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RESEARCH ARTICLE

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The Critically Endangered western chimpanzee declines by 80%

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African large mammals are under extreme pressure from unsustainable hunting and habitat loss. Certain traits make large mammals particularly vulnerable. These include late age at first reproduction, long inter-birth intervals, and low population density. Great apes are a prime example of such vulnerability, exhibiting all of these traits. Here we assess the rate of population change for the western chimpanzee, *Pan troglodytes verus*, over a 24-year period. As a proxy for change in abundance, we used transect nest count data from 20 different sites archived in the IUCN SSC A.P.E.S. database, representing 25,000 of the estimated remaining 35,000 western chimpanzees. For each of the 20 sites, datasets for 2 different years were available. We estimated site-specific and global population change using Generalized Linear

Models. At 12 of these sites, we detected a significant negative trend. The estimated change in the subspecies abundance, as approximated by nest encounter rate, yielded a 6% annual decline and a total decline of 80.2% over the study period from 1990 to 2014. This also resulted in a reduced geographic range of 20% (657,600 vs. 524,100 km^2). Poverty, civil conflict, disease pandemics, agriculture, extractive industries, infrastructure development, and lack of law enforcement, are some of the many reasons for the magnitude of threat. Our status update triggered the uplisting of the western chimpanzee to “Critically Endangered” on the IUCN Red List. In 2017, IUCN will start updating the 2003 Action Plan for western chimpanzees and will provide a consensus blueprint for what is needed to save this subspecies. We make a plea for greater commitment to conservation in West Africa across sectors. Needed especially is more robust engagement by national governments, integration of conservation priorities into the private sector and development planning across the region and sustained financial support from donors.

KEYWORDS
habitat loss, IUCN Red List of Threatened Species, *Pan troglodytes verus*, poaching, West Africa

1 | INTRODUCTION

The African megafauna, including elephants, rhinoceros, large ungulates, and predators, has come under enormous pressure due to rapidly intensifying human impacts resulting in dramatic population declines (Craigie et al., 2010; Maisels et al., 2013). The major reasons for such declines are the rapidly growing human populations with a growing middle class, urbanization and economic development, all associated with rising demands for and consumption of natural resources (Baillie, Hilton-Taylor, & Stuart, 2004; Kharas, 2010). Additionally, global demand for animal products, timber and mineral resources is driving overexploitation of the African megafauna and their habitats (Edwards et al., 2014; Maisels et al., 2013; Wich et al., 2014). These factors combined have led to the disappearance of large species in parts of their former range (Bauer et al., 2015; Henschel et al., 2014; Maisels et al., 2013; Tranquilli et al., 2012).

Great apes are no exception and have already disappeared from parts of their historic range (Funwi-Gabga et al., 2014); their suitable habitat is disappearing rapidly (Jantz, Pintea, Nackoney, & Hansen, 2016; Junker et al., 2012), and dramatic declines have been reported for several taxa (Campbell, Kuehl, Kouamé, & Boesch, 2008; Plumptre et al., 2016; Walsh et al., 2003). Similar to other species of megafauna, great apes are particularly vulnerable to human impacts, characterized by hunting and habitat destruction (Walsh et al., 2003; Wich et al., 2016) and infectious disease transmission (Köndgen et al., 2008). Great apes are expected to be particularly vulnerable to human impact in comparison to other organisms due their low reproductive rate and late age of first reproduction, long interbirth intervals and low population densities (Purvis, Gittleman, Cowlishaw, & Mace, 2000; Williamson, Maisels, & Groves, 2013).

Historically, African great apes inhabited the tropical rainforest and woodland savannas along the equator (Butynski, 2001). However, the behavioral flexibility of great apes allows them to also persist in human dominated agro-forestry mosaic, which strongly differs from their natural habitat (Brncic, Amarasekaran, McKenna, Mundry, & Kühl, 2015; McCarthy et al., 2015). Whether this is only a transient phenomenon, or whether great apes are able to survive therein in the long-term, is not yet clear.

Of the nine great ape taxa occurring in Africa, bonobo (*Pan paniscus*), chimpanzee (*Pan troglodytes ellioti*, *P. t. schweinfurthii*, *P. t. troglodytes*, *P. t. verus*), western lowland gorilla (*Gorilla gorilla diehli*, *G. g. gorilla*), and eastern gorilla (*Gorilla beringei beringei*, *G. b. graueri*), chimpanzees are considered to be the most adaptable in changing environments, due to their flexible and diverse behavior and resilience to anthropogenic stressors relative to other great ape taxa (Hockings et al., 2015). This flexibility is demonstrated by the fact that, of all great ape taxa, chimpanzees have the largest range across Africa, and that they occur in a wide spectrum of habitats and ecological conditions, ranging from tropical lowland to mountain forest, inundated forests and extremely dry woodland savannas at their range limits close to the Sahel belt (Williamson et al., 2013). Chimpanzees may also occur in agricultural mosaics, where they have survived via behavioral and dietary adaptations, such as eating crops cultivated by humans as well as wild foods (McCarthy, Lester, & Stanford, 2016; McLennan & Hockings, 2014).

A wide variety of conservation interventions for the protection of great apes and sympatric wildlife have been implemented during recent decades, including legal regulations and law enforcement, creation of protected areas, environmental education and awareness campaigns, mitigation of the impacts of mineral and timber extraction, community development and veterinary interventions (Caldecott & Miles, 2005). However, the effectiveness of most interventions is uncertain, as only a few studies have evaluated the usefulness and efficiency of specific activities, such as the effectiveness of law enforcement (N'Goran et al., 2012; Robbins et al., 2011), long-term conservation presence of research and tourism (Campbell, Kuehl, Diarrassouba, N'Goran, & Boesch, 2011; Robbins et al., 2011; Tagg, Willie, Duarte, Petre, & Fa, 2015; Tranquilli et al., 2012), environmental education (Borchers et al., 2014), veterinary interventions (Robbins et al., 2011), or mitigation of the impact of the extractive industry (Rabanal, Kuehl, Mundry, Robbins, & Boesch, 2010).

Among the four currently recognized chimpanzee subspecies, the western chimpanzee shows the greatest behavioral diversity (Whiten et al., 1999), with higher richness of behaviors as compared to the other subspecies. This subspecies diverged from the Central African lineage around 0.5 m years ago (Bowden et al., 2012; Prado-Martinez et al., 2013). Like other great ape taxa, the western chimpanzee has come under enormous human pressure; for example a 90% decline of the chimpanzee population in Côte d'Ivoire has been recorded (Campbell et al., 2008). Throughout its range, the western chimpanzee is losing its natural rainforest and savanna woodland habitat. It is also hunted illegally in most parts of its range, mainly for food, but also as retribution for damage to crops and occasionally to capture and sell their infants (e.g., Pruetz & Kante 2010). Previously practiced taboos against hunting are being eroded due to changing traditions, loss of alternative big game and ungulate populations for protein supply, and redistribution of ethnic groups with different belief systems.

In this study, we provide a status update of the western chimpanzee, including an evaluation of the change in population size over the last three decades, an update of their geographic range, and an overview of estimated current population sizes. We also discuss possible reasons for their decline and outline what is needed to substantially improve conservation of this subspecies.

2 | METHODS

2.1 | Study area

The geographic range of the western chimpanzee extends across eight West African countries and until recently was estimated to be 657,600 km^2 large (Figure 1). Historically, the western chimpanzee also occurred in Benin, Burkina Faso, and Togo, but was extirpated in these countries during the 20th century (Campbell & Houngbedji, 2015; Kormos, Boesch, Bakarr, & Butynski, 2003). The western chimpanzee's habitat ranges from tropical lowland forest, mainly in Liberia, Côte d'Ivoire, and Sierra Leone, to woodland savanna in Guinea, Guinea-Bissau, Senegal, and Mali, to extremely human-dominated agro-forest mosaics in several of the range countries.

2.2 | Data collection and compilation methods

Protocols for field research were in compliance with the EU Commission's legislation for animals used for scientific purposes and adhered to the legal requirements in the respective countries. All data collection was performed in accordance with government regulations and approved by the respective national authority.

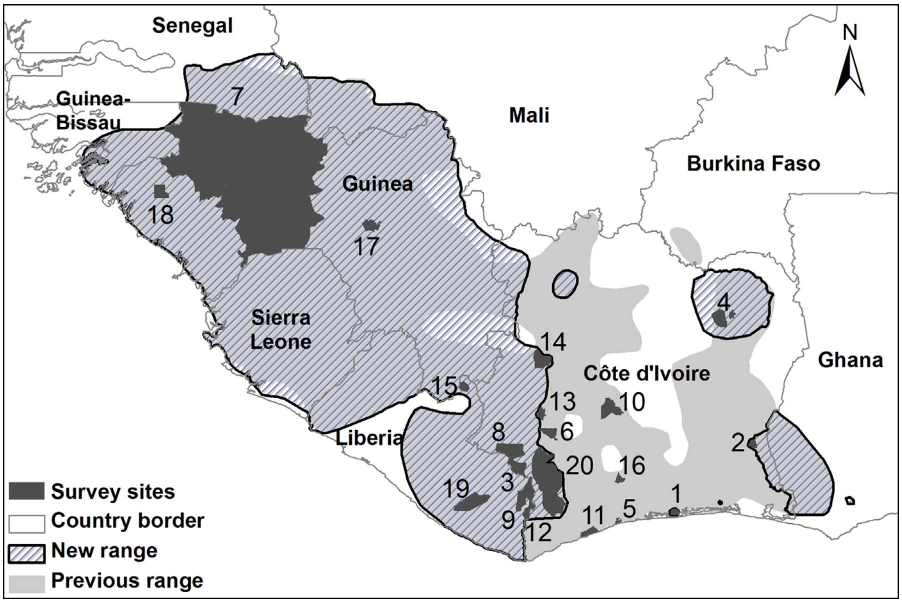

FIGURE 1 Map of both the previous and the updated geographic range of the western chimpanzee, also indicating the 20 sites for which survey information was available. The numbers given for each site correspond to the IDs and site names listed in Table 3

Lastly, all field methods and research adhered to the American Society of Primatologists Principles for Ethical Treatment of Non-Human Primates, as well as ethical guidelines established by the Max Planck Society.

2.2.1 | Abundance information

Information on the abundance of western chimpanzee populations was compiled from all available survey reports and peer-reviewed literature. Most information on western chimpanzee abundance is not available in the peer-reviewed literature, but only in the grey literature. Therefore, we also considered unpublished reports. If several reports were available for the same area, but different years, we used the most recent one.

2.2.2 | IUCN SSC A.P.E.S. database

The data used to estimate temporal change in abundance and for updating the geographic range were extracted from the IUCN SSC A.P.E.S. database (http://apes.eva.mpg.de). This database is a repository for field survey data and other population information on all great ape taxa and aims to inform conservation bodies and decision makers about the status of great apes, the threats and conservation opportunities. Currently, more than 60 field survey datasets are archived in the database (defined as distinct field surveys during different, non-continuous time periods) for the western chimpanzee. For the purpose of estimating change in abundance, datasets were extracted only where at least two surveys for two different time periods were available. This produced 40 datasets from 20 sites (Table 1). The area surveyed ranged from 98 to 66,634 km^2 and survey effort ranged from 9 to 366 km of total transect length per site and survey.

All survey data used were collected following distance sampling methods (Buckland, 2004; Buckland et al., 2001) and IUCN best practice guidelines (Kühl, Maisels, Ancrenaz, & Williamson, 2008). The standard method of surveying chimpanzees is to count nests along line transects. Most, but not all of the surveys analyzed were designed using DISTANCE software (Thomas et al., 2010).

2.3 | Analytical methods

2.3.1 | Updating the geographic range

To update the geographic range of the western chimpanzee, we extracted all new surveys archived in the IUCN SSC A.P.E.S. database since the 2008 Red List assessment. All chimpanzee presence and absence points based on transect and recce surveys were superimposed in QGIS (http://www.qgis.org/) on the previously defined range layer (IUCN, 2008). Areas outside this range with confirmed chimpanzee presence were added, and areas where chimpanzee nests were no longer found were removed from the previous range map. A buffer of 100 km was set around isolated presence points.

2.4 | Estimating change in abundance

2.4.1 | Data processing

The 40 datasets were formatted to the same standard, with the number of observed nests, total transect length, date of survey, and the start and end coordinates per surveyed transect line. We used the number of nests detected on each transect as a proxy for chimpanzee density. While this may be problematic when making spatial comparisons of density due to varying nest decay times across habitats with different climatic and vegetation conditions, it is not a problem, when making within site comparisons. Such approaches have been frequently applied (e.g., Walsh et al., 2003). Another common issue with these kinds of data is the frequency distribution of nests per transect, as a disproportionate number of transects have no nests and a few transects have a large number of nests. Issues with frequency distribution are unlikely to arise because of imperfect detection of nests, but rather because ape densities are generally low and most randomly-located transects fall in areas with no ape nests at the time of survey. Such skewed data distribution can create problems when fitting models (e.g., overdispersion) and requires careful selection of the model (further details below).

2.4.2 | Modeling approaches

To model the impact of date on nest encounter rate (i.e., temporal change in number of nests per km of transect), we first fitted a Generalized Linear Mixed Model (GLMM) (Baayen, 2008) using a negative binomial error structure and log link function (McCullagh & Nelder, 1996). We included date of the survey as a fixed effect, site and country as random intercepts, and also random slopes for survey date within country and site, and an offset term for transect length. Since model convergence proved difficult with this model, we used a Poisson error structure instead. This turned out to be problematic as well, because of overdispersion, which can lead to increased type I error rates, namely erroneous effects of variables tested and underestimated uncertainty of model coefficients (Gelman & Hill, 2007). We hence abandoned the idea of fitting a single GLMM to all sites and used instead the following two approaches based on site-level analysis and subsequent averaging of yielded estimates of population changes.

We based our first approach on the use of Generalized Linear Models (GLM) (McCullagh & Nelder, 1996). Due to data distribution issues described above, it was not possible to model temporal change in nest encounter rates for all sites with the same error structure (e.g., negative binomial, Poisson, or zero-inflated negative binomial). Instead, we used different models for the different sites. In a first step, we fitted a negative binomial model for each site. However, when this appeared to be overdispersed (dispersion parameter >1.5; four out of 20 sites; see Tables 2 and 3 for site names), we fitted a zero-inflated Poisson and a zero-inflated negative binomial model and chose whichever revealed the smaller Akaike Information Criterion (AICc, corrected for small samples)

TABLE 1 List of the 20 sites considered in the trend analysis

Site	Area (km^2)	Status	Pop. Est.	Effort (km)	Date	Source
Azagny	200	National Park	47	12	2007	Herbinger (2007)
			NA	20	2012	WCF (2012) unpub. data
Bossematié	233	Classified Forest	118	12	1990	Marchesi et al. (1995)
			0	12	2007	Campbell et al. (2008)
Cavally	791	Classified Forest	52	39.5	2008	Normand et al. (2010)
			44	35.5	2010	Normand et al. (2010)
Comoé	1450	Community Area	NA	100	1990	Marchesi et al. (1995)
			NA	18	2014	PANAF (2014) unpub data
Dagbego	98	Classified Forest	98	9	1990	Marchesi et al. (1995)
			0	9	2007	Campbell et al. (2008)
Duékoué	524	Classified Forest	356	12	1990	Marchesi et al. (1995)
			0	12	2007	Campbell et al. (2008)
Fouta Djallon	66634	Mixed Management Area	17700	366	2011	WCF (2012)
			NA	62	1996	Ham (1998)
Goin-Débé	1366	Classified Forest	213	186	2006	Normand et al. (2010)
			27	244	2009	Normand et al. (2010)
Grebo	1667	Proposed Protected Area	NA	58	2005	Kouakou et al. (2012)
			204	248	2014	Kouakou et al. (2014)
Marahoué	1056	National Park	1407	15	1990	Marchesi et al. (1995)
			NA	15	2007	Campbell et al. (2008)
Monogaga	366	Classified Forest	165	9	1990	Marchesi et al. (1995)
			0	9	2007	Campbell et al. (2008)
Mount Kopé	104	Classified Forest	50	9	1989	Marchesi et al. (1995)
			NA	9	2007	Campbell et al. (2008)
Mount Péko	318	National Park	320	13	2001	Herbinger & Lia (2001)
			NA	9	2012	WCF (2012) unpub. data
Mount Sangbé	935	Classified Forest	260	21	2001	Herbinger (2007)
			NA	15	2012	WCF (2012). unpub. data
Nimba	216	Strict Nature Reserve	28	178	2010	WCF (2011) unpub. data
			NA	76	2014	PANAF (2014) unpub data
Nizoro	233	Classified Forest	14	12	1990	Marchesi et al. (1995)
			0	12	2007	Campbell et al. (2008)
PNHN Mafou	557	National Park	275	103	2001	Fleury-Brugière & Brugière (2002)
			288	99	2009	WCF (2012)
Sangaredi	715	Mining Concession	266	397	2008	WCF (2011)
			174	247	2014	WCF (2014)
Sapo	1529	National Park	1517	44	2009	N'Goran et al. (2010)
			NA	148	2014	FFI (2014) unpub. data
Taï	5453	National Park	288	363	2014	Tiédoué et al. (2014)
			480	362	2005	N'Goran (2007)

Columns include site name, area size, protection status of survey area, population estimate ("NA"- estimate not available for this site and year), total survey effort, date of survey, and source of information.

(Burnham & Anderson, 2003). In three cases (Fouta Djallon, Monogaga, Mt. Kopé), the negative binomial model was over-dispersed, and neither of the zero inflated models converged, so we used the negative binomial model without zero-inflation.

In each model, we included date (converted to Julian date) as the single predictor (survey dates with unknown day were set to the 15th of the respective month, and dates with unknown day and month were set to June 30th of the respective year) and controlled for the length of

TABLE 2 Population estimates available for the western chimpanzee

Country	Site	Abundance	Min	Max	Source	Year of survey	Field survey
Guinea	Fouta Djallon	17,750	8,127	40,575	WCF (2012)	2011	SCNC Line transects + nest decay study
	All other sites, except Fouta Djallon	1,100	–	–	WCF (2012)	2009–2010	SCNC Line transects
	Bafing area[a] (half of the area is part of Fouta Djallon)	4,720[a]	3,760	5,918	WCF (2014)	2014	SCNC Line transects
Liberia	Nationwide	7,010	4,260	11,590	Tweh et al. (2014)	2011–2012	SCNC Line transects + nest decay study
Sierra Leone	Nationwide	5,580	3,052	10,446	Brncic et al. (2010)	2009	SCNC Line transects + nest decay study
Ghana	Bia-Gaoso Forest Block (BGFB)	264	–	–	Danquah et al. (2012)	2009	Line transects
Guinea-Bissau	Lagoas NP	137	51	390	Carvalho, Marques, and Vicente (2013)	2010–2011	SCNC & MNC Line transects
	Boé NP	Not yet estimated	–	–	PANAF (2014) unpub. data	2014	SCNC Line transects
Côte d'Ivoire	Taï National Park	540	321	909	Tiédoué et al. (2015)	2015	SCNC Line transects
	Azagny National Park	47	18	125	Herbinger (2007)	2007	SCNC Line transects
	Goin-Débé Classified Forest	27	13	57	Normand et al. (2010)	2009	SCNC Line transects
	Mount Nimba Strict Nature Reserve	28	8	39	Granier, Hambuckers, Matsuzawa, and Huynen (2014)	2010–2011	SCNC Line transects
	Banco National Park	20	–	–	Normand (2010) pers. comm.	2015	SCNC & MNC Line transects
	Cavally Classified Forest	52	28	96	Normand (2010)	2010	SCNC Line transects
	Bossematié Classified Forest	Present	–	–	Campbell et al. (2008)	2007	SCNC Line transects
	Comoé National Park	Present	–	–	PANAF (2014) unpub. data	2009	SCNC Line transects
	Mount Sangbé National Park	Present	–	–	PANAF (2014) unpub. data	2014	SCNC Line transects + camera trapping
	Mabi Classified Forest	Present	–	–	Campbell et al. (2008)	2007	SCNC Line transects
	Mount Kopé Forest	Present	–	–	Campbell et al. (2008)	2007	SCNC Line transects
	Dassikro Classified Forest	Extirpated	–	–	Campbell et al. (2008)	2007	SCNC Line transects
	Duékoué Classified Forest	Extirpated	–	–	Campbell et al. (2008)	2007	SCNC Line transects
	Gobodienou Classified Forest	Extirpated	–	–	Campbell et al. (2008)	2007	SCNC Line transects
	Marahoué National Park	Extirpated	–	–	WCF	2015	SCNC Informed guess
	Monogaga Classified Forest	Extirpated	–	–	Campbell et al. (2008)	2007	SCNC Line transects
	Mount Péko National Park	Extirpated	–	–		2014	SCNC Informed guess
	Niouniourou Classified Forest	Extirpated	–	–	Campbell et al. (2008)	2007	SCNC Line transects
	Haute Dodo Classified Forest	Extirpated	–	–		2015	Guess

(Continues)

TABLE 2 (Continued)

Country	Site	Abundance	Min	Max	Source	Year of survey	Field survey
	Nizoro Classified Forest	Extirpated	-	-	Campbell et al. (2008)	2007	SCNC Line transects
	Okromodou Classified Forest	Extirpated	-	-	Campbell et al. (2008)	2007	SCNC Line transects
	Port Gauthier Classified Forest	Extirpated	-	-	Campbell et al. (2008)	2007	SCNC Line transects
Senegal		Present	400	500	Kormos et al. 2003	2015	Guesstimate based on recent surveys
Mali	Bafing	Present, but population size not yet estimated	-	-	PANAF (2014): unpub. data	2014	SCNC Line transects
Benin	Various protected areas	Extinct	-	-	Campbell and Houngbedji (2015)	2015	Interviews
Togo	Various protected areas	Extinct	-	-	Campbell and Houngbedji (2015)	2015	Interviews
Burkina Faso	Various protected areas	Likely extinct	-	-	Ginn et al. (2013)	2012	Interviews, recce survey

We considered all surveys conducted in recent years in West Africa to derive a global estimate of total population size for *Pan troglodytes verus*. By summing all existing population estimates from Côte d'Ivoire, Ghana, Guinea, Guinea-Bissau, Liberia, and Sierra Leone the total population of western chimpanzee ranges from 18,000 to 65,000 with the point estimate being around 35,000 individuals. This is, however, a minimal estimate as the chimpanzee populations of unsurveyed areas remain unknown. Column headers indicate the name of range country and survey site, estimated abundance, estimated minimum and maximum abundance, the source of information, year of survey, and type of field survey (SCNC-Standing crop nest count; MNC-Marked nest count).

[a]Half of the Bafing area is part of the Fouta Djallon that was surveyed in 2010–2011. We considered only half of the Bafing's estimate in the calculation of the western chimpanzee's population.

the transects by including them (log transformed) as an offset term into the models. In the zero-inflated models, we fitted the same model for the count and the zero-inflation part (for the latter, we inverted transect length to account for increasing probability of not finding nests on shorter transects, log-transformed it and then included it as an offset term in the zero-inflation part).

Regardless of the particular model used, we aimed to control for spatial autocorrelation. Autocorrelation may arise if an unknown factor causes similar values in the observed pattern in a spatially aggregated manner, which in turn can cause autocorrelated, non-independent residuals and, thus, violate the assumption of the models. We chose the following approach: as a first step, we fitted the model and extracted the residuals. Separately for each data point, we then averaged all other residuals, whereby we weighted their contribution by their distance to the respective data point. The weight function had the shape of a Gaussian distribution with a mean of zero (i.e., maximal weight at a distance of zero) and a standard deviation chosen such that the likelihood of the model with the derived autocorrelation term included was maximized (Fürtbauer, Mundry, Heistermann, Schülke, & Ostner, 2011). Where the model revealed a negative coefficient for the autocorrelation term, we removed it (see Table 3 for details). Thus the negative binomial model and the count part of the zero-inflated negative binomial model were

$$n_{ij} \sim \exp(\beta_0 + \beta_1 \text{date} + \beta_2 \text{autocorrelation} + \text{offset} + \theta) \quad (1)$$

where n_{ij} is the number of nests on transect i in survey period j, β_0 is the intercept, β_1 and β_2 are the coefficients for date and the autocorrelation term, respectively, offset is the log-transformed transect length and θ is the dispersion parameter of the negative binomial distribution. We estimated uncertainty for the yielded population change estimate by conducting a non-parametric bootstrap ($n = 1000$ bootstraps). For this, we resampled site estimates for rate of change and then extracted the 2.5% and 97.5% quantile values to derive the 95% confidence limits.

We derived the percentage annual change in nest encounter rate (x) by taking the ratio of predicted nest encounter rate for two consecutive years based on the fitted models' estimated parameters. We calculated the percentage change in nest encounter rate over the 24 years (y) from 1990 to 2014, using:

$$y = 1 - (1 - x)^{24} \quad (2)$$

In a second approach, we used a simple exponential model based on mean nest encounter rates per site and survey period. For this approach, we summed all nest observations per site and survey period and divided by total transect length for the same survey and site. Thus we had two values for each site for further analysis, as well as the time difference between the surveys. Using

$$N_{i_1} = N_{i_0} \times e^{r_i t} \quad (3)$$

TABLE 3 List of sites with information about model details and results

Id	Country	Site	Ac	Error term	No. transects	Dispersion param	Estimate	SE	*p*-value
1	Côte d'Ivoire	Azagny NP	Yes	Negbin	28	1.37	−0.077	0.408	0.849
2	Côte d'Ivoire	Bossematié CF	No	Negbin	8	1.12	−0.314	0.532	0.555
3	Côte d'Ivoire	Cavally CF	No	Negbin	97	1.04	0.372	0.176	0.035
4	Côte d'Ivoire	Comoé Geprenaf	Yes	Negbin	30	0.83	**−1.524**	**0.289**	**<0.001**
5	Côte d'Ivoire	Dagbego CF	No	Negbin	6	0.49	**−64.032**	**11.199**	**<0.001**
6	Côte d'Ivoire	Duékoué CF	No	Negbin	8	1.05	**−1.86**	**0.616**	**0.003**
7	Guinea	Fouta Djallon	No	Negbin	137	1.88	0.067	0.259	0.795
8	Côte d'Ivoire	Goin-Débé CF	Yes	Negbin	1121	1.27	**−1.162**	**0.271**	**<0.001**
9	Liberia	Grebo NF	Yes	Negbin	153	1.46	−0.251	0.149	0.093
10	Côte d'Ivoire	Marahoué CF	No	Negbin	8	1.22	**−2.903**	**0.554**	**<0.001**
11	Côte d'Ivoire	Monogaga CF	No	Negbin	6	5.11	**−1.361**	**0.57**	**0.017**
12	Côte d'Ivoire	Mount Kopé NP	Yes	Negbin	6	2.56	**−1.128**	**0.262**	**<0.001**
13	Côte d'Ivoire	Mount Péko NP	No	Negbin	7	0.8	**−1.635**	**0.649**	**0.012**
14	Côte d'Ivoire	Mount Sangbé	Yes	Negbin	12	0.88	**−2.153**	**0.402**	**<0.001**
15	Liberia	Nimba NP	No	Negbin	213	1.41	**−0.621**	**0.385**	**0.107**
16	Côte d'Ivoire	Nizoro CF	No	Negbin	6	0.5	−11.066	8103	0.999
17	Guinea	PNHN Mafou	Yes	Negbin	145	1.05	**−0.418**	**0.166**	**0.012**
18	Guinea	Sangaredi GAC concession	Yes	Zeroinfl, negbin	202	1.7	0.044	0.094	0.64
19	Liberia	Sapo NP	Yes	Negbin	118	1.49	**−1.463**	**0.152**	**<0.001**
20	Côte d'Ivoire	Taï NP	yes	Negbin	366	0.9	−0.321	0.237	0.176

"Ac" indicates whether an autocorrelation term was included in the model or not, "Error term" indicates whether a negative binomial GLM (negbin) or zero-inflated negative-binomial GLM (zeroinfl) was fitted; "No. transects" indicates the total transect length per site in km and "Dispersion param" indicates the dispersion parameter. For model results: estimated coefficients for the variable Julian date (indicated in year), as well as their standard errors (SE) and *p*-values.

Significant negative estimates, their SE and *p*-values are printed in bold.

where N_{i_0} and N_{i_1} are the mean nest encounter rates in the first and second survey for site i, t is the time difference between the first and second survey in years and r_i is the annual rate of change in nest encounter rate. r_i was estimated separately for each site and then averaged across sites by weighting it with the site-specific chimpanzee population sizes (see Table 2). We calculated mean annual and total change in nest encounter rate across all sites by inserting $t = 1$ and $t = 24$ (years).

All analyses were conducted in R [version 3.1.x, R Core Team 2015]. We used the functions "zeroinfl" from the package pscl (Jackman, 2015; Zeileis, Kleiber, & Jackman, 2008), "glm.nb" of the package MASS (Venables & Ripley, 2002), and "glm" of the R stats package.

3 | RESULTS

3.1 | Abundance

We estimated the total population of the western chimpanzee to be between 15,000 and 65,000 individuals (Table 2). Most recent information from published and unpublished abundance data indicates that there are probably about 35,000 chimpanzees remaining. This estimate is based on surveys covering roughly 40% of the western chimpanzee's geographic range, including nationwide surveys in Sierra Leone and Liberia and a large-scale survey in Fouta Djallon, Republic of Guinea. Due to lack of information, the chimpanzee populations in Mali, Senegal, and Guinea-Bissau are underrepresented.

3.2 | Estimation of rate of change

Overall, there was a clear impact of "date" on chimpanzee nest encounter rate in the GLM analysis (Table 3, Figure 2). The percentage annual change averaged across sites and weighted by site-level population size revealed an annual decline of −5.96%. The 95% lower and upper confidence limits for the percentage annual change, based on the non-parametric bootstrap, were estimated as −0.00006% and −35%, respectively. For the entire 24-year study period (1990–2014), a −77.1% decline was estimated. For some sites (in particular Dagbego and Nizoro Classified Forests in Côte d'Ivoire), the estimates for the variable "date" and the standard error were relatively large due to small sample sizes, highly-skewed distributions of nest data for the first and second surveys, and a complete separation issue (Field, 2005) during model fitting. The exponential population change model revealed an annual percentage change of −7.1% and a population change over the 24-year study period of −82.9%. The percentage change averaged from the two modeling approaches gave estimates of −6.53% decline per year and −80.2% decline between 1990 and 2014.

According to IUCN criteria, classification of a species as Critically Endangered requires >80% decline over three generations. Using the observed generation time of 23 years for western chimpanzees (Langergraber et al., 2012), a projection of the observed population decline over three generations would yield a 99% decline in abundance for the western chimpanzee.

3.3 | Geographic range

The population decline also resulted in a considerably reduced geographic range of the western chimpanzee. The likely extinction of chimpanzees in Burkina Faso and regional extinctions in Côte d'Ivoire reduced the geographic range by 20% (133,500 km^2) from 657,600 to 524,100 km^2 (Figure 1). The observed range contraction shifts the center of the western chimpanzee geographic range much further to the west. In Senegal, the formerly known range was adjusted to new field data and the range limit was expanded 20 km to the north.

4 | DISCUSSION

Our analysis provided the quantitative basis for the recent upgrading of the western chimpanzee as "Critically Endangered" (Humle et al., 2016). The IUCN criterion that triggered this uplisting was "A2." This criterion requires that the observed decline of a taxon is ≥80% over three generations, also assuming that the reduction or causes of it may not have ceased or been understood or may not be reversible. The observed decline of the western chimpanzee was about 80% in 24 years, which is only one generation. Assuming that the decline would continue over two more chimpanzee generations, this would accumulate in a projected decline of 99%.

The 20 sites included in this study harbor approximately 25,000 chimpanzees, which is near to 70% of the estimated remaining total population of 35,000 individuals. This, and the fact that the sites are distributed across a large part of the western chimpanzee range, and within a broad range of habitat types, suggests that our estimate is likely to be representative of the overall western chimpanzee population. The use of nest encounter rate to infer change in abundance over time instead of estimated individual density could be considered as a factor affecting the accuracy of this estimate. In principle, dramatically changing climate conditions causing nest decay times to decrease could theoretically generate the pattern observed in our study in that wetter conditions could decrease nest decay times and thus lower nest encounter rate at the same chimpanzee density. However, there is no indication that the mean rainfall for this region has increased (Sanogo et al., 2015). Furthermore, we used available abundance estimates only to calculate weighted mean of site-specific trend estimates. Any potential bias in estimated abundance due to differing techniques and use of non-site and survey-specific nest decay times had therefore only a minimal impact on our yielded estimate of 80% decline. Last, the estimated abundance of the western chimpanzee used in our study is supported by another study, which provides very similar estimates based on spatial modeling techniques and modeled site-specific nest decay time (Heinicke et al. in prep).

The causes of the western chimpanzee decline are well known and comprise illegal hunting, habitat loss (Kormos et al., 2003) and infectious diseases (Köndgen et al., 2008). The western chimpanzee's remarkable behavioral diversity will not be enough to allow the subspecies to survive the magnitude and severity of the threats. Clearly, there is large spatial variation in the importance of these threats and their underlying drivers. In some countries, such as Côte

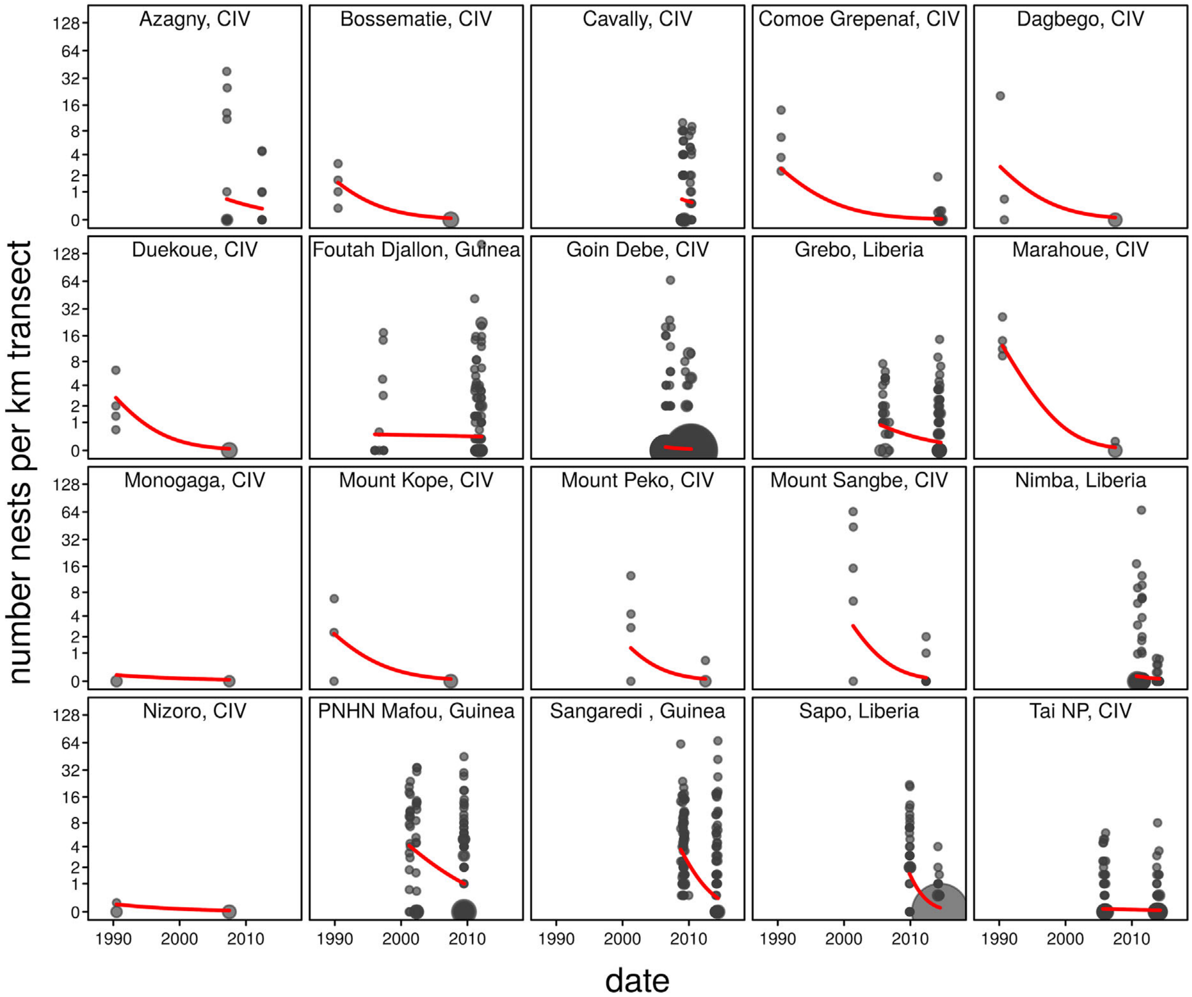

FIGURE 2 Change in nest encounter rate of western chimpanzees at the different survey sites. The area of the circles is proportional to the number of transects in the respective class of nest encounter rate (Y-axis). The red line represents the fitted response (CIV-Côte d'Ivoire)

d'Ivoire or Ghana, extreme habitat loss due to deforestation and large-scale industrial agriculture, and poaching have extirpated most chimpanzee populations. Recent surveys in Burkina Faso indicate that chimpanzees have likely become locally extinct (Ginn & Nekaris, 2014; Ginn, Robison, Redmond, & Nekaris, 2013). As threats to a population living on the edge of the geographic range likely had a greater impact, the population was disconnected from others, and experienced intense habitat loss and hunting due to rapid human population growth. With their likely extirpation in Benin, Burkina Faso, and Togo, chimpanzees have now disappeared from three former range countries in West Africa.

Ghana has only a few individuals remaining (Danquah, Oppong, Akom, & Sam, 2012; Elleni Vendras & Adam Welsh pers. comm.) that are scattered throughout the southwest of the country. As such, the complete disappearance of chimpanzees in Ghana is likely in the very near future unless serious efforts to protect the remaining individuals are initiated immediately.

The once very large chimpanzee population in Côte d'Ivoire has experienced the worst decline of the West African range states and only several hundred individuals remain in Taï National Park and in the vicinity of Comoé National Park. Other remnant populations are very small and mostly below 100 individuals. A major cause of this catastrophic development was large-scale deforestation in and outside protected areas and classified forests, driven by the rapidly growing human populations, massive immigration from the Sahel Belt, as well as development of the industrial agricultural sector for coffee, cacao, and palm oil (Campbell et al., 2008, Marchesi, Marchesi, Fruth, & Boesch, 1995).

The remaining strongholds of the western chimpanzee are in Guinea, Liberia and Sierra Leone. Guinea and Liberia have lower human population densities than Côte d'Ivoire and Ghana (http://countrymeters.info) and have not yet developed large-scale industrial agriculture, which was one of the driving factors of habitat loss in Côte d'Ivoire and Ghana. Liberia still has the largest rainforest population of western chimpanzees. The survival of chimpanzees in this country is most threatened by bushmeat hunting, even inside protected areas (Greengrass, 2016) and the rapidly developing mining, forestry and industrial-agricultural sectors (Junker, Boesch, Mundry, et al., 2015; Junker, Boesch, Freeman, et al., 2015; Tweh et al., 2014). In Sierra Leone, chimpanzees occur at low density throughout the country, even in human-dominated landscapes (Brncic, Amarasekaran, & McKenna, 2010; Brncic et al., 2015). There seems to be an increasing density gradient from south to north, with strongholds occurring close to the border with Guinea. The major threats in Sierra Leone include the expansion of mining and industrial agriculture, and bushmeat hunting. Guinea has the largest remaining chimpanzee population in West Africa (Ham, 1998; Kormos et al., 2003). A nationwide chimpanzee survey from 1995 to 1997 found the majority of Guinea's chimpanzees to be living in the Fouta Djallon region (Ham, 1998) and in 2012, new surveys in the Fouta Djallon estimated this population at approximately 17,000 individuals (Regnaut & Boesch, 2012). This region of Guinea is characterized by traditional small-scale farming practices. The most numerous ethnic group, the Fulani, hold traditional beliefs that chimpanzees are the ancestors of humans and therefore do not kill or eat them (Ham, 1998). The region of the Fouta Djallon also has the world's largest bauxite deposits and large-scale and widespread open-pit mining will occur in much of the chimpanzee habitat within the next decade (Kormos et al., 2014). If the mining proceeds at the scale planned, it will most certainly cause further population declines, and thus threatens this stronghold of the subspecies.

The chimpanzee populations at the western and northern limits of their range, in Mali, Senegal, and Guinea-Bissau, are likely to be small. Their very dry habitat of woodland savanna and human-dominated landscapes makes them particularly vulnerable to environmental change, including aridification and desertification, intensification of agriculture, open-pit mining, infrastructure development and resulting loss of vital habitat, such as gallery forests.

The deteriorating conservation status of western chimpanzees is echoed by other ape taxa: both orangutan and both gorilla species are now classified as Critically Endangered. For example, Grauer's gorillas declined by more than 80% over just two decades (Plumptre et al., 2016). Given the high human population growth rates in great ape range countries, global demands for natural and mineral resources, as well as a lack of efficient protection of great apes both inside and outside protected areas, we will likely see these taxa continuing to decline in the years to come.

4.1 | Implications for the conservation of the western chimpanzee

The countries that make up the region of West Africa have suffered tremendous challenges that have hampered their ability to prevent the destruction of their biological resources. Many countries of this region have been fraught with civil conflicts that have had both direct and indirect consequences for forest and wildlife protection, including large migrations of people, unsustainable use of resources due to lack of security, illegal sale of resources for purchase of weapons, and prevention of the continuation of protected area management. Many countries in this region suffered tremendously during the 2014–2016 Ebola epidemic. During this time, many conservation activities were put on hold, and their funding was suspended. West Africa has the largest bauxite deposits in the World, and while mining these riches holds promise to bring some countries out of poverty, it also risks eroding the very natural resources and ecosystem services upon which many of the rural poor depend. In the face of the magnitude of pressures, the response from the global community has not been adequate.

Long-term, sustainable protection of the region's biodiversity is going to depend on a spectrum of interventions that also addresses poverty, governance, agricultural practices, land-use planning, and improvement of environmental safeguards. While these are long-term goals, imminent action is needed as well. We suggest here immediate first steps that could be taken to prevent the extinction of the western chimpanzee through improved engagement and coordination from the international conservation community, additional financial support to conservation initiatives, and further commitment from governments to increase each country's protected area coverage and to improve the management of existing protected areas.

4.2 | Increased international conservation commitment

Although many small conservation organizations have been working on the ground for decades, their efforts have not been at the scale needed to prevent the rapid disappearance of chimpanzee habitat and the precipitous decline in their numbers. Most of the large international conservation NGOs that implement on great ape conservation programs in Central and East Africa do not have equivalent programs in West Africa. This has been in part due to the lack of funds available for the region. Several countries in West Africa, including Guinea (where the largest-known western chimpanzee population occurs in the Fouta Djallon region), do not fall within the designated "Guinean Hotspot," which guides the geographical and financial commitment of several of the large conservation organizations and funds. Lack of engagement is also a consequence of the magnitude and complexity of the challenges facing the region, which may result in fewer opportunities to demonstrate conservation successes than in other regions of Africa. Hence, donors often may be hesitant to support conservation in the region. West Africa also suffers from a lack of regional conservation programs, such as ECOFAC (Programme de Conservation et Utilisation Rationale des Ecosystèmes Forestiers en Afrique Centrale) and CARPE (Central African Regional Program for the Environment). However, the recently developed EU strategy for African wildlife conservation (European Union, 2015) is a very promising step forward and may help advancing conservation in the region

4.3 | Increased national commitment

Not only does great ape conservation in West Africa need increased support from the international conservation and donor community, it also needs greater commitment to habitat protection by national governments. Protected area coverage in West Africa is lower than in many other areas within the great ape range (Table 4). Several countries in the range of western chimpanzees have not yet reached the percentage coverage of protected areas aspired to by the "Aichi Biodiversity Targets" of "The Convention on Biological Diversity"

TABLE 4 Number, total area and percentage coverage of national parks within the chimpanzee's range by country and region

Region	Country	Number of NPs	Total area	% coverage
West Africa	Côte d'Ivoire	7	17,061	7.7
	Ghana	2	811	5.0
	Guinea	2	891	0.4
	Guinea-Bissau	1	1,057	7.9
	Liberia	2	1,687	2.2
	Mali	2	990	5.1
	Senegal	1	8,045	38.2
	Sierra Leone	5	2,294	3.5
Central Africa	Nigeria	2	7,930	17.3
	Cameroon	12	19,966	7.0
	Equatorial Guinea	2	2,632	10.6
	Gabon	13	27,643	11.4
	Republic of the Congo	4	25,668	11.4
	Central African Republic	1	1,251	1.0
	Democratic Republic of the Congo	5	25,903	3.2
East Africa	Rwanda	1	1,019	50.1
	Burundi	1	470	7.6
	Uganda	6	4,474	22
	Tanzania	2	1,484	9.1
	South Sudan	4	1,568	4.6

Data derived from World Database on Protected Areas (www.protectedplanet.net).

(Woodley et al., 2012). Consequently, there is a great need for the designation of new protected areas to maintain large intact habitats, particularly in the countries with the largest remaining chimpanzee populations, namely in Guinea, Liberia, and Sierra Leone. However, these sites alone will not be sufficient to halt the current population decline, unless they are also well managed. Several parks in West Africa that existed on paper and in law, were not well managed, and the result was severe degradation and the complete loss of chimpanzees within them. For instance, Marahoué National Park in Côte d'Ivoire disappeared in just a few years (Campbell et al., 2008), due to inadequate park management, law enforcement and immigration controls. Only two conservation interventions have been demonstrated to build effective resistance to threats in protected areas—these are the strict regulation of access through law enforcement, and ranger patrols (N'Goran et al., 2012), as well as protection through long-term presence of research or tourism projects (Campbell et al., 2011; Tagg et al., 2015; Tranquilli et al., 2012). Tourism may be an option in some countries in West Africa, but not in others due to lack of infrastructure. In those cases, adequate long-term resources need to be available for enforcement and ranger patrols. Other regions of Africa have ranger-training centers, but West Africa lacks such opportunities and therefore a focus on ranger training and employment would be beneficial in these countries.

However, building resistance within protected areas will never be sufficient alone. If human pressure on a protected area is high and increasing, a protected area system will eventually collapse without interventions to mitigate or control human demands for natural resources in and around them (Imong, Kühl, Robbins, & Mundry, 2016). Although, research showing how socio-economic context or development actually affect pressure on protected areas is rare, a study in Liberia has shown that areas with increased literacy have higher densities of chimpanzees (Junker, Boesch, Mundry, et al., 2015). As socio-economic status and resulting consequences for chimpanzee survival may differ even on a relatively small scale, it is crucial to study the relevant effects at the appropriate scale, identify those that successfully reduce pressure on protected areas, and promote them in such neighborhoods.

4.4 | Increased engagement of private and development sector, lending banks

Finally, one of the greatest future threats to chimpanzees and their habitats throughout this region is extraction of timber and minerals. Guidelines that specifically address impacts to chimpanzees and how these can be mitigated are crucial (Morgan & Sanz, 2007). However, it is also important for mechanisms to be put in place to ensure that companies adhere to best practices and guidelines. These could include the further development of national legislation and policies throughout the region, as well as strengthening of the policies and standards of international lending banks and the companies themselves. It is essential that extractive industries follow the mitigation hierarchy, that they contribute to offset schemes to compensate for residual impacts on chimpanzees and their habitats and that they are held accountable for these standards (Kormos et al., 2014; Morgan & Sanz, 2007). Certainly, this is most feasible with those companies with existing internal environmental standards. Strengthening of governmental standards, therefore, is essential to prevent considerable and irreversible damage by companies who have little concern for the environment. Last, rapid development of the industrial agricultural sector in the region poses severe threats to remaining chimpanzee populations. Large-scale monocultures, such as cocoa, coffee, rubber and oil-palm plantations, destroy natural habitat with massive negative consequences for the survival of great apes (Wich et al., 2014).

5 | CONCLUSION

In essence, western chimpanzees have declined dramatically, due not only to increasing levels of threat, but also to lack of political, financial and conservation commitment. Spatial variation in threats and chimpanzee persistence has revealed the human population in the Fouta Djallon to be particularly “chimpanzee friendly,” due to a cultural taboo against killing and eating them. Certainly, this may be only part of the reason of why chimpanzees persist there; a specific set of environmental conditions likely contributes as well. Nevertheless, the Fouta Djallon landscape deserves particular attention for any conservation planning in the region, for understanding how chimpanzees and humans can co-exist, how factors contributing to this co-existence can be maintained over time, and whether conservation planning in other parts of the western chimpanzee range may apply any lessons learned from this region. The central question for any conservation planning must be how effective any interventions will be. Better application and coordination of available assessments of conservation intervention effectiveness will help to invest funding resources in the most effective way.

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