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Title: Human impact erodes chimpanzee behavioral diversity

One Sentence Summary: Wild chimpanzees living in areas with high human impact have lower behavioral and cultural diversity

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Abstract:

Chimpanzees possess a large number of behavioral and cultural traits among non-human species. The 'disturbance hypothesis' predicts that human impact depletes resources and disrupts social learning processes necessary for behavioral and cultural transmission. We used an unprecedented data set of 144 chimpanzee communities, with information on 31 behaviors, to show that chimpanzees inhabiting areas with high human impact have a mean probability of occurrence reduced by 88%, across all behaviors, compared to low impact areas. This behavioral diversity loss was evident irrespective of the grouping or categorization of behaviors. Therefore, human impact may not only be associated with the loss of populations and genetic diversity, but also affects how animals behave. Our results support the view that 'culturally significant units' should be integrated into wildlife conservation.

Main Text:

Many animals show population specific behavioral variation, with chimpanzees (*Pan troglodytes*) exhibiting exceptionally high levels of behavioral diversity(*1*, *2*). This diversity has been documented in a variety of contexts, including communication, thermoregulation and extractive foraging (table S1). Chimpanzees are also proficient tool-users, using sticks, leaves and stones to access honey, insects, meat, nuts and algae (table S1). Many of these behaviors are inferred to be socially learned and therefore cultural(*2*), although the influence of genetic and environmental variation cannot always be ruled out(*3*). Culture in chimpanzees is supported by the occurrence of local traditions irrespective of resource or tool abundance(*1*, *2*), and controlled experiments demonstrating that naïve chimpanzees can socially learn new behaviors(*4*, *5*).

Moreover, new behaviors, or variants, are regularly discovered when observing previously unstudied populations(*5*) (table S1).

Cultural behaviors in great apes, notably chimpanzees(*1*) and orang-utans(*7*), are maintained by cultural processes including innovation, diffusion, and vertical and horizontal transmission(*2*, *8*). These behaviors are vulnerable to environmental disturbance, in that if crucial conditions are modified, the overall rate of opportunities for social transmission may be reduced(*8*). This proposition, named the ‘disturbance hypothesis’, predicts that under anthropogenically disturbed conditions behavioral traditions in great apes may disappear not only with the complete extinction of a population, but also when the population remains, due to resource depletion or a breakdown in opportunities for social learning(*8*). Major elements of human impact include habitat loss, degradation and fragmentation, which reduce population size, gregariousness and long-distance dispersal, weakening behavioral transmission(*8*).

In the current Anthropocene era, Earth’s biosphere is being heavily degraded by unsustainable resource use and high rates of biodiversity loss(*9*). This overexploitation is substantially impacting chimpanzees and their habitat, namely African tropical forests and savanna woodlands(*10*). All four chimpanzee subspecies are severely threatened by deforestation and poaching, caused by a rapidly growing human population(*9–11*). These factors have already led to major population declines, fragmentation and regional extirpations(*11*) and reduced genetic diversity(*12*).

The large behavioral diversity of chimpanzees coupled with rapid population decline makes investigation of the disturbance hypotheses timely: to what extent are chimpanzee behavioral and cultural diversity affected by habitat fragmentation and population loss resulting from human activities? To address this question, we applied a range of non-invasive techniques to collect a wide spectrum of environmental, social, demographic and behavioral information on previously unstudied chimpanzee communities, or communities not fully habituated to human observers, at 46 locations (Fig. 1). The actual number of chimpanzee communities represented is likely to be higher, as individuals from more than one community may have been observed at a location. Therefore, we define a chimpanzee community as those individuals which occur at a specific geographic location, with associated observations on behaviors. With few exceptions, we collected data over a minimum of one annual cycle (observation period between 12-30 months at 37 locations; observation period 1-10 months at 9 locations) in a systematic grid design (grid size range: 9-143 km^2).

We compiled presence and absence data on 31 known chimpanzee behaviors (table S1) from these 46 chimpanzee communities and complemented the data set with additional information about these same behaviors on another 106 chimpanzee communities from the published literature. In total, 144 unique chimpanzee communities comprised the full data set (Fig. 1, Data S1). We recorded observations on these behaviors via 1) extensive camera trapping; 2) fecal samples that provided evidence of ingestion of insects, algae and honey, resources often exploited with the aid of tools; 3) artifacts of tool use identified during reconnaissance, line and strip transect surveys. We selected behaviors that were detectable via indirect evidence (e.g., tools and artifacts) or direct evidence from camera traps, and that exhibit variation across populations rather than being universal traits of chimpanzees(*1*, *2*, *13*) (table S1). Importantly, although we do not explicitly test for cultural transmission, we infer that much of chimpanzee behavioral diversity reflects cultural diversity owing to an accumulation of observational and experimental evidence(*1*, *4*–*6*). Moreover, many behaviors included here have already been classified as cultural(*1*).

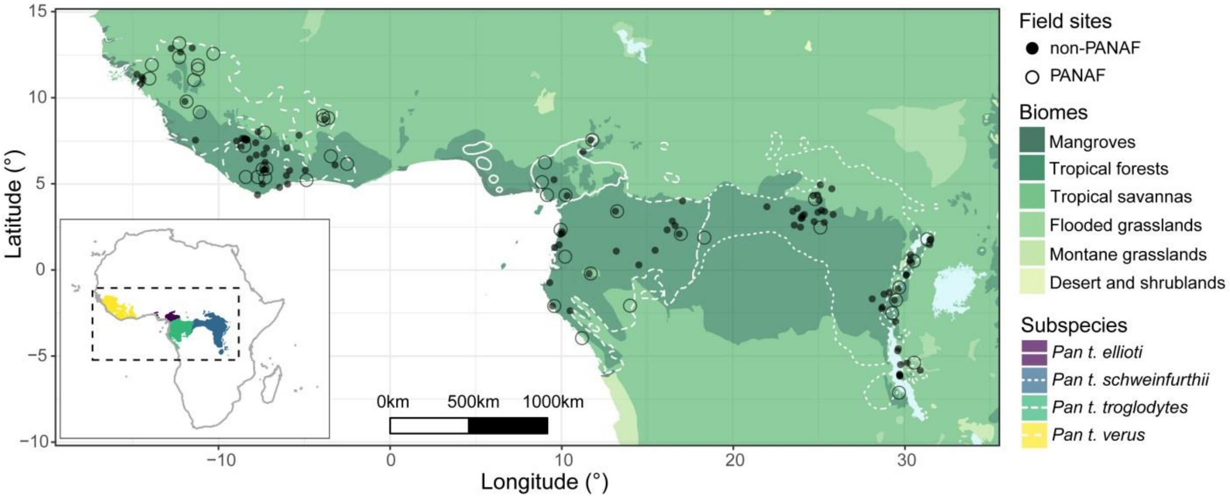

Fig. 1 Locations of all 144 unique chimpanzee communities for which information on select behaviors was collected for this study. This includes 46 communities from the Pan African Programme (PanAf) and 106 communities for which information was also available from the published literature (non-PanAf). Of these, eight communities had both PanAf and non-PanAf data available. Habitat type represented as biomes modified from the Terrestrial Ecoregions of the World Map 2001.

According to the disturbance hypothesis, potential behavioral diversity loss is expected to manifest across multiple chimpanzee generations, so human impact should be assessed over long time periods. We used the ‘human footprint’, a spatial composite layer integrating human impact over time by combining infrastructure, human population density, forest cover and remoteness, to provide a geographically explicit variable quantifying the overall effect of humans on the environment with a 1km grid resolution(*14*). We used both Bayesian Regression (BR) and Maximum Likelihood (ML) mixed models to test the hypothesis that variation in human impact among chimpanzee populations predicts variation in the number of behaviors present(*13*). We controlled for observation effort in number of months, spatial autocorrelation, and chimpanzee subspecies in the analyses(*13*)(tables S2 to S6 and figs S1 to S5).

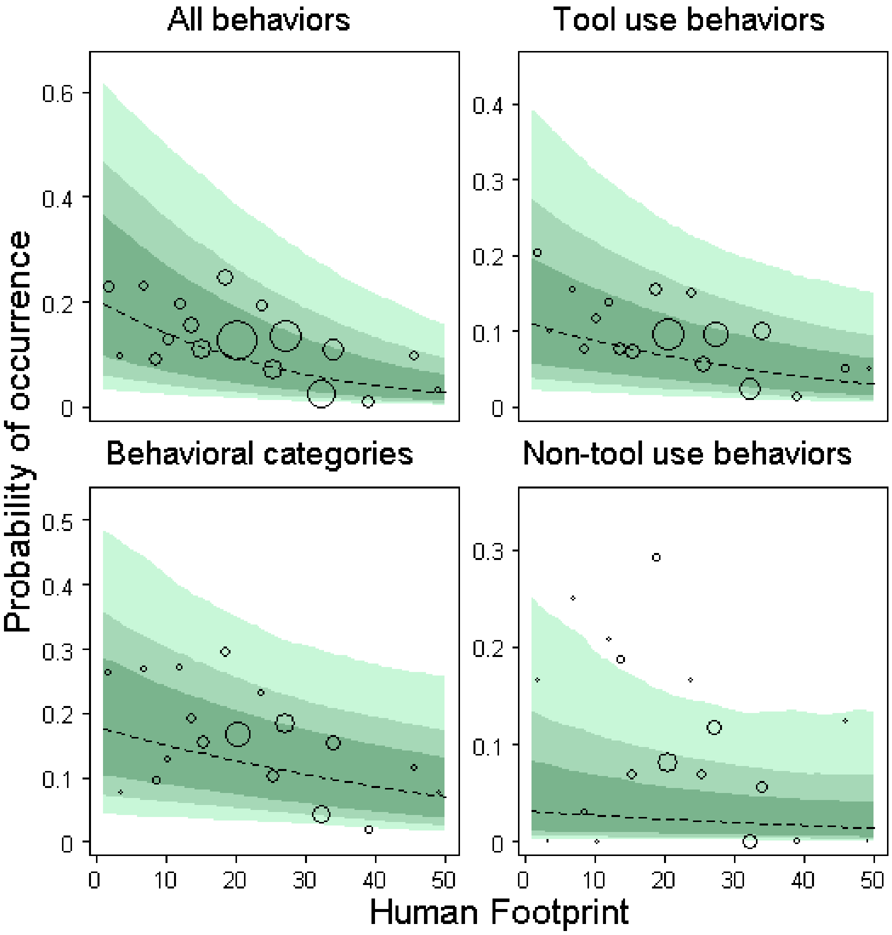

Fig. 2. The probability of occurrence of a behavior per chimpanzee community decreases with human impact. Human impact negatively affects the probability of occurrence of behaviors (top left), irrespective of grouping behaviors by category (bottom left), or by tool use

and non-tool use behaviors (top and bottom right, respectively). The probability of occurrence across behaviors is depicted by 67%, 87%, 97% credibility intervals (*green areas*) of the mean predicted posterior distribution (*dashed*), plotted excluding random effects and for all subspecies combined. The area of the points corresponds to the respective number of chimpanzee communities constituting that data point (range: 1-36 communities).

We found that chimpanzee communities located in areas with a high degree of human impact exhibited an 88% lower mean probability of occurrence, across all behaviors, compared to communities with the least human impact observed (Fig. 2, Estimate (mean of the posterior distribution) = -0.40, CI (95% credible interval) = [-0.73, -0.10], P =0.009). We found this effect irrespective of the grouping of behaviors, i.e., when behaviors were grouped into broader categories such as foraging for termites or thermoregulation (table S1, Estimate = -0.30, CI =[-0.80, 0.139], P=0.006), or when considering non-tool use behaviors only (Estimate = -0.75, CI =[-1.77,0.03], P=0.018), or tool use behaviors only (Estimate = -0.37, CI =[-0.73, -0.01], P =0.018; Fig. 2 and tables S1 to S4). We assessed the reliability of our analyses by testing various subsets of the data and by removing a single behavior at a time, which showed that no single behavior was responsible for our results (figs S3 to S4; table S6). The control predictor ‘subspecies’ showed highly overlapping effects, indicating minimal subspecies specific effects. As expected, the control variable observation months revealed a strong positive effect for all models (figs S1 and S2; tables S2 to S5).

Several potential mechanisms may explain the observed pattern. First, areas with high human impact generally have decreased chimpanzee density and abundance(*11*). As has been shown for humans(*3*, *15*), population size can play a major role in maintaining cultural traits although this relationship is debated(*16*). A similar mechanism may occur in declining chimpanzee populations(*17*). Second, chimpanzees may reduce the frequency of conspicuous behaviors as human impact increases(*8*). Third, climate change may play a role. For example, nut production is strongly dependent on weather conditions and a changing climate is causing greater inter-annual variation in nut availability(*18*), stochastically increasing the potential loss in nut cracking behavior over time. Fourth, habitat degradation and resource depletion may lead to a lower carrying capacity of individuals, thereby reducing opportunities for social learning. This may eventually lead to the disappearance of the behavior. Most likely, a combination of these mechanisms interacts with environmental stability, demography and population connectedness, to create the overall loss of chimpanzee behavioral diversity associated with human impact.

Some studies on chimpanzees living in human-dominated landscapes suggest that a reduction in behavioral diversity will eventually be partially compensated for by new inventions(*10*). Moreover, genetic and ecological variation are expected to continue to be important drivers of behavioral and cultural diversity(*3*). Chimpanzees do show adaptations to modified environments(*10*) and one may ask whether the processes of behavioral loss and innovation act on similar, or different, timescales, and at which point they might reach equilibrium(*8*).

We are currently witnessing a decline in great ape populations at a rate of 2.5-6% per year due to human impact(*11*, *19*). Our results suggest that chimpanzee populations are losing their characteristic sets of behavioral traits and that a number of not yet discovered behaviors may be lost without having ever been described. Considerable effort is urgently needed to protect these populations if we are to fully understand the underlying mechanisms and drivers of their cultural diversification. As such, our findings support the concept of ‘culturally significant units’, whereby a more integrative approach to conservation is needed which considers behavioral diversity in addition to population size and trends for wildlife management(*20*, *21*). Given our limited understanding of the potentially adaptive value of local traditions, we advocate using the precautionary principle of aiming for maximal protection of behavioral variation. We suggest that, for chimpanzees, specific interventions are needed to protect their natural resources and tool-use sites in order to maintain behavioral plasticity and safeguard their capacity for cultural evolution. Therefore, we anticipate the necessity for a new concept, ‘chimpanzee cultural heritage sites’, with which the behavioral and cultural diversity of this species might be recognized and protected. Such a concept could easily be extended to other species exhibiting a high degree of cultural variability, such as orang-utans(*7*) and whales(*20*). This proposition is in accordance with the Convention on Biological Diversity, as well as recent recommendations by the Convention on the Conservation of Migratory Species of Wild Animals, of the United Nations Environment Programme(*22*), which calls for the protection of physiological, genetic and behavioral diversity of culturally rich wildlife.

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Authors contributions:

HSK, CB, MA and AKK designed the study and oversaw data collection; FH, MA, PD, GB and AKK compiled data for this study; HSK, LK, and AKK analyzed the data; GB and LK prepared figures; HSK, LK and AKK wrote the manuscript with input from all co-authors. AA, SA, EAA, EB, DB, MBe, GBr, HC, CC, ED, PD, OD, VEE, HE, RF, YG, AGr, JH, DH, VH, II, SJ, JJ, PK, AKK, MK, MoK, IK, JL, BL, KL, VLe, ML, GM, SM, TJM, ACM, DM, FM, MM, ENe, PN, LJO, JP, SR, CS, JvS, EV, AW, EGW, JW and KY collected data in the field. CB, MBM, RC, CC, TD, DD, AD, AGo, II, KJJ, DK, KL, BM, DM, LP, AP, SR, AR, CS, VS, FS, NT, VV, RMW and KZ provided logistical support and infrastructure for data collection.

Competing interests: The authors declare no competing interests.

Data and materials availability: All data and model script are in the supplementary materials or otherwise publicly available as per the main text.

List of Supplementary Materials:

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Supplementary Text

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Science

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Supplementary Materials for

Human impact erodes chimpanzee behavioral diversity

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Captions for Data S1 to S2

Other Supplementary Materials for this manuscript include the following:

Data S1 to S2 [Data matrix with all 144 chimpanzee communities and the occurrence of each behavior along with the sources of data and publications consulted; Model script and result output for the analyses of the full model using all behaviors in R]

Materials and Methods

Experimental Design

In an effort to understand the ecological and evolutionary processes of behavioral and cultural diversification in chimpanzees, we launched the Pan African Programme: The Cultured Chimpanzee in 2010 (hereby referred to as the ‘PanAf’, http://panafrican.eva.mpg.de). Due to the extensive cost and time involved in the traditional approach of habituating chimpanzees to human observers for longitudinal behavioral studies, we used an alternative methodological approach, relying on a space-for-time substitution concept(*36*). This is based on the assumption that a temporal process, such as the loss of behaviors due to human impact, can also be investigated by studying different populations in a cross-sectional manner. At the time of sampling, chimpanzee communities are positioned at different locations on the behavioral loss trajectory as a function of the level of human impact they have experienced and should therefore show different sized sets of behavioral traits. We collected data via a uniform field protocol and gathered information on behaviors using camera traps (Bushnell Trophy cameras) as well as line (0- 144 km) and strip (0-51km) transects. Prior to setting up a PanAf site, we conducted a reconnaissance survey over a larger area (~100 km²) to identify a suitable research area with contiguous occurrence of chimpanzee signs (dung, feeding signs, nests, vocalizations and sightings). We then set a grid of cell size 1 by 1 km covering the study area. Grid size varied between 9-143km², depending on biome (rainforest vs savanna) and detected signs of chimpanzee presence. Within each cell of the grid we placed one camera at a location visited regularly by chimpanzees, such as a fruit tree, natural bridge across water, animal path, or tool-using sites, such as those where the apes exploit nests of social insects, crack nuts, fish for algae, or a tree showing signs of accumulative stone throwing. We also installed additional cameras to target tool-using sites across the grid. Note that these cameras could be moved throughout the study period since chimpanzee tool-use behavior often targets seasonally available resources.

In addition, we compiled information on chimpanzee behavioral diversity by screening the literature, including printed and electronic articles, doctoral theses(*37*, *38*) and books(*2*, *39*–*46*). First, we defined a list of behaviors to be considered. The key criterion for selection was detectability of behaviors by the PanAf methodology and behaviors that exhibit population variation (table S1). We downloaded publications using the key words “tool-use”, “tool” and the names of the specific behaviors defined, by first searching in Google Scholar and subsequently identifying more articles by following the reference lists of already compiled sources. This resulted in screening of approximately 450 publications from 1951 to 2017, but most of them after the 1980s.

We considered behaviors as being present in a community if either direct or indirect evidence had been documented, irrespective of the frequency or number of observations. Indirect evidence is only possible for behaviors that leave behind observable traces in the dung (e.g. insect remains) or artefacts (e.g. tools). We classified the 31 behaviors as tool use or non-tool use based on the consensus in the literature and further grouped them according to their function or the targeted resource (table S1). Importantly, we recorded a behavior as absent for a specific community if no evidence was found by the PanAf or reported in the published literature.

The combined effort of the PanAf and additional data compilation resulted in a total sample size of 144 chimpanzee communities spanning all four subspecies from 107 different research sites. Multiple communities could be present at a single site, such as neighboring chimpanzee communities (e.g., Taï) because a site was defined as communities occurring within 2.5 km of one another. Of these 144 communities, eight had both PanAf and published studies available about the selected behaviors. A limitation of our study rests with the fact that we cannot be certain of whether our classification as a behavior as absent is true due to observational constraints. Therefore, the effect of observation effort is illustrated further with respect to the number of behaviors (figs S1 and S2).

Statistical Analysis

To investigate how the observed behavioral diversity in chimpanzee communities is influenced by human disturbance we used Bayesian Regression Models (BRM) with Bernoulli response distribution and logit link function. Our dataset comprised 31 combinations for 144 communities with the occurrence (yes/no) of a particular behavior within it. Due to the possibility that, for some behaviors, the resource or the necessary tool (e.g., rocks) was not available within the presumed territory of the community, we coded those cases as NA ('not applicable') and excluded them from the dataset. As the response variable, we used four different measures to account for behavioral diversity. First, we used the occurrence (yes / no) of a behavior per community; second, we categorized the behaviors into 13 categories (table S1) and used the occurrence of a category per community; third, we considered only the occurrence of tool-use behaviors, and fourth, we used the occurrence of non-tool use behavior. As fixed effects, we included a human footprint value for each community based on the coordinates at its center(*13*). We included as control effects the number of months the community was observed or surveyed, and the chimpanzee subspecies (*Pan troglodytes verus/ ellioti/ schweinfurthii/ troglodytes*). The effect of observation months is twofold. First, an increase in observation time is expected to increase the number of recorded behaviors, asymptoting at some point. However, increased observation effort also has a protective effect for chimpanzees(*23*). This suggests that the loss of behaviors due to human impact may occur at a much lower rate in communities undergoing long-term observation (fig S1 and S2).

We included the site and behavior as random effects into the model (Data S1). As random slopes we included the human footprint, the number of months of observation for the community and the chimpanzee subspecies within behavior, as well as the correlation parameters between the random intercepts and random slope terms(*47*, *48*). We controlled for spatial autocorrelation by including a Gaussian process over longitude and latitude for each community(*49*) by using the function "gp" from the R package "brms"(*51*). Before running the models, we z-transformed the two numerical covariates to a mean of zero and a standard deviation of one(*44*).

We additionally ran reduced models to account for variation in PanAf data quality. One model excluded four PanAf communities that comprised study durations shorter than 12 months and recorded no observations of the 31 chimpanzee behaviors targeted in this study and another excluded PanAf communities where camera trap video data were not yet fully cleaned. For another model we removed all long-term research sites from the dataset since these communities have a disproportionately large amount of observation effort (figs S1, S2 and S4).

We fitted the models in R(*50*) by using the function 'brm' from the R- package "brms"(*51*), which runs 2,000 iterations by default over four MCMC chains, with a 'warm-up' period of 1,000 iterations per chain resulting in 8,000 usable posterior samples(*51*). We are confident in the accuracy of the MCMC results because: (1) visual inspection showed stationarity and convergence to a common target, (2) all Rhat(*52*) values were below 1.01, and (3) there were no divergent transitions after warmup. As priors we used the default flat priors and in addition, we tested all models with a weakly informative and an informative prior for the human footprint predictor. As weak prior we chose a normal distribution with a mean of 0 and a standard deviation of 1. Since human disturbance on wildlife is predicted to have mostly negative effects, we assumed a negative effect of the predictor human footprint on the occurrence probability of chimpanzee behavior; therefore, we chose as informative prior a normal distribution with a mean of -0.4 and a standard deviation of 0.3. As we assumed a positive effect of observation time we chose as informative prior a normal distribution with a mean of 0.4 and a standard deviation of 0.3.

Moreover, we also fitted Maximum Likelihood mixed models (MLM)(*53*) in order to verify our results with the commonly used statistical approach that provides P values. For calculation we used the function ‘glmer’ from the R package “lme4”(*54*). We used the same model structure as described above with binomial error distribution and logit link function. As our dataset was likely to show spatial autocorrelation, where the assumption of independent residuals might be violated, we aimed to include an autocorrelation term into the MLM’s for each community, to account for spatial autocorrelation in the data. However, the autocorrelation term was non-significant and had a negative estimate; therefore we dropped it from the models. We checked the MLM’s for various model assumptions. First, we checked for overdispersion, and found slight underdispersion for some of the models (range: dispersion parameter=0.634-0.819, χ^2=717.0-3571.3, df=1131-4401, P=1). Second, we checked for model stability by excluding each level of the random effects one at a time from the data and comparing the model estimates derived for these data with those derived from the full dataset. This indicated no influential cases existed. Third, we calculated Variance Inflation Factors (VIF(*55*)) using the function ‘vif’ of the R-package “car”(*56*) applied to a standard linear model excluding the random effects. The results did not indicate collinearity to be an issue (largest VIF=1.128). For the MLM’s we determined statistical significance of the full model by comparing its fit with that of the null model comprising only the random effects, using a likelihood ratio test (LRT(*57*)), available as R function ‘anova’, package “stats”. The results revealed for all models a significant difference between the full and the null model (LRT: χ^2=32.773-68.614, df=5, P<0.001). P-values for the individual effects were based on likelihood ratio tests comparing the full with their respective reduced models(*47*) (R function “drop1”). Additionally, effect sizes were calculated with the R-package “piecewiseSEM” using the function ‘rsquared’(*58*). The effect sizes for the MLM’s measured as 'marginal' R^2 ranging from 0.025 to 0.063 and as 'conditional' R^2 (including fixed and random effects) ranging from 0.148 to 0.321. Since we found large standard deviations and correlation parameters of the random intercepts and slopes for the MLM’s, we ran additional models to the full dataset: one without the correlation parameter and one with random intercepts only (see also fig S3 to S5 and tables S2 to S6).

Supplementary Text

Mathematical Formulation of the Statistical Model

$$\text{Observed.YN}_{\text{i}} \sim \text{Binomial}(1,\text{Y}_{\text{i}})$$

$$\text{logit}(Y_{\text{i}}) = \beta_{0\text{i}}+\beta_{1\text{i}}Footprint_{\text{i}}+\beta_{2\text{i}}ObsTime_{\text{i}}+\beta_{3\text{i}}Subspecies_{\text{i}}+GP_{\text{i},}$$

$$\beta_{0\text{i}} = \beta_0 + \beta_{0\text{Site i}} + \beta_{0\text{Behavior i}}\ ,$$

$$\beta_{1\text{i}} = \beta_1 + \beta_{1\text{Site i}} + \beta_{1\text{Behavior i}}\ ,$$

$$\beta_{2\text{i}} = \beta_2 + \beta_{2\text{Site i}} + \beta_{2\text{Behavior i}}\ ,$$

$$\beta_{3\text{i}} = \beta_3 + \beta_{3\text{Behavior i}}\ ,$$

$$\begin{bmatrix} \beta_{0\text{Site i}} \\ \beta_{1\text{Site i}} \\ \beta_{2\text{Site i}} \end{bmatrix} \sim \text{MVN}\left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \text{Sigma}_{\text{Site}} \right),$$

$$\text{Sigma}_{\text{Sites}} = \text{S}_{\text{Sites}}\ \text{Rho}_{\text{Sites}}\ \text{S}_{\text{Sites}},$$

$$\text{S}_{\text{Sites}} \sim \begin{bmatrix} \sigma_{0\text{Site i}} & 0 & 0 \\ 0 & \sigma_{1\text{Site i}} & 0 \\ 0 & 0 & \sigma_{2\text{Site i}} \end{bmatrix},$$

$$\begin{bmatrix} \beta_{0\text{Behavior i}} \\ \beta_{1\text{Behavior i}} \\ \beta_{2\text{Behavior i}} \\ \beta_{3\text{Behavior i}} \end{bmatrix} \sim \text{MVN}\left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \text{Sigma}_{\text{Behavior}} \right),$$

$\mathrm{Sigma}_{Behavior} = \mathrm{S}_{Behavior}\ \mathrm{Rho}_{Behavior}\ \mathrm{S}_{Behavior}$,

$$\mathrm{S}_{Behavior} \sim \begin{bmatrix} \sigma_{0Behavior\ i} & 0 & 0 & 0 \\ 0 & \sigma_{1Behavior\ i} & 0 & 0 \\ 0 & 0 & \sigma_{2Behavior\ i} & 0 \\ 0 & 0 & 0 & \sigma_{3Behavior\ i} \end{bmatrix}$$

$GP \sim MVN(0,k)$

$k_{longlat\ i,longlat\ j} = sdgp^2\ exp(-\ ||\ _{longlat\ i\ -\ longlat\ j}\ ||\ /\ (2\ lscale^2)$,

$\beta_0 \sim$ student_t(3, 0, 10),
$\beta_1 \sim$ Flat or Normal(0,1) or Normal(-0.4,0.3),
$\beta_2 \sim$ Flat or Normal(0,1) or Normal(0.4,0.3),
$\beta_3 \sim$ Flat or Normal(0,1) or Normal(0,1),
$\sigma \sim$ student_t(3, 0, 10),
$\mathrm{Rho}_{Sites} \sim$lkj_corr (1)
$\mathrm{Rho}_{Behavior} \sim$lkj_corr (1)
lscale ~ normal(0,1)
sdgp ~ normal(0,1)

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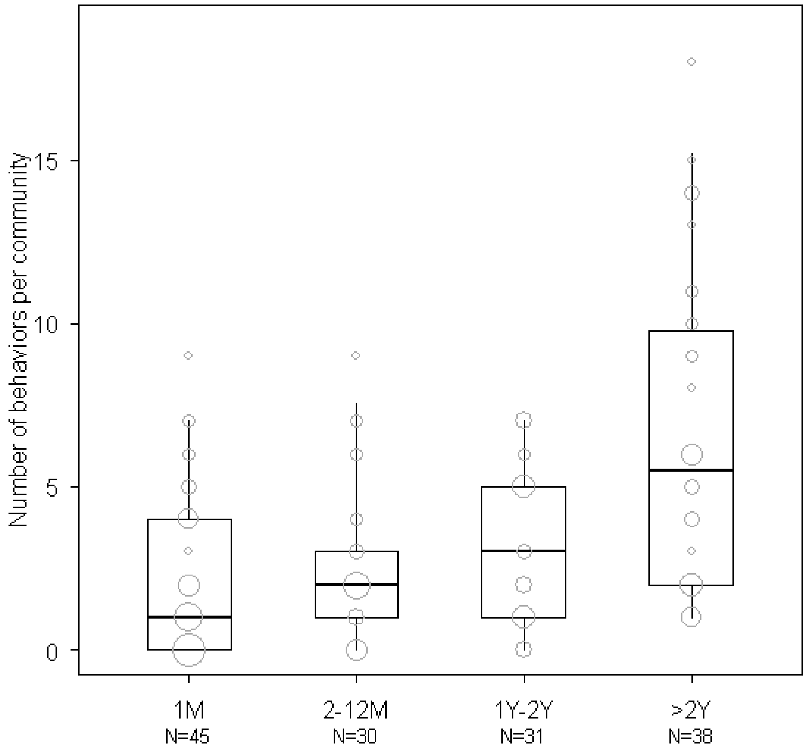

Fig. S1.

The effect of observation time on the number of behaviors per chimpanzee community. Horizontal black lines represent medians, the boxes are the 25 and 75% quantiles, the vertical lines the 2.5and 97.5% quantiles Circles show aggregated data where sample size is proportional to the size of the circle. The number of communities per observation effort class is shown on the x-axis.

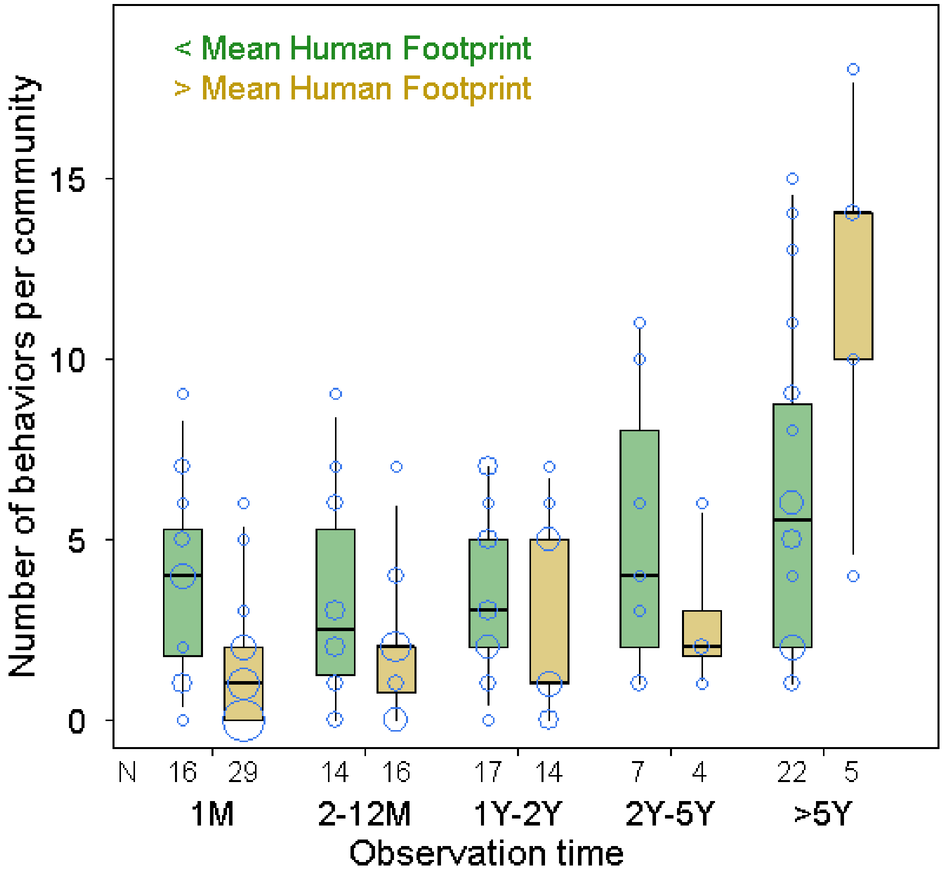

Fig. S2.

The effect of observation time on the number of behaviors per chimpanzee community for above and below the mean human footprint values of the dataset. Horizontal black lines represent medians, the boxes are the 25 and 75% quantiles, the vertical lines the 2.5 and 97.5% quantiles. Circles show aggregated data where sample size is proportional to the size of the circle. The number of communities per observation effort class is shown on the x-axis.

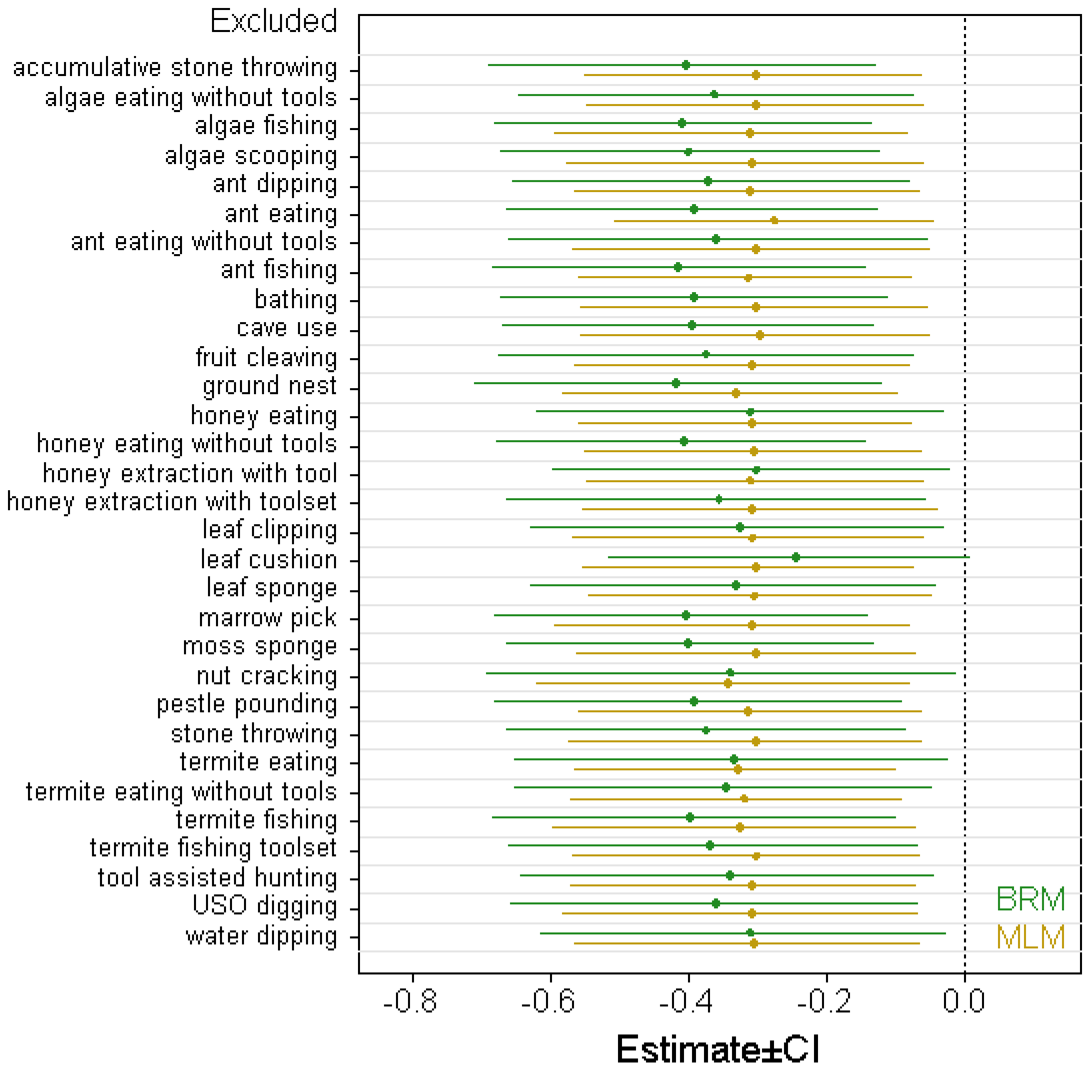

Fig. S3.

Model estimates for the predictor human footprint revealed when the full model for all behaviors is run by excluding one behavior at a time from the dataset. The estimates (dots) and confidence intervals (lines) for MLMs (black) and the estimate (mean of the posterior distribution) and the 95% credibility interval for the BRMs (green) for the predictor do not depend on any particular behavior being included in the model.

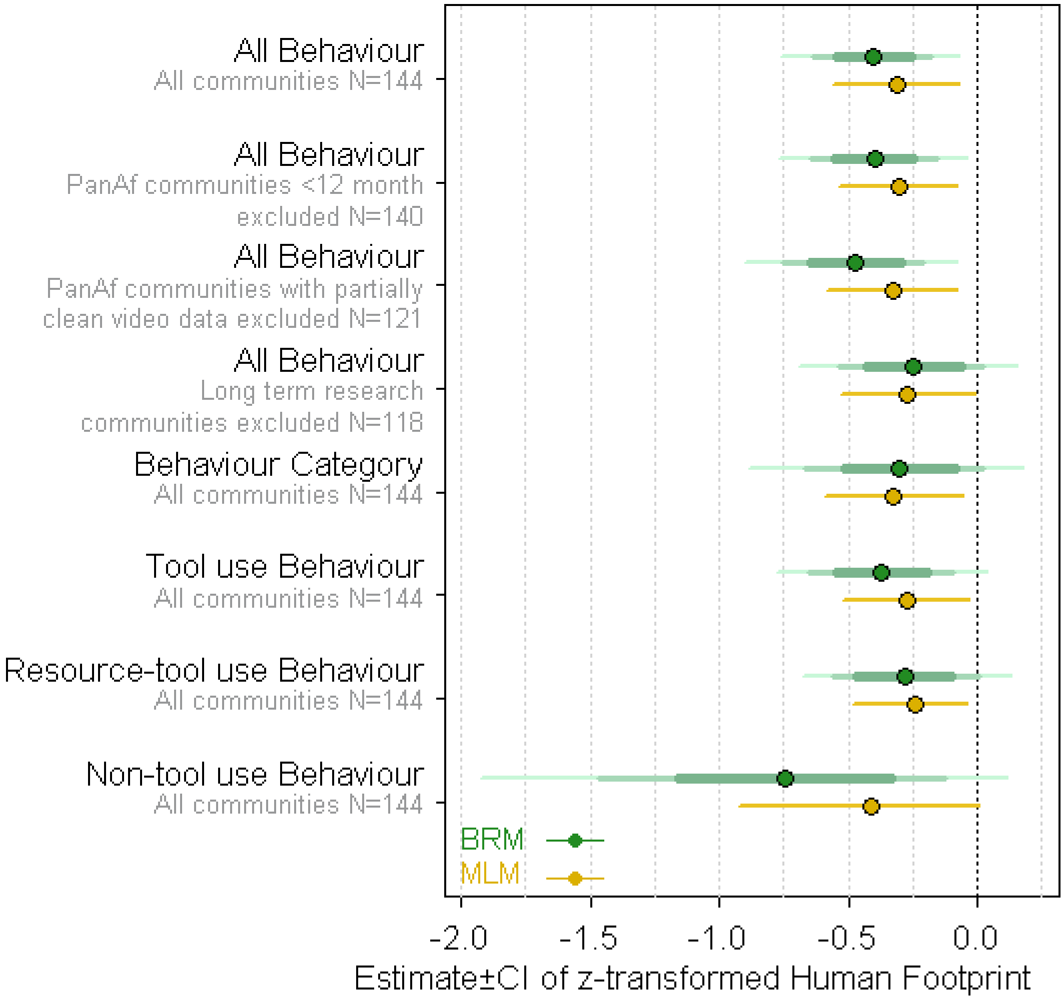

Fig. S4.

Model estimates for the predictor human footprint revealed by applying MLMs and BRMs on the four different response variables and reduced datasets. The plots shows the estimates (dots) and confidence intervals (lines) for MLMs (brown) and the estimate (mean of the posterior distribution) and the 67%, 87%, 97% credibility intervals (*green areas*)for the BRMs (green).

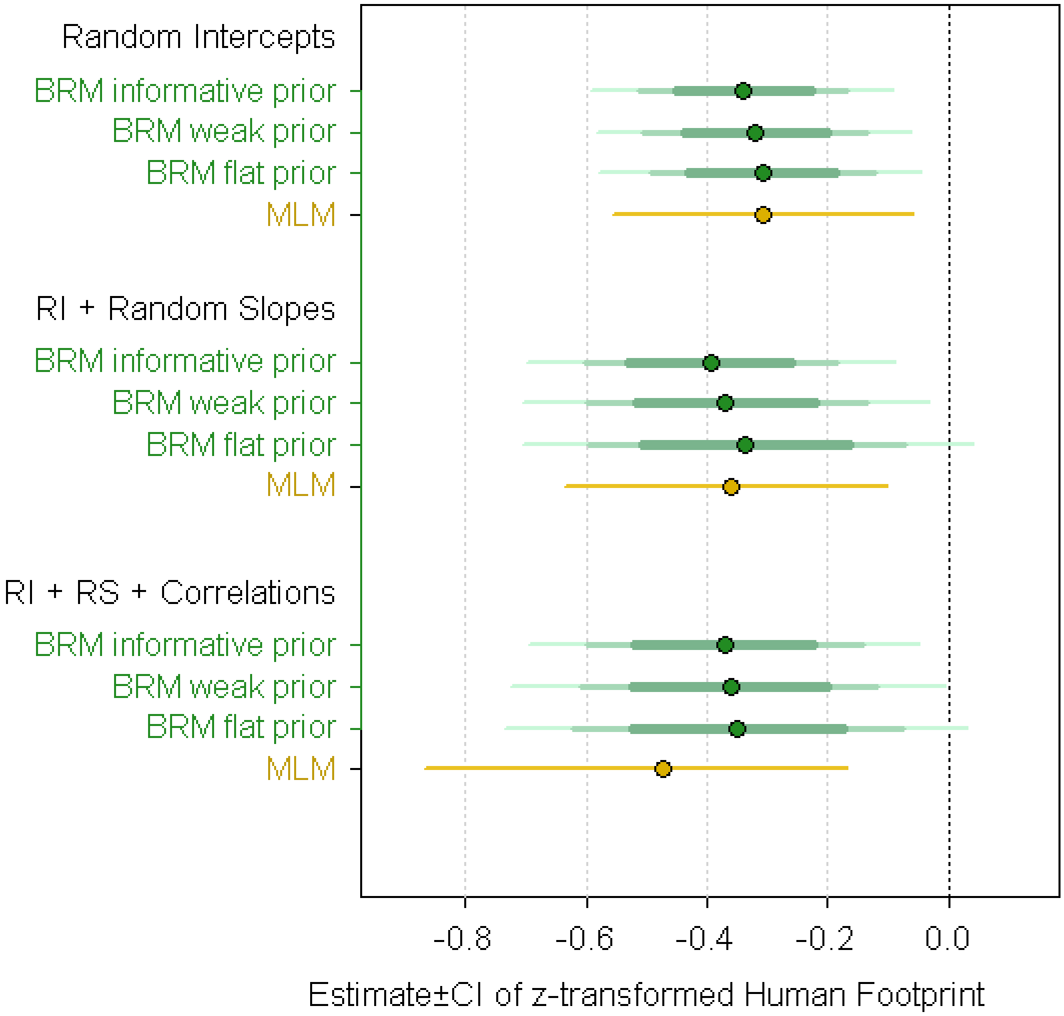

Fig. S5.

Model estimates for the predictor human footprint revealed by conducting MLMs and BRMs with different priors and different random effect structures. The plots shows the estimates (dots) and confidence intervals (lines) for MLMs (black) and the estimate (mean of the posterior distribution) and the 95% credibility interval for the BRMs (green).

Behavior	Tool use	Category	Definition
accumulative stone throwing	yes	communication	repeated throwing of stones at a tree with accumulation of stones at the base and wound marks visible on the tree
algae fishing	yes	foraging algae	fish algae with plant part from bottom of water source
algae scooping	yes	foraging algae	scoop algae with plant part from surface of water source
algae eating without tools	no	foraging algae	collect algae from water with bare hands
ant dipping	yes	foraging ants	collect army ants (*Dorylus* spp.) from trail or nest using plant part
ant eating	unknown	foraging ants	ant remains in feces; tool-use cannot be inferred
ant fishing	yes	foraging ants	use plant part to obtain non-*Dorylus* spp. ants
ant eating without tools	no	foraging ants	eat ants with bare hands
bathing	no	thermoregulation	immerse in pools of water to presumably cool down
cave use	no	thermoregulation	enter caves during the day for short or long period, presumably to aid cooling
fruit cleaving	yes	foraging fruit	pound fruit with a tool to fracture it
ground nest	no	ground protection	create overnight sleeping platform on the ground from foliage
honey eating	unknown	foraging honey	traces of honey, bees, or honeycomb in feces; tool-use cannot be inferred
honey extraction with tool	yes	foraging honey	extract honey from beehives using a plant part
honey extraction with toolset	yes	foraging honey	extract honey from beehives using functionally different types of tools i.e., perforation and probing
honey eating without tools	no	foraging honey	eat honey with bare hands
leaf clipping	yes	communication	audible ripping with teeth or pressed lips and side-to-side moving of detached leaves without ingesting them
leaf cushion	no	ground protection	sit on detached leaves placed on ground to without creating full sleeping platform
leaf sponge	yes	water extraction	use chewed wad of leaves as a sponge to soak up water and squeeze into mouth
marrow pick	yes	foraging vertebrates	pick brain matter or bone marrow using plant part
moss sponge	yes	water extraction	use chewed moss as a sponge to soak up water and squeeze into mouth
nut cracking	yes	foraging nuts	crack nuts using hammer and anvil from wood or stone
pestle pounding	yes	foraging pith	open crown of oil palm by pounding with palm frond petiole
stone throwing	yes	communication	directed throw at predators or intruders, including humans, to chase them off
termite eating	unknown	foraging termites	termite remains in feces; tool-use cannot be inferred
termite fishing	yes	foraging termites	extract termites from nest using plant part
termite fishing toolset	yes	foraging termites	extract termites from nest using functionally different types of tools
termite eating without tools	no	foraging termites	use hands to break open termite mounds; no tool-use seen
tool-assisted hunting	yes	foraging vertebrates	use sticks to spear and kill small vertebrates
USO digging	yes	foraging	use sturdy plant part to dig up underground storage organs such as tubers
water dipping	yes	water extraction	chew on plant part to create a brush tip to soak-up water and ingest

Table S1.

Definitions of the 31 chimpanzee behaviors coded for all 144 chimpanzee communities*(1,2, 24-35).*

	BRM				**MLM**						
Predictor	**E**	**SD**	**CI2.5**	**CI97.5**	**E**	**SE**	**CI2.5**	**CI97.5**	**χ^2**	**df**	**P**
(Intercept)	-3.613	0.431	-4.498	-2.827	-3.382	0.319	-4.117	-2.812	(1)	(1)	(1)
Human footprint (2)	-0.401	0.155	-0.725	-0.106	-0.307	0.115	-0.556	-0.074	6.900	1	0.009
N month of observation(2)	0.972	0.281	0.418	1.524	0.820	0.109	0.589	1.031	47.401	1	<0.001
Pan troglodytes ellioti	-0.529	0.977	-2.739	1.137	0.194	0.493	-0.892	1.164	7.510	3	0.057
Pan troglodytes schweinfurthii	-0.963	0.629	-2.224	0.239	-0.252	0.314	-0.919	0.408			
Pan troglodytes troglodytes	-0.399	0.796	-2.088	1.074	0.729	0.337	0.014	1.406			

(1): not shown because of not having a meaningful interpretation

(2): predictors were z-transformed to a mean=0 and sd=1

Table S2.

Model results for the probability of behavioral occurrence per community.

	BRM				MLM						
Predictor	**E**	**SD**	**CI2.5**	**CI97.5**	**E**	**SE**	**CI2.5**	**CI97.5**	**χ^2**	**df**	**P**
(Intercept)	-2.539	0.784	-4.113	-1.013	-2.572	0.479	-3.543	-1.664	(1)	(1)	(1)
Human footprint (2)	-0.304	0.233	-0.802	0.129	-0.326	0.116	-0.589	-0.059	7.674	1	0.006
N month of observation(2)	1.044	0.367	0.324	1.781	0.803	0.106	0.567	1.036	47.974	1	<0.001
Pan troglodytes ellioti	-2.004	2.026	-6.731	0.944	-0.474	0.506	-1.665	0.543	4.846	3	0.183
Pan troglodytes schweinfurthii	-1.809	1.132	-4.234	0.278	-0.690	0.317	-1.490	-0.070			
Pan troglodytes troglodytes	-1.830	1.623	-5.348	1.016	-0.116	0.342	-0.884	0.646			

(1): not shown because of not having a meaningful interpretation
(2): predictors were z-transformed to a mean=0 and sd=1

Table S3.
Model results for the probability of occurrence of a behavioral category per community.

	BRM				MLM						
Predictor	**E**	**SD**	**CI2.5**	**CI97.5**	**E**	**SE**	**CI2.5**	**CI97.5**	**χ^2**	**df**	**P**
(Intercept)	-4.099	0.894	-6.047	-2.508	-3.493	0.453	-4.713	-2.545	(1)	(1)	(1)
Human footprint (2)	-0.746	0.455	-1.770	0.032	-0.415	0.183	-0.926	0.004	5.620	1	0.018
N month of observation(2)	1.153	0.621	-0.071	2.398	0.807	0.153	0.457	1.183	27.780	1	<0.001
Pan troglodytes ellioti	-12.619	12.820	-47.146	-0.339	-1.827	1.303	-13.665	-0.161	3.459	3	0.326
Pan troglodytes schweinfurthii	-1.989	1.966	-6.308	1.587	-0.618	0.530	-1.882	0.479			
Pan troglodytes troglodytes	-1.281	1.758	-5.116	1.886	-0.281	0.593	-1.822	0.918			

(1): not shown because of not having a meaningful interpretation
(2): predictors were z-transformed to a mean=0 and sd=1

Table S4.

Model results for the probability of occurrence of a non-tool use behavior per community.

	BRM				MLM						
Predictor	**E**	**SD**	**CI2.5**	**CI97.5**	**E**	**SE**	**CI2.5**	**CI97.5**	χ^2	**df**	**P**
(Intercept)	-3.398	0.51	-4.450	-2.446	-3.101	0.327	-3.796	-2.480	(1)	(1)	(1)
Human footprint (2)	-0.370	0.18	-0.734	-0.009	-0.274	0.114	-0.524	-0.032	5.553	1	0.018
N month of observation(2)	0.892	0.28	0.336	1.450	0.771	0.095	0.576	0.980	52.331	1	<0.001
Pan troglodytes ellioti	-1.172	1.39	-4.470	0.950	-0.013	0.443	-1.002	0.759	13.392	3	0.004
Pan troglodytes schweinfurthii	-1.635	0.81	-3.431	-0.168	-0.883	0.295	-1.500	-0.308			
Pan troglodytes troglodytes	-1.497	1.25	-4.287	0.668	0.312	0.310	-0.343	0.921			

(1): not shown because of not having a meaningful interpretation

(2): predictors were z-transformed to a mean=0 and sd=1

Table S5.

Model results for the probability of occurrence of a tool use behavior per community.

	BRM				**MLM**						
Excluded behavior	**Estimate**	**SD**	**CI2.5**	**CI97.5**	**Estimate**	**SE**	**CI2.5**	**CI97.5**	χ^2	**df**	**P**
Accumulative stone throwing	-0.403	0.143	-0.690	-0.131	-0.302	0.116	-0.550	-0.064	6.539	1	0.011
Algae eating without tools	-0.362	0.147	-0.647	-0.076	-0.300	0.115	-0.548	-0.060	6.488	1	0.011
Algae fishing	-0.408	0.140	-0.680	-0.136	-0.309	0.114	-0.594	-0.083	6.973	1	0.008
Algae scooping	-0.399	0.140	-0.673	-0.125	-0.306	0.116	-0.576	-0.060	6.670	1	0.010
Ant dipping	-0.370	0.146	-0.654	-0.081	-0.309	0.113	-0.566	-0.065	7.184	1	0.007
Ant eating	-0.390	0.136	-0.664	-0.128	-0.274	0.112	-0.507	-0.045	5.757	1	0.016
Ant eating without tools	-0.359	0.154	-0.662	-0.054	-0.302	0.114	-0.569	-0.051	6.765	1	0.009
Ant fishing	-0.415	0.138	-0.685	-0.145	-0.312	0.115	-0.560	-0.078	7.062	1	0.008
Bathing	-0.391	0.142	-0.672	-0.111	-0.302	0.114	-0.557	-0.055	6.684	1	0.010
Cave use	-0.394	0.136	-0.671	-0.134	-0.296	0.115	-0.555	-0.051	6.319	1	0.012
Fruit cleaving	-0.375	0.153	-0.675	-0.076	-0.307	0.115	-0.564	-0.080	6.890	1	0.009
Ground nest	-0.418	0.150	-0.710	-0.121	-0.331	0.118	-0.583	-0.097	7.444	1	0.006
Honey eating	-0.310	0.150	-0.619	-0.031	-0.306	0.113	-0.559	-0.077	6.992	1	0.008
Honey eating without tools	-0.405	0.136	-0.677	-0.145	-0.305	0.113	-0.550	-0.063	6.909	1	0.009
Honey extraction with tool	-0.300	0.146	-0.597	-0.021	-0.310	0.112	-0.547	-0.061	7.399	1	0.007
Honey extraction with toolset	-0.355	0.155	-0.663	-0.057	-0.306	0.115	-0.553	-0.041	6.716	1	0.010
Leaf clipping	-0.324	0.155	-0.630	-0.032	-0.307	0.114	-0.568	-0.060	6.963	1	0.008
Leaf cushion	-0.244	0.137	-0.515	0.007	-0.302	0.113	-0.554	-0.075	6.777	1	0.009
Leaf sponge	-0.330	0.152	-0.630	-0.042	-0.305	0.114	-0.544	-0.048	6.825	1	0.009
Marrow pick	-0.403	0.136	-0.681	-0.142	-0.306	0.114	-0.593	-0.080	6.876	1	0.009
Moss sponge	-0.401	0.137	-0.663	-0.132	-0.302	0.116	-0.562	-0.071	6.465	1	0.011
Nut cracking	-0.338	0.175	-0.694	-0.015	-0.342	0.131	-0.619	-0.080	6.563	1	0.010
Pestle pounding	-0.391	0.150	-0.682	-0.092	-0.313	0.116	-0.559	-0.063	7.006	1	0.008
Stone throwing	-0.375	0.147	-0.664	-0.087	-0.302	0.113	-0.573	-0.064	6.857	1	0.009
Termite eating	-0.332	0.162	-0.653	-0.025	-0.328	0.116	-0.565	-0.102	7.653	1	0.006
Termite eating without tools	-0.346	0.156	-0.651	-0.048	-0.319	0.116	-0.570	-0.092	7.170	1	0.007
Termite fishing	-0.398	0.147	-0.683	-0.102	-0.325	0.118	-0.598	-0.073	7.291	1	0.007
Termite fishing toolset	-0.367	0.150	-0.661	-0.070	-0.302	0.115	-0.568	-0.067	6.551	1	0.010
Tool-assisted hunting	-0.340	0.153	-0.643	-0.046	-0.307	0.114	-0.571	-0.073	6.874	1	0.009
USO digging	-0.360	0.151	-0.657	-0.068	-0.307	0.115	-0.582	-0.070	6.854	1	0.009
Water dipping	-0.309	0.150	-0.615	-0.027	-0.305	0.114	-0.566	-0.066	6.938	1	0.008

Table S6.

Model results for the predictor human footprint revealed stable estimates, 95% credible intervals or confidence intervals, and significance ($P < 0.05$) when the full model based on single behaviors was run by excluding one behavior at a time.

Data S1. (separate file)

Data matrix with the list of all 144 chimpanzee communities and the presence of each behavior along with the sources of data and publications consulted. To our knowledge, the dataset is up to date as of December 2017.

Data S2. (separate file)

Model script and result output for the analyses of the full model using all behaviors in R.