cardoso 2012), but also other features, such as exceptional life cycles and/
or species existing in small and isolated relict populations in Europe, where they are at the margin of their distribution range (Hochkirch et al. 2013a).

Examples of species that were included in the Habitats Directive annexes based on a mixture of beauty and ecological speciality are the three “Large Blues” of the genus *Phengaris* (formerly *Maculinea*). These species show highly peculiar parasitic interactions with ants (e.g. Witek et al. 2013; Filz and Schmitt 2015), but also their beauty was scored well above average in our enquiry. Due to their specific and highly sensitive life cycles, these species are vanishing across Europe, and consequently they are red-listed (Van Swaay et al. 2010). Thus, these species are of high relevance for regional nature conservation (Mun-guira and Martín 1999), but do not meet the requirements to be of high conservation priority (SCP), as most of their distribution ranges is located outside of the EU, where most of the populations are non-threatened in the centres of their distributions further east (Tshikolovets 2011). Similarly, the Festoon *Zerynthia polyxena* and the Large Copper *Lycaena dispar* also have comparatively high beauty scorings according our enquiry (> 3) due to their colourful wings with a filigree patterning of the former and the shiny red wing colour of the latter. In addition, both have a relatively large size. However, both species are considered as least concern in the red list of Europe (Van Swaay et al. 2010).
distribution areas again are beyond the EU (Tshikolovets 2011), and their conservation will also not preserve a specific habitat of particular threat. Consequently, such species can generate public awareness for nature conservation, but their specific protection is unlikely to achieve the objective of the most efficient and targeted conservation.

Our second hypothesis states that HD species cover a larger trait space than SCP because HD species include charismatic species as well as species of high ecological relevance, but underrepresent species of high geographic relevance as well as the truly threatened species. Since the selection of the butterfly species of the Habitats Directive annexes covers aesthetic, ecological, biogeographical and conservation aspects as a whole, it is not surprising that they occupy the largest trait space in our analyses. This is even larger than for the species selected for their charismatic wing features and the not listed species, both representing groups with high ecological and biogeographical diversity. SCPs occupy the by far smallest trait space as they only include specialists who usually have low dispersal capabilities, a limited number of larval food plants and often inhabit small ranges (Habel et al. 2019). These findings support our second hypothesis. Since similar phenomena are also obvious in other taxonomic groups, it is not surprising that the composition of the Habitats Directive annexes is often criticised (e.g. Cardoso 2012; Hochkirch 2013a, b; Habel et al. 2019). However, there are also opinions that on the one hand accept these criticisms, but fear that an intensive discussion of the annex species could weaken nature conservation in Europe. Such voices advise that it is better to have an effective nature conservation tool with known deficiencies than to jeopardise it by attempting to optimise it (e.g. Maes et al. 2013).

Therefore, we have to scrutinise the value of charismatic species in nature conservation. In general, the use of such species is also known as flag-ship species concept (Heywood 1995), which also can be successfully applied to invertebrates (Barua et al. 2012). Rodrigues and Brooks (2007) showed that such flag-ships, in addition to being charismatic and thus attractive to people, can represent suitable surrogates to conserve entire species communities and ecosystems under threat. However, surrogates have their strong limitations. Thus, Rodrigues and Brooks (2007) clearly underlined that surrogates have a particularly high probability of being effective if they are part of the target group. Nevertheless, even in this case, careful verification is necessary. For example, it has been shown that the large mammalian species in Africa are a good surrogate for all mammals, but not the famous "Big Five" (Williams et al. 2000). Surrogates across major taxonomic units performed substantially less well (Rodrigues and Brooks 2007), suggesting that the focus on vertebrates in European nature conservation could be one reason for the on-going decline of terrestrial invertebrates (e.g. Habel et al. 2016; Hallmann et al. 2017; Seibold et al. 2019; Van Klink et al. 2020). The selection of accurate invertebrate surrogates is therefore elementary for an optimised nature conservation addressing biodiversity as a whole.

The political and societal acceptance of charismatic flag-ship species is high and thus a prerequisite to implement nature conservation in real-life action (Barua et al. 2012). The willingness to protect species is increasing with their beauty (Landová et al. 2018). However, these species frequently miss conservation targets because of rather limited ecological significance for the conservation goal (Rodrigues and Brooks 2007). Therefore, the use of charismatic flagship species has already been severely criticised (Lorimer 2007; Brichetti and Gariboldi 1997; Ballourad et al. 2011; Brambilla et al. 2013). Previous studies also underlined that focusing on a few charismatic species not only neglect other (relevant) species (Pillon and Chase 2007; Amori et al. 2008), but may have even negative effects towards “non-charismatic species” (i.e. “background species”) due to specifically adapted management regimes (Simberloff 1998; Andelman and Fagan 2000).
If one compares the HD and the SCP species, the iterative selection process of the latter ensures that they are good surrogates for the general conservation of butterflies in Europe and might also represent other groups of invertebrates. Thus, they might be a suitable group for the general conservation of invertebrates. However, the large majority of these butterfly species have rather limited public awareness, because most of them are neither big, colourful or otherwise particularly charismatic. This lack of appealing characteristics might be detrimental for the political formulation of conservation laws and their local and regional implementation (cf. Landová et al. 2018). Although the existing list of butterfly species in the Habitats Directive annexes does not have the problem of lack of acceptance, as several of them belong to the exceptionally beautiful species (see above), their suitability as surrogates must be questioned, partly because of their lack of ecological significance and partly because of their highly specialised and rare niches. If we focus exclusively on species of the Habitat Directive, we would likely miss the conservation of many ecologically relevant species and species communities. It is therefore important to establish a link between species appeal and their suitability to act as flagship and umbrella for as many diverse species communities as possible (see Lorimer 2007; Caro 2010; Macdonald et al. 2015; Verissimo and McKinley 2016).

In conclusion, we suggest that prioritisation is first made on the basis of objective (i.e. science-based) ecological criteria, such as for the SCPs, in order to identify the most relevant species for the conservation of their respective communities. In a second step, these communities can then be further supplemented by some charismatic flagships, which will achieve highest possible acceptance in politics and the society. With respect to our study, several aspects should be considered when interpreting the results: 1. Local perceptions of beauty by people and the relation of local people to nature may strongly vary and might play a stronger role in conservation acceptance than the charisma of single species (Kellert 1996a, b; Czech et al. 1998; Brackney and McAndrew 2001; Knight 2008; Tam et al. 2013; Ahn et al. 2014). For example, Macdonald et al. (2017) indicated cultural differences in stakeholder attitudes (see also Bowen-Jones and Entwistle 2002) and thus underlined that beauty is a very subjective value, which may strongly vary among ethnic groups. 2. In our study, we exclusively considered butterflies, because of the broad ecological knowledge available for this group. By selecting this generally rather charismatic group within the order Lepidoptera we included a bias associated with beauty in our study. However, our result show clear biases associated with beauty even within this group and we expect this to be even much clearer when including moths or other less charismatic groups. 3. We have to critically request the robustness of our scoring of charisma. The different factors were not weighted, which may lead to a bias in subjective perception, but also every applied weighting might be subjective as clear and universal measures of what makes an animal beautiful do not exist. 4. Lastly, butterflies, the selected group in this study, already underline this dilemma, since they represent a small group of all lepidoptera with the moths being much more species-rich and even of greater ecological relevance. However, moths neither scientifically nor socially enjoys the same attention as do butterflies. Thus, the selection of butterflies for this study also is largely a consequence of charisma consideration.

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Author contributions All authors developed the idea. JCH and TS compiled the data. MMG did the statistics. TS performed the enquiry with citizens. All authors contributed with writing and the interpretation of data.

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Authors and Affiliations

Jan Christian Habel¹ · Martin M. Gossner²,³ · Thomas Schmitt⁴,⁵,⁶

¹ Evolutionary Zoology, Department of Biosciences, University of Salzburg, Hellbrunner Str. 34, 5020 Salzburg, Austria
² Forest Entomology, Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland
³ Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, Universitätsstr. 16, 8092 Zurich, Switzerland
⁴ Senckenberg Deutsches Entomologisches Institut, 15374 Müncheberg, Germany
⁵ Department of Zoology, Institute of Biology, Faculty of Natural Sciences I, Martin Luther University Halle-Wittenberg, 06099 Halle (Saale), Germany
⁶ Entomology and Biogeography, Institute of Biochemistry and Biology, Faculty of Science, University of Potsdam, 14476 Potsdam, Germany