



Characteristics of Positive Deviants in Western Chimpanzee Populations

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With continued expansion of anthropogenically modified landscapes, the proximity between humans and wildlife is continuing to increase, frequently resulting in species decline. Occasionally however, species are able to persist and there is an increased interest in understanding such positive outliers and underlying mechanisms. Eventually, such insights can inform the design of effective conservation interventions by mimicking aspects of the social-ecological conditions found in areas of species persistence. Recently, frameworks have been developed to study the heterogeneity of species persistence across populations with a focus on positive outliers. Applications are still rare, and to our knowledge this is one of the first studies using this approach for terrestrial species conservation. We applied the positive deviance concept to the western chimpanzee, which occurs in a variety of social-ecological landscapes. It is now categorized as Critically Endangered due to hunting and habitat loss and resulting excessive decline of most of its populations. Here we are interested in understanding why some of the populations did not decline. We compiled a dataset of 17,109 chimpanzee survey transects (10,929 km) across nine countries and linked them to a range of social and ecological variables. We found that chimpanzees seemed to persist within three

social-ecological configurations: first, rainforest habitats with a low degree of human impact, second, steep areas, and third, areas with high prevalence of hunting taboos and low degree of human impact. The largest chimpanzee populations are nowadays found under the third social-ecological configuration, even though most of these areas are not officially protected. Most commonly chimpanzee conservation has been based on exclusion of threats by creation of protected areas and law enforcement. Our findings suggest, however, that this approach should be complemented by an additional focus on threat reduction, i.e., interventions that directly target individual human behavior that is most threatening to chimpanzees, which is hunting. Although changing human behavior is difficult, stakeholder co-designed behavioral change approaches developed in the social sciences have been used successfully to promote pro-environmental behavior. With only a fraction of chimpanzees and primates living inside protected areas, such new approaches might be a way forward to improve primate conservation.

Keywords: behavioral change, conservation planning, hunting, mimicking, positive deviance, West Africa, *Pan troglodytes verus*

INTRODUCTION

With continued human population growth and the associated expansion of human-dominated areas, 75% of land surface areas have been anthropogenically modified (Ellis and Ramankutty, 2008). Human disturbance resulted in an average population decline of 25% for terrestrial vertebrates and of 45% for the majority of invertebrates, with the main drivers being habitat destruction, overexploitation, and invasive species (Dirzo et al., 2014). However, in some instances, species are able to persist and co-exist with humans (Gardner et al., 2009). Threats to species and the resulting species decline are relatively well studied, but considerably less is known about the social-ecological conditions under which some species tend to persist while others disappear.

One approach to understand why species are persisting at certain sites is to understand the heterogeneity across populations with a focus on analyzing positive outliers (Post and Geldmann, 2018). Similarities between areas where species are doing exceptionally well, called exceptional responders (Post and Geldmann, 2018), bright spots (Cinner et al., 2016), or positive deviants (Marsh et al., 2004), could highlight novel solutions to conservation challenges (Cinner et al., 2016; Post and Geldmann, 2018). While this approach has been used widely in medicine and social sciences, applications in ecology and conservation are still rare (Cinner et al., 2016; Frei et al., 2018). Applied to species conservation this approach entails identifying those social-ecological conditions in which a species is likely to persist.

Primates are a taxon that is strongly impacted by anthropogenic factors, and despite their social, cultural, and ecological importance, most populations are severely threatened (Estrada et al., 2017). However, evidence on the effectiveness of conservation interventions for primates remains scarce (Junker et al., 2017). Nonetheless, some primates, and great apes in particular, seem to be able to adapt to and persist in anthropologically impacted landscapes (Hockings et al., 2015; McCarthy et al., 2017; Spehar et al., 2018). The identification of

conditions that are enabling species persistence can guide the design of conservation interventions that are mimicking these favorable conditions.

Here we focus on the western chimpanzee (*Pan troglodytes verus*), that occurs in a variety of social-ecological landscapes, meaning that different combinations of biophysical and socio-economic variables characterize their range (Liu et al., 2007). For example, western chimpanzees occur in isolated patches of intact habitat surrounded by human-dominated areas (e.g., Nimba mountains), protected primary rainforest (e.g., Taï National Park), or in agricultural landscapes with forest remnants (e.g., parts of Sierra Leone). A recent evaluation of their status showed a dramatic decline in abundance of 80% and a range reduction of 20% since 1990 (Kühl et al., 2017). This resulted in the up-listing of the species' IUCN status to Critically Endangered (Humble et al., 2016). However, from the 20 sites for which longitudinal data were available, Kühl et al. (2017) found that three sites were exceptions to the general trend of population decline, with two sites in Guinea and one in Côte d'Ivoire seeming to support stable populations. The aim of this study was to apply the positive deviance approach across the entire range of western chimpanzees, to identify social-ecological conditions that might enable chimpanzee persistence. For this we compiled a range-wide dataset of chimpanzee densities, identified drivers of chimpanzee density, and characterized social-ecological conditions across 66 sites.

METHODS

General Workflow

We compiled a western chimpanzee density dataset covering the entire range of this taxon and extracted publicly available social-ecological data for all surveyed sites. We first determined which of the factors influenced chimpanzee densities significantly by fitting a Generalized Linear Mixed Model (McCullagh and Nelder, 1989; Baayen, 2008). After the model established

which factors influenced chimpanzee densities significantly, we compared the configuration of significant social-ecological factors across a total of 66 sites.

Statistical Modeling

Model Response and Offset Term

Great ape density estimates are usually based on the counting of nests they built as resting places, instead of counting individuals themselves. Nests are more visible, more numerous, and do not move, meaning that there is no correlation between detectability of nests and intensity of threats (Kühl et al., 2008). Following a procedure that is commonly used for modeling ape densities, we used number of nests per transect as the model response and constructed an offset term to let the model output directly express chimpanzee densities (Murai et al., 2013; Wich et al., 2016; Voigt et al., 2018).

The number of nests was derived from chimpanzee nest surveys. In total we compiled 52 chimpanzee nest surveys across nine countries (Figure 1, Supplementary Table 1) via the IUCN SSC A.P.E.S. database (Kühl et al., 2007). These included line transect and reconnaissance surveys (Kühl et al., 2008) conducted between 2001 and 2015. We only included reconnaissance surveys for which the survey effort was known, based on GPS tracklog data. The entire dataset consisted of 17,109 transect or reconnaissance segments (hereafter referred to as “transect”) with a total survey effort of 10,929 km (mean transect length: 0.64 km, range: 0.02–14.00 km).

The offset term (McCullagh and Nelder, 1989) was calculated as $D = N / (2 * L * ESW * p * r * t)$ where D is chimpanzee density, N number of nests, L transect length, ESW effective strip width, p proportion of nest builders, r nest production rate, and t nest decay time (Kühl et al., 2008). Hence, the offset term in the model was the log of the denominator of the above equation [i.e., $\log(2 * L * ESW * p * r * t)$].

To determine the ESW we only used nests for which the perpendicular distance from the transect line was recorded ($n = 12,728$ nests), meaning that we did not use nest observations from reconnaissance surveys for this specific analysis. We determined the ESW separately for different habitat types to account for varying nest detectability due to habitat type. For nest observations the habitat type was typically recorded during the survey. To standardize habitat types across datasets we assigned them to the land cover categories defined by the Global land cover dataset (Friedl et al., 2010), namely “evergreen broadleaf forest,” “mixed forest,” “permanent wetlands,” “woody savanna,” “savanna,” “croplands,” “cropland natural vegetation mosaic.” For <10% of nest observations the habitat was not recorded during the survey, and we extracted habitat type from satellite data (Global land cover dataset, Friedl et al., 2010). To get approximately balanced sample sizes for each habitat type we pooled habitat type to three categories: forest (“evergreen broadleaf forest,” “mixed forest,” “permanent wetlands”), savanna (“savannah,” “woody savannah,” “closed shrubland”), and cropland (“cropland,” “cropland/natural vegetation mosaic”). We determined the ESW using DISTANCE (6.2 Release 1, Thomas et al., 2010, further details in Supplementary Material, Supplementary Tables 2, 3,

Supplementary Figure 1). We then extracted the habitat type for an area of 0.5 km around each transect from the Global land cover dataset (Friedl et al., 2010), and used the same assignment to the three habitat categories as above. Lastly, we assigned the habitat-specific ESW to each transect. ESW assignment for transects that traversed more than one habitat type was based on a majority vote.

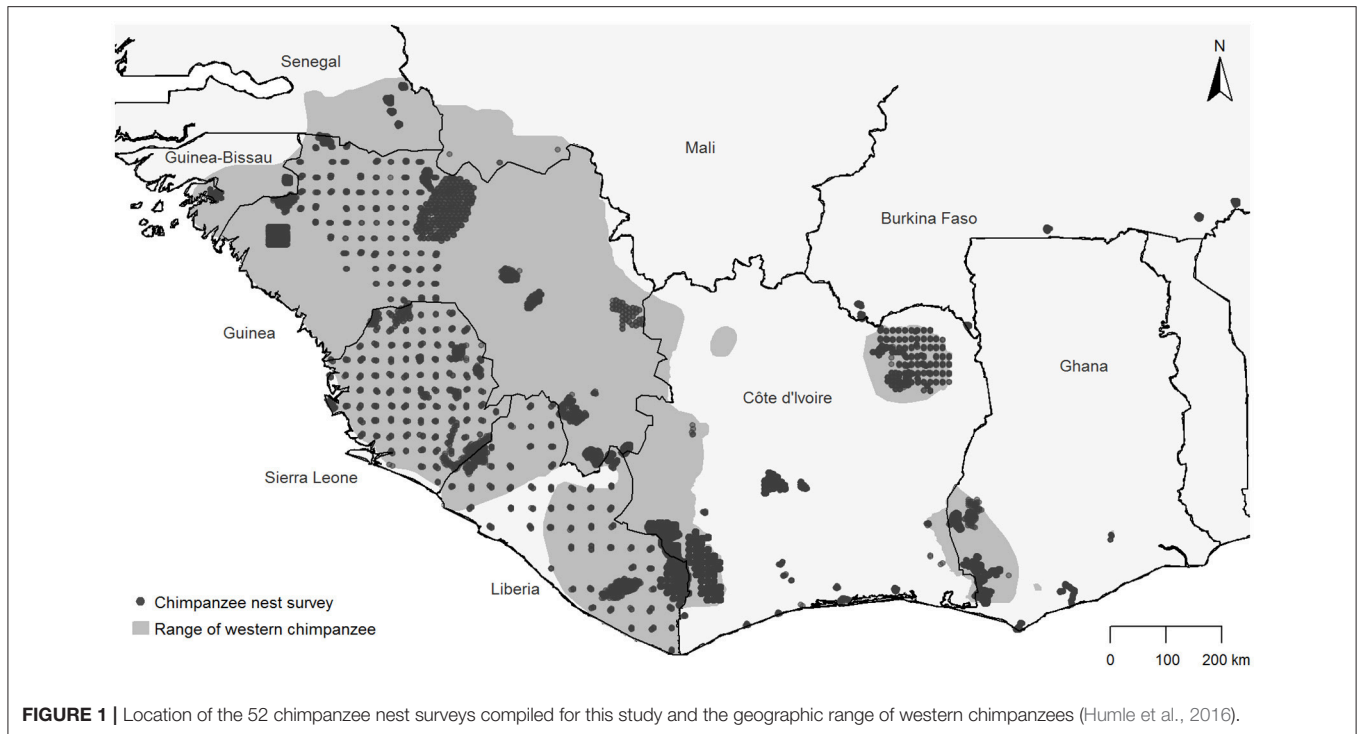
Nest decay times vary between sites and seasons and are influenced by rainfall (Walsh and White, 2005; Kühl et al., 2008; Kouakou et al., 2009). Hence, we first fitted models to determine the mean nest decay time separately for each of the eight nest decay datasets and then fitted a separate model to estimate decay time as a function of rainfall. We then assigned a nest decay time to each transect based on that model and the mean rainfall at the respective transect. The model revealed a minimum fitted decay time of 85.45 days and a maximum fitted decay time of 229.03 days. Model uncertainty was assessed by deriving 10,000 bootstraps (additional details on nest decay methods and results in Supplementary Tables 4, 5, Supplementary Figures 2, 3). We used a proportion of nest builders of 0.83 (Plumptre and Cox, 2006) and a nest production rate of 1.143 (Kouakou et al., 2009).

Model Predictors

We modeled chimpanzee density as a function of different social-ecological factors relevant for chimpanzee abundance, such as habitat, climate, topography, and socio-economic context. For this we used 19 predictor datasets that were available for the entire study area (predictor descriptions, temporal and spatial resolution of datasets detailed in Table 1). For quantitative predictors we calculated the mean of values within a fixed extraction radius around each transect, and for categorical predictors we determined the proportion of each category within the extraction radius. We transformed predictors when necessary to derive approximately symmetric distributions (details on predictor data extraction, transformation, and post-processing in Supplementary Table 6).

Spearman correlations among predictors indicated that some predictors were highly interrelated (Supplementary Table 7); hence, we used factor analyses to reduce redundancy among them, which resulted in three factors. On the factor that we termed “environment” *tree cover* and *vegetation height* loaded negatively, while *savanna*, *temperature*, and *rainfall seasonality* loaded positively (Supplementary Table 8). On the factor termed “socio-economic status” *education* and *corruption control* loaded positively, while *poverty* and *malnourishment* loaded negatively. On the factor termed “human activity” *settlements*, *human density*, *nighttime light*, and *conflicts* loaded positively (details on factor analyses in Supplementary Table 9). We did not include the variables *cropland*, *forest loss*, *hunting taboo*, *slope*, *river*, and *road* in the factor analyses either because they did not load strongly on any factor with Eigenvalue ≥ 1 , or because it was the only predictor that loaded strongly on a factor. We therefore included them as separate predictors in the model.

We differentiated between test and control predictors (Mundry, 2014), and included 13 model terms as test predictors into the model (details on anticipated effects, also for interactions and squared terms, in Table 2). Distance to the closest river and



road were included as control predictors, because they are known to influence animal densities (Boesch et al., 2017). All predictors were standardized to a mean of zero and a standard deviation of one to facilitate comparability of model parameters and ease interpretation of interactions (Schielzeth, 2010).

Model Implementation

We fitted a Generalized Linear Mixed Model (McCullagh and Nelder, 1989; Baayen, 2008) with a negative binomial error distribution and log link function, because the response was highly skewed with no nest observations on most transects (90.24%) and a large number of nests on some transects (range number of nests per transect: 0–430). The latter speaks against a Poisson distribution. With ape surveys being very cost and time intensive, they are usually targeted toward areas with possible chimpanzee presence, and hence we decided against a zero-inflated error distribution.

We included an autocorrelation term into the model to account for spatial autocorrelation, i.e., nest counts from transects that were closer to one another were more similar, even after accounting for the predictors in the model, and therefore the model residuals were not independent (details on implementation in **Supplementary Material**). The full model was:

number of nests per transect \sim cropland + date + environment + forest loss + human activity + hunting taboo + slope + socio-economic status + socio-economic status² + human activity:hunting taboo + human activity:slope + human activity:socio-economic status + human activity:socio-economic status² + hunting taboo:slope + hunting taboo:socio-economic

status + hunting taboo:socio-economic status² + river + road + spatial autocorrelation + offset term.

Chimpanzee densities are likely to differ among countries. This can be due to past events, for example chimpanzee densities are likely to be lower in Sierra Leone due to excessive chimpanzee captures in the 70's and 80's (Hanson-Alp et al., 2003). To account for these between-country differences and to control for the non-independence of data points from the same country, i.e., pseudoreplication, we included country as a random effect.

Additionally, the strength of effects can differ among countries, i.e., the slopes of the response against the predictor. For example, in a country with high poaching intensity, forests have lower than expected mammal densities, so that the positive effect of forests on mammal density will be smaller than in a country with less intense poaching. Such country-specific differences in poaching intensity can have many reasons among which could be differences in law enforcement capacity, or access to alternative protein sources or livelihoods. Consequently, we included the random slopes of all predictors within country (Schielzeth and Forstmeier, 2009; Barr et al., 2013).

The check of model assumptions revealed overdispersion (dispersion parameter = 1.71), causing standard errors to be underestimated. We corrected for this by adjusting the estimated standard errors and then re-determining z - and p -values (Gelman and Hill, 2007). We also tested for multicollinearity and found that it was not an issue (details on implementation in **Supplementary Material**, **Supplementary Table 10**, **Supplementary Figure 4**).

To test the significance of fixed effects as a whole, we compared the fit of the full model with that of a null model lacking all test predictors, but comprising the same control predictors

TABLE 1 | Dataset sources for predictors in the statistical model.

Predictor	Dataset	Variable used	References	Temporal resolution*	Spatial resolution
Conflicts	Armed Conflict Location and Event Data project (ACLED)	Location of violent conflicts	Raleigh et al., 2010	1997–2015 (continuous)	Point locations
Corruption control	Worldwide governance indicators	Control of corruption (measures perception of extent of corruption, ranges from –2.5 to 2.5)	World Bank, 2015	2000–2014 (annually, not 2001)	Country
Cropland	Global land cover MCD12Q1	Land cover classified as “cropland” and “cropland/natural vegetation mosaic”	Friedl et al., 2010	2001–2012 (annually)	0.5 km
Education	Sub-national African education and infrastructure access data	Net secondary attendance rate (proportion of children attending secondary school)	CCAPS, 2013	year of DHS/MICS survey (2005–2011)	Subnational region
Forest loss	Global forest change—forest loss year	Year of forest cover loss	Hansen et al., 2013	2000–2014 (annually)	0.03 km
Human density	AfriPop	Estimated number of people	Linard et al., 2012	2010	0.0083° (ca. 0.10 km)
Hunting taboo	World religion database based on USAID demographic and health survey (DHS)	Proportion of Muslims	Johnson and Grim, 2008	most recent DHS survey available in database (2003–2008)	Subnational region
Malnourishment	World Health Organization Global Database on Child Growth and Malnutrition	Prevalence of stunting among 0–5 year-old children (stunting is the result of suboptimal health and/or nutritional conditions)	de Onis and Blössner, 2003	1992–2013 (1–6 datasets per region)	Subnational region
Nighttime light	Nighttime lights composite	Stable lights (presence of lighting, is associated with intensity of economic activity, integer scale from 0 to 63)	NOAA, 2013	2000–2013 (annually)	30 arc s (ca. 1.00 km)
Poverty	Multidimensional poverty index 2015 [based on most recent USAID demographic and health survey (DHS) and UNICEF multiple indicator cluster survey (MICS)]	Poverty index (ranges from 0 to 1)	Alkire and Robles, 2015	most recent DHS or MICS survey (2006–2014)	Subnational region
Rainfall	Tropical rainfall measuring mission (TRMM) 3B43	Rainfall	TRMM and GES DISC, 2011	Jan 2000–Oct 2015 (monthly)	0.25°
River	River-surface water body network (RWDB2)	Location of rivers	FAO, 2007	2006	Vector map
Road	Roads of the world (Vmap0)	Location of roads	FAO, 2005	1997	Vector map
Savanna	Global land cover MCD12Q1	Land cover classified as “savannah,” “woody savannah,” “open shrubland,” or “closed shrubland”	Friedl et al., 2010	2001–2012 (annually)	0.50 km
Settlements	Global urban footprint	Land cover classified as built-up area	Esch et al., 2012	2011/2012	0.084 km
Slope	Global multi-resolution terrain elevation data (GMTED2010)	Slope (derived as maximum elevation change between a cell and its eight neighbors)	Danielson and Gesch, 2011	2010	7.5 arc s (ca. 0.25 km)
Temperature	Land surface temperature and emissivity MOD11B3	Day time land surface temperature	Wan and Hulley, 2015	Feb 2000–Dec 2011 (monthly)	6.00 km
Tree cover	Vegetation continuous fields MOD44B	% tree cover	DiMiceli et al., 2011	2000–2010 (annually)	0.25 km
Vegetation height	Vegetation height estimate	Average vegetation height	Woods Hole Research Center, 2007	2007	0.03 km

*“most recent” refers to the latest data point prior to when the area was surveyed.

TABLE 2 | Anticipated effects of model terms included as test predictors into the model.

Model term*	Anticipated effect	Explanation/hypothesis
Cropland	negative	Land-use conversion to cropland results in habitat loss and fragmentation. It also increases contact between humans and chimpanzees, e.g., when chimpanzees feed on crops, increasing the likelihood of conflict or disease transmission.
Date	negative	Chimpanzee populations have continuously declined over the last decades Kühl et al., 2017.
Environment	negative	<i>Tree cover</i> and <i>vegetation height</i> loaded negatively on this factor, and <i>savanna</i> , <i>temperature</i> and <i>rainfall seasonality</i> loaded positively, i.e., low values of this factor indicate rainforest conditions and high values indicate savanna conditions. It can be expected that chimpanzee densities are lower in savanna than in forest habitat due to differences in resource availability.
Forest loss	negative	Forest loss leads to habitat loss and fragmentation. It entails secondary threats such as increased bush meat hunting around settlements in resource concessions.
Human activity	negative	<i>Conflicts</i> , <i>human density</i> , <i>nighttime light</i> , and <i>settlements</i> loaded positively on this factor. Increased intensity of human activity leads to increased resource use which negatively influences chimpanzees.
Hunting taboo	positive	Due to cultural traditions Muslims are less likely to kill great apes for food than non-Muslims Davis et al., 2013. In areas with a higher proportion of Muslims there is a higher prevalence of cultural taboos against eating chimpanzee meat Ham and Carter, 1998.
Slope	positive	Steep terrain is characterized by less anthropogenic disturbances and could serve as a refuge area for chimpanzees.
Socio-economic status ²	positive quadratic	<i>Education</i> and <i>corruption control</i> loaded positively on this factor, and <i>poverty</i> and <i>malnourishment</i> loaded negatively. Improvement of the socio-economic status, e.g., economic development, is often accompanied by an increase in resource use resulting in environmental degradation. Based on the concept of the environmental Kuznets curve Mills and Waite, 2009, further economic growth might allow a community or country to invest into environmental protection.
Human activity : Hunting taboo	positive	The effect of hunting taboos increases when the intensity of human activity increases, because in areas with a very low intensity of human activity the pressure on chimpanzees might be too low to reveal the positive effect of hunting taboos.
Human activity : Slope	positive	The effect of steep terrain as a refuge area increases with increasing intensity of human activity in surrounding areas.
Human activity : Socio-economic status ²	positive quadratic	The effect of socio-economic status increases with increasing intensity of human activity, because in areas with a low intensity of human activity the pressure on chimpanzees might be too low to reveal an effect of socio-economic status.
Hunting taboo : Slope	positive	The effect of steep terrain as a refuge area increases with decreasing hunting pressure, because the positive effect of steep terrain might not be observable in areas with very strong hunting pressure.
Hunting taboo : Socio-economic status ²	positive quadratic	In areas with a high prevalence of hunting taboos changes in socio-economic conditions might impact chimpanzee densities, while there could be no such effect in areas without hunting taboos.

*Model term followed by superscripted 2 refers to a squared term.

and random effects structure as the full model (Forstmeier and Schielzeth, 2011) using a likelihood ratio test (Dobson and Barnett, 2008). All models were fitted with the R function “glmer.nb” of the R package “lme4” (version 1.1–11, Bates et al., 2015). Model stability was assessed by comparing model estimates based on all data, with model estimates based on data excluding countries one at a time. The model was stable regarding the effects of all significant predictors (minimum and maximum estimates in **Table 3**). To derive confidence limits, we fitted parametric bootstraps. For this, we randomly selected one nest decay bootstrap, determined the fitted nest decay rate, and derived an adjusted offset term. We then fitted the full model with the new offset term and derived one bootstrap with the R function “bootMer” (package “lme4”). This was repeated 1,000 times. Unless specified otherwise, all analyses were implemented in R (version 3.2.3, R Core Team, 2015).

Characterization of Positive Deviant Sites

We assigned the transects to 19 of the 20 sites delineated in the previous study on western chimpanzee population trends

(Kühl et al., 2017). We did not have data for Mount Péko in Côte d'Ivoire, but it is thought that chimpanzees are now extirpated there (Kühl et al., 2017). The remaining transects covered 47 additional sites, usually according to protected area delineation. For each of the total 66 sites and each factor that was significant in the statistical model we calculated the median, lower and upper quartile of the predictor variable. We then compared characteristics for the three sites that were previously identified as having stable populations, namely Fouta Djallon and Sangaredi in Guinea and Cavally in Côte d'Ivoire (Kühl et al., 2017). We also analyzed sites with transects that deviated by more than two standard deviations from the mean chimpanzee density of transects with chimpanzee presence, as suggested by Post and Geldmann (2018). Due to lower densities of feeding trees, chimpanzee densities are naturally lower in savanna-mosaics than in rainforest habitat (Pruetz and Bertolani, 2009). As chimpanzees have adapted to these challenging conditions (Wessling et al., 2018a,b), low chimpanzee densities in these habitats do not imply population decline. We therefore, focus interpretation of results on populations which have been shown

TABLE 3 | Results of the full model to identify drivers of chimpanzee densities (Generalized Linear Mixed Model, $n = 17,109$).

Predictor ^a	Estimate	SE	z	p	SE _{cor} ^b	z _{cor} ^b	p _{cor} ^b	min ^c	max ^c	CL _{lower} ^d	CL _{upper} ^d
Intercept	-3.176	0.761	e	e	0.995	e	e	-3.783	-2.765	-4.359	-2.101
Cropland	-0.160	0.231	-0.695	0.487	0.301	-0.532	0.595	-0.507	0.009	-0.689	0.302
Date	-0.390	0.291	-1.338	0.181	0.381	-1.023	0.306	-0.586	-0.255	-1.075	0.246
Environment	-1.037	0.414	-2.501	0.012	0.542	-1.913	0.056	-1.649	-0.789	-2.312	-0.302
Forest loss	-0.571	0.085	-6.736	< 0.001	0.111	-5.152	< 0.001	-0.681	-0.496	-0.743	-0.399
Human activity	-0.009	0.136	e	e	0.178	e	e	-0.462	0.256	-0.216	0.349
Hunting taboo	0.385	0.424	e	e	0.554	e	e	-0.058	1.201	-0.250	1.645
Slope	0.490	0.200	e	e	0.261	e	e	0.225	0.594	0.072	0.869
Socio-economic status	0.469	0.239	e	e	0.313	e	e	-0.578	0.463	-1.510	1.081
Socio-economic status ²	-0.259	0.232	e	e	0.304	e	e	-0.632	0.050	-0.963	0.399
Human activity : hunting taboo	-0.302	0.099	-3.053	0.002	0.130	-2.335	0.020	-0.430	-0.052	-0.531	-0.078
Human activity : slope	0.175	0.050	3.476	0.001	0.066	2.658	0.008	-0.050	0.259	0.042	0.283
Human activity : socio-economic status	-0.047	0.126	-0.370	0.711	0.165	-0.283	e	-0.096	0.333	-0.301	0.321
Human activity : socio-economic status ²	0.004	0.098	0.040	0.968	0.128	0.031	0.976	-0.166	0.310	-0.289	0.189
Hunting taboo : slope	0.217	0.102	2.118	0.034	0.134	1.620	0.105	0.162	0.291	-0.064	0.472
Hunting taboo : socio-economic status	0.122	0.313	0.389	0.697	0.409	0.298	e	-0.298	0.548	-0.632	0.953
Hunting taboo : socio-economic status ²	0.504	0.207	2.437	0.015	0.271	1.864	0.062	0.054	0.692	-0.084	0.939
River ^f	-0.419	0.130	-3.228	0.001	0.170	-2.469	0.014	-0.533	-0.328	-0.683	-0.124
Road ^f	0.013	0.140	0.095	0.924	0.184	0.073	0.942	-0.039	0.124	-0.284	0.329
Spatial autocorrelation ^f	0.704	0.074	9.502	< 0.001	0.097	7.267	< 0.001	0.660	0.756	0.532	0.852

^aAll predictors were z-transformed to a mean of zero and a standard deviation of one (mean and sd of predictors before being z-transformed in **Supplementary Table 13**).

^bCorrected for overdispersion.

^cMinimum and maximum value of model stability.

^d95% confidence limits.

^eP- and z-values not shown for intercept and model terms that are conditional on other model terms because of very limited interpretation.

^fControl predictor.

to have remained stable (Kühl et al., 2017) and also ordered sites in **Figure 3** according to environmental conditions.

RESULTS

In total, 13,464 nests were recorded. Estimated chimpanzee density ranged between 0.00 and 46.33 individuals/km², with average densities of 0.14 ± 0.93 individuals/km² (mean \pm SD) across all transects and average densities of 1.42 ± 2.67 individuals/km² on transects with chimpanzee presence.

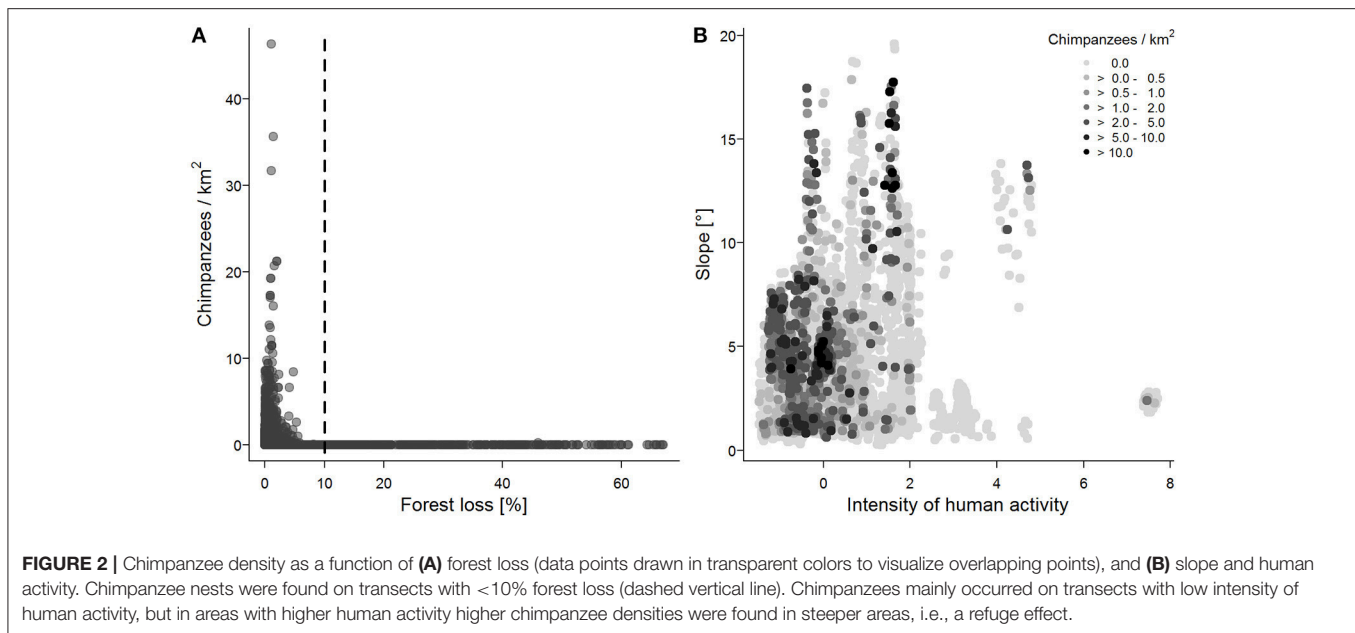
Statistical Model

The full model explained chimpanzee density significantly better than the null model (likelihood ratio test comparing full model and null model without test predictors: $\chi^2 = 40.28$, $df = 16$, $p < 0.001$, model results in **Table 3**, random effects and random slopes in **Supplementary Tables 11, 12**). The factor “environment” had a marginally significant negative effect, with lower chimpanzee densities in dry and sparsely forested areas, and higher chimpanzee densities in rainforest habitat (**Table 3**). “Forest loss” had a significant negative effect on chimpanzee density. Except for two transects in Marahoué National Park, Côte d’Ivoire, chimpanzee nests were only found on transects with <10% forest loss (**Figure 2A**). We also found a positive synergistic effect of human activity and slope. Chimpanzee densities were higher in areas with low

intensities of human activity. However, in areas characterized by relatively high intensities of human activity, chimpanzee densities were higher in steeper terrain (**Figure 2B**). There was also a positive synergistic effect of human activity and hunting taboo, with the highest chimpanzee densities in areas with a high prevalence of hunting taboos and low degree of human activity. Socio-economic status had no significant effect (**Table 3**), i.e., chimpanzee density was not significantly influenced by education, poverty or malnourishment levels. Cropland did not have a significant effect on chimpanzee densities, but highest densities were recorded on transects with <25% cropland. Overall, absolute model estimates showed that the factor “environment” had the strongest influence on chimpanzee densities, followed by “forest loss” and “slope”.

Characteristics of Positive Deviant Sites

In addition to the three sites identified as exceptional based on stable populations in a previous study (Kühl et al., 2017), we identified five sites with transects with very high estimated chimpanzee densities (>6.76 individuals/km² corresponding to the mean+2SD), namely Tai (Côte d’Ivoire), Grebo (Liberia), Nimba (Côte d’Ivoire and Guinea part), and Boé (Guinea-Bissau, **Figure 3, Supplementary Figure 5**). Characterization of those sites could be grouped into three social-ecological configurations. The first group was characterized by rainforest habitats with low degree of forest loss and low intensity of human activity,



e.g., Cavally (Côte d'Ivoire), Grebo (Liberia), and Tai (Côte d'Ivoire). The second group was characterized by steep terrain, e.g., Nimba mountains in Guinea and Côte d'Ivoire. The third was characterized by a high prevalence of hunting taboos and low intensity of human activity, e.g., Boé in Guinea-Bissau, and Fouta Djallon and Sangaredi in Guinea (**Figure 3**). Nimba (Liberian part), Gola (Sierra Leone), and Goin-Débé (Côte d'Ivoire) also each had one transect with exceptionally high chimpanzee densities, but as this was only one transect each, we did not base any conclusions on these three sites.

DISCUSSION

In our study we found that three configurations of social-ecological factors enabled chimpanzee persistence: rainforest habitat with low degree of human impact, steep areas, and areas with a high prevalence of hunting taboos and low degree of human impact. While the conditions of the first and second configuration are mirrored in conservation interventions aiming at threat exclusion, such as the expansion of protected areas and law enforcement, conservation interventions focusing on threat reduction, as reflected in the third configuration, are still very rare in primate conservation.

Social-Ecological Conditions Enabling Chimpanzee Persistence

The results underlined the importance of intact habitat for chimpanzee persistence, as chimpanzees seemed to only be able to tolerate a surprisingly low threshold of a maximum of 10% forest loss (**Figure 2A**). Habitat loss not only implies a loss of feeding and nesting trees, but often also an increase in other disturbances, such as hunting or human-wildlife conflicts (Estrada et al., 2017). This is in line with previous findings that chimpanzees are sensitive to habitat disturbance (Junker

et al., 2015; Morgan et al., 2018). At those sites in our dataset for which we found high forest loss levels, such as Monogaga (median forest loss: 40.88%), Duékoué (14.19%) and Marahoué (15.20%) in Côte d'Ivoire, chimpanzees are now thought to be extirpated (Campbell et al., 2008; Kühl et al., 2017). In contrast, median forest loss ranged between 0.09 and 1.51% at sites with exceptional chimpanzee densities. Consequently, very low levels of forest loss seem to be a prerequisite for chimpanzee persistence.

Regarding the three social-ecological configurations enabling chimpanzee persistence, we first found exceptionally high chimpanzee densities at rainforest sites with low human activity. The low level of human activity in some of these areas is due to conservation interventions, such as law enforcement, presence of researchers and NGOs, which have a scientifically proven positive effect on great ape persistence (Campbell et al., 2011; Tranquilli et al., 2012; Tagg et al., 2015). For other sites in this category, the relative remoteness and the large distances to the next city (Weiss et al., 2018) might have enabled chimpanzee persistence, as it has been shown that increased market integration has a negative influence on chimpanzee densities (Boesch et al., 2017).

Second, exceptionally high chimpanzee densities were found in steep terrain, especially when surrounding areas were strongly impacted by humans (**Figure 2B**). The steep terrain likely reduced access for humans, as has been found elsewhere (Adanu et al., 2011; Sesink Clee et al., 2015), and such areas are less favorable for conversion to other land-uses (Kinnaird et al., 2003; Silva et al., 2007), so that they seem to function as refuge areas for chimpanzees. In savanna environments, steep terrain also seem to be favored sleeping sites due to the higher tree cover and access to water sources (Pintea and Plumpre, 2006). Consequently, individual transects with very high densities may indicate favored sleeping sites, while surrounding areas are likely characterized by less favorable conditions. For those sites in

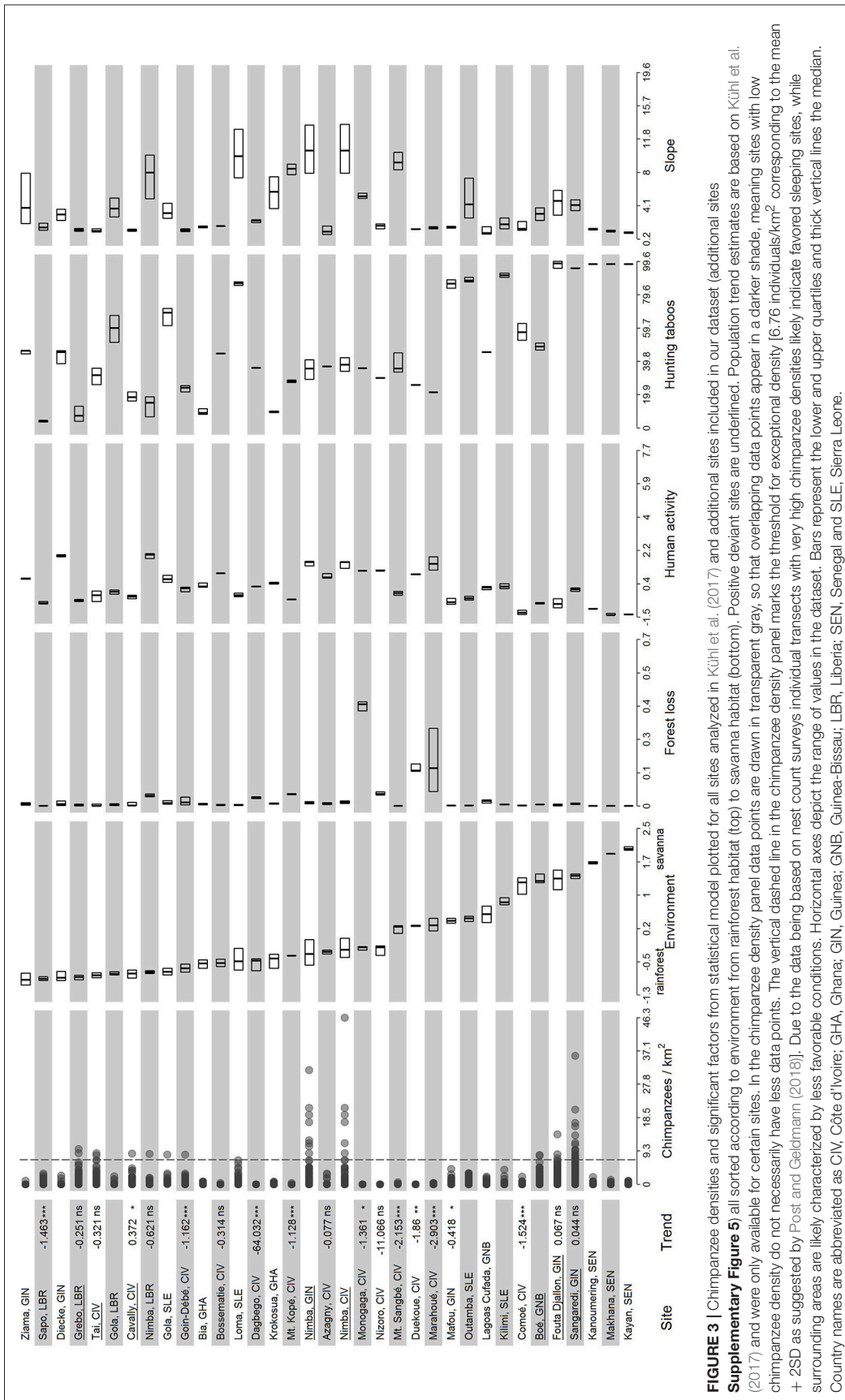


FIGURE 3 | Chimpanzee densities and significant factors from statistical model plotted for all sites analyzed in Kühl et al. (2017) and additional sites included in our dataset (additional sites **Supplementary Figure 5**) all sorted according to environment from rainforest habitat (top) to savanna habitat (bottom). Positive deviant sites are underlined. Population trend estimates are based on Kühl et al. (2017) and were only available for certain sites. In the chimpanzee density panel data points are drawn in transparent gray, so that overlapping data points appear in a darker shade, meaning sites with low chimpanzee density do not necessarily have less data points. The vertical dashed line in the chimpanzee density panel marks the threshold for exceptional density [6.76 individuals/km² corresponding to the mean + 2SD as suggested by Post and Geldmann (2018)]. Due to the data being based on nest count surveys individual transects with very high chimpanzee densities likely indicate favored sleeping sites, while surrounding areas are likely characterized by less favorable conditions. Horizontal axes depict the range of values in the dataset. Bars represent the lower and upper quartiles and thick vertical lines the median. Country names are abbreviated as CIV, Côte d'Ivoire; GHA, Ghana; GIN, Guinea; GNB, Guinea-Bissau; LBR, Liberia; SEN, Senegal and SLE, Sierra Leone.

our dataset with steep terrain and high chimpanzee densities, including the Nimba mountains in Guinea and Côte d'Ivoire, and to a lesser extent Loma mountains in Sierra Leone, the population trend is not known. Chimpanzees might be restricted to small refuge areas, and their long-term survival at those refuges could be constrained due to reduced dispersal possibilities and increased vulnerability, for example to diseases. This is illustrated by examples from Côte d'Ivoire such as Mount Kopé and Mount Sangbé for which strong population declines have been shown (Kühl et al., 2017). While these mountains are isolated areas of steep terrain, there are regions where extensive areas are characterized by relatively steep slopes, for example the Fouta Djallon (**Figure 3, Supplementary Figure 6**). Here, loss in dispersal ability is less likely to be of concern for chimpanzee survival. In addition, mineral exploitation poses a threat as mountains often contain mineral deposits, and several mining sites operate in the Nimba mountains, entailing further threats to wildlife such as infrastructure expansion (Edwards et al., 2014).

The third social-ecological configuration was characterized by relatively low levels of human activity in combination with a high prevalence of hunting taboos at sites characterized by higher proportions of savanna habitat. It was surprising to find that this group of sites not only has seemingly stable populations (Kühl et al., 2017), but also exceptionally high chimpanzee densities, despite the fact that our analysis showed that overall chimpanzee densities are lower in savanna areas compared to rainforest areas (**Table 3**). It appears that the adherence to hunting taboos by humans reduced hunting pressure on chimpanzees, and thereby the key threat to chimpanzees was removed. This is in accordance with a site-based sociological study from Côte d'Ivoire that showed that people adhering to hunting taboos generally do not eat primate meat (Bachmann et al. submitted). These important chimpanzee areas are now partly protected by the recently established Boé National Park (Guinea-Bissau) and the Moyen Bafing National Park (Guinea) that is currently being created. However, large-scale open pit mining is underway at Sangaredi (Guinea), and the current status of the chimpanzee communities there is unclear.

However, there are exceptions to these patterns, i.e., there are sites which are characterized by one of the above-mentioned combination of factors but still have low chimpanzee densities or decreasing populations. This shows that additional factors for which data were not available across the entire study area and could therefore not be included in our analysis might influence chimpanzee persistence, for example absence of diseases (Ryan and Walsh, 2011). Also, historic events, such as intensive hunting in the past at specific sites (Hanson-Alp et al., 2003), might influence current chimpanzee densities. Due to their slow life history apes are especially susceptible to such threats and communities can take decades to recover from single mortality events (Ryan and Walsh, 2011). In addition, due their behavioral flexibility, chimpanzees might be able to adapt to savanna and anthropogenic habitat mosaics and persist there long-term, though likely at lower densities (Hockings et al., 2015). For example, it has been shown that although chimpanzees at Fongoli, Senegal, a site with strong seasonality in temperature and rainfall, experience heat and dehydration

stress, chimpanzees likely developed mechanisms for avoiding costs of energetic constraint (Wessling et al., 2018b). However, these types of landscapes are still less surveyed, and longitudinal data from more sites are needed to determine the population trend, especially from Guinea-Bissau, Mali, Senegal, and Sierra Leone for which such data are lacking. Consequently, this study can only be regarded as a first step and follow-up studies are needed to substantiate our findings.

Threat Reduction Through Behavioral Change

Our study revealed three factors having a positive effect on chimpanzee densities; habitat protection, reduced accessibility, and hunting taboos. The first two factors are already reflected in commonly implemented conservation interventions, such as protected areas, law enforcement, and the presence of researchers, NGOs and tourism activities, which have also been shown to have a positive effect on ape persistence (Campbell et al., 2011; Tranquilli et al., 2012; Strindberg et al., 2018). The mechanism underlying those activities is threat exclusion, meaning threats are excluded from delineated areas. In contrast, the positive effect of hunting taboos is based on a different mechanism, namely the reduction of a threat, in this case due to a particular human behavior. While threat exclusion addresses the symptoms of conservation challenges, threat reduction aims to focus on the root causes. Previous studies argued that for conservation to be successful, threats need to be actively reduced (Allison et al., 1998; Clout, 2001; Challender and MacMillan, 2014; Crees et al., 2016). Considering that only a small proportion of chimpanzees are living in protected areas (Kühl et al., 2017), conservation interventions reducing threats outside of protected areas are needed, that thereby also reduce the pressure on protected areas. However, in a recent compilation of available evidence for the effectiveness of conservation interventions for primates, the majority of interventions was aimed at threat exclusion, for example through protected areas, law enforcement, and species management (Junker et al., 2017). There is considerably less evidence for interventions targeting threat reduction (Junker et al., 2017).

While the positive effect of hunting taboos we found for chimpanzees cannot be directly transferred to other areas, conservation interventions mimicking these conditions could complement current conservation efforts. The positive effect of hunting taboos is a challenge for conservationists, because they generally have a religious or a supernatural basis, both in their origin and in their maintenance (Colding and Folke, 2001). While taboos can be strengthened or reinforced where they already exist (Junker et al., 2017), they cannot simply be introduced to other areas, where they never existed or disappeared. An additional concern is the loss of power of traditional taboos through modernization and migration, with people from different cultural or religious background being less likely to accept local taboos (Golden and Comaroff, 2015).

Mimicking hunting taboos would mean to reduce the demand for chimpanzees by consumers and discourage the supply by hunters and traders. From a consumer perspective, chimpanzees

are not a notable protein source, and the provision of alternative protein sources is a common intervention aimed at reducing the economic incentive to consume bushmeat, including chimpanzee. Junker et al. (2015) have, for example, shown that affordable fish protein correlated positively with chimpanzee densities. Another important conservation intervention includes awareness raising activities, especially because in certain areas medicinal or magical properties are assigned to chimpanzee parts and chimpanzee bone powder (Hanson-Alp et al., 2003). There are studies that have shown a positive effect of such interventions on bushmeat consumption, for example in the context of repeated multimedia campaigns (Kouassi et al., 2017) and Ebola information campaigns (Ordaz-Németh et al., 2017). However, hunting chimpanzees is also strongly driven by a demand for chimpanzee parts and live animals from urban areas and even international markets (Kuehl et al., 2009; Greengrass, 2016; Strindberg et al., 2018). Awareness raising activities at national or even regional scale specifically targeting urban consumers is absent from West Africa, but could be an important tool to reduce the acceptability of chimpanzee consumption. Evidence from China suggests that an ambitious nation-wide awareness raising campaign championed by the most popular Chinese athlete, Yao Ming, resulted in a change in government policy and a strong decrease in shark fin demand across China (Whitcraft et al., 2014). In general, research on behavioral change in conservation highlights the need to go beyond awareness raising because often a change in awareness alone is not enough to lead to pro-environmental behavior (Schultz, 2011; Amel et al., 2017). Stakeholder co-designed behavioral change tools therefore try to identify barriers to behavioral change as well as providing benefits (Schultz, 2014). Successful examples of behavioral change interventions aimed at reducing bushmeat consumption include the so-called community-based social marketing tool, that has been implemented to reduce consumer demand for wild meat in a Brazilian town, and that explicitly identified and then reduced barriers to the consumption of domesticated meat (Chaves et al., 2018).

From a supplier perspective, chimpanzees are mostly killed or captured opportunistically, but because of their large size, hunters make high profits from a single catch, and young chimpanzees can be sold for the pet trade (Hanson-Alp et al., 2003). Even such single catches can have detrimental effects on chimpanzee populations due to their long time to maturation and long inter-birth intervals. As discussed above, law enforcement aiming to exclude hunters from certain areas often seems not to be sufficient, mainly due to the virtual impossibility of stopping every single hunter. Conservation interventions aiming at reducing chimpanzee supply are scarce, and here again stakeholder co-designed behavioral change tools might be a way forward to first understand what is driving certain behaviors and how hunters could be motivated to not kill or capture chimpanzees despite their high monetary value. While there is evidence that monetary and non-monetary benefits can have a positive effect on primate populations, there are also studies showing no effect (Junker

et al., 2017). In addition, studies looking at the entire supply chain from individual hunters via traders to sellers have identified multiple entry points for conservation interventions (Bachmann et al., submitted).

Application of the Positive Deviance Approach to Other Study Systems and Challenges

The positive deviance approach can be a useful tool for conservation science because it focuses on identifying conditions or mechanisms that have already proven to work. While understanding threats to species is a prerequisite for conservation planning, solutions are often a lot less understood. The positive deviance approach allows directing research toward possible answers to conservation challenges. In general, this approach can be applied to any taxon, region and at different spatial scales, if matched with data of corresponding resolution and quality. Importantly, the spatial scale needs to be chosen so that there is sufficient variation along multiple predictor variables.

Similarly to Frei et al. (2018) who applied this approach to agricultural landscapes, we found that applying it to a specific species comes with several challenges. First, it is difficult to differentiate between the influence of historic and current conditions, i.e., past events such as disease outbreaks might have long-lasting effects on a population independent of current conditions. This is of particular concern for species with slow life histories. Second, the data, especially when it pertains to human behavior or socio-economic context, might not be available at a small resolution for a large area, which makes large-scale analyses difficult. Here, multi-scale studies might give additional insights. In general, many more studies using the positive deviance approach would be needed to determine whether this is truly a useful approach that can provide novel insights for species conservation.

CONCLUSIONS

Conservation interventions, especially for the conservation of primates, still largely focus on habitat protection and reducing accessibility for humans through protected areas and law enforcement. However, with about 80% of western chimpanzees living outside of high-level protected areas, i.e., national parks and strict nature reserves, the focus on excluding threats from delineated areas might not be sufficient to ensure the long-term survival of western chimpanzees. By using the positive deviance approach, we found high chimpanzee densities and seemingly stable population trends for sites with a high prevalence of hunting taboos, even though those areas were not set aside under any high-level protective status. This suggests that these enabling conditions can be mimicked by using stakeholder co-designed behavioral change approaches (Schultz, 2011, 2014; Chaves et al., 2018) to reduce hunting pressure and thereby complement current conservation interventions. While new behavioral change tools have been applied to different environmental problems, they remain largely absent

from primate conservation (Junker et al., 2017). With a lot of organizations already working for the protection of chimpanzees across West Africa and the relatively strong support that chimpanzee protection garners within and outside its range, this might be an opportunity to pioneer and test new conservation approaches, which, if successful, could inform protection of other primates. Applications of the positive deviance approach to species conservation are still rare, and many more studies and methodological advancements would be needed to establish this method as a useful conservation science tool.

DATA AVAILABILITY

The raw data will be made available via the IUCN SSC A.P.E.S. database (<http://apesportal.eva.mpg.de>).

AUTHOR CONTRIBUTIONS

HK, SH, RM, and CB conceived and designed the study; SH and TS curated the data; SH and RM analyzed the data; SH and HK wrote the initial draft; all remaining authors contributed data, and provided comments on model formulation. All authors contributed to the reviewing and editing of the manuscript, and approved its submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00016/full#supplementary-material>

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The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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