CONSERVATION

Human impact erodes chimpanzee behavioral diversity

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Chimpanzees possess a large number of behavioral and cultural traits among nonhuman species. The "disturbance hypothesis" predicts that human impact depletes resources and disrupts social learning processes necessary for behavioral and cultural transmission. We used a dataset 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.

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 by 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*).

Cultural behaviors in great apes, notably chimpanzees (*1*) and orang-utans (*6*), are maintained by cultural processes including innovation, diffusion, and vertical and horizontal transmission (*2*, *7*). 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 (*7*). 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, owing to resource depletion or a breakdown in opportunities for social learning (*7*). Major elements of human impact include habitat loss, degradation, and fragmentation, which reduce population size, gregariousness, and long-distance dispersal, weakening behavioral transmission (*7*).

In the current Anthropocene era, Earth's biosphere is being heavily degraded by unsustainable resource use and high rates of biodiversity loss (*8*). This overexploitation is substantially affecting chimpanzees and their habitat, namely African tropical forests and savanna woodlands (*9*). All four chimpanzee subspecies are severely threatened by deforestation and poaching, caused by a rapidly growing human population (*8*–*10*). These factors have already led to major population declines, fragmentation and regional extirpations (*10*), and reduced genetic diversity (*11*).

The large behavioral diversity of chimpanzees, coupled with rapid population decline, makes investigation of the disturbance hypothesis 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 noninvasive 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 that occur at a specific geographic location, with associated

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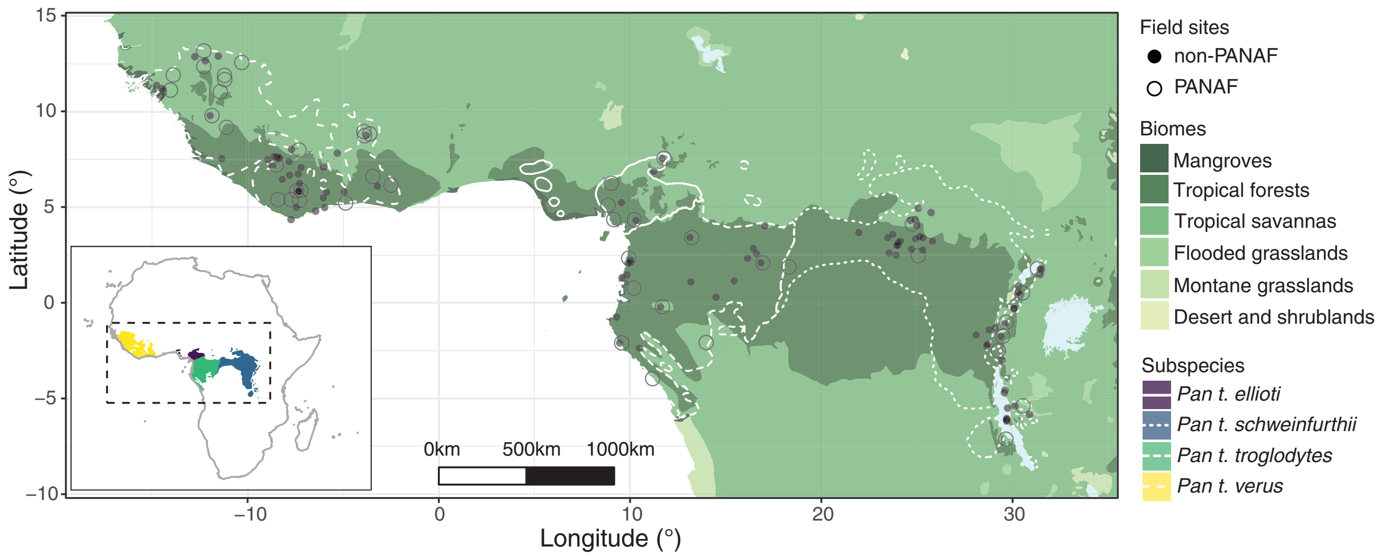

Fig. 1. Locations of all 144 unique chimpanzee communities for which information on select behaviors was collected for this study. This dataset includes 46 communities from the Pan African Programme (PanAf) and 106 communities for which information was also available from the published literature (non-PanAf). 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.

observations on behaviors. With few exceptions, we collected data over a minimum of one annual cycle (observation period between 12 and 30 months at 37 locations; observation period from 1 to 10 months at 9 locations) in a systematic grid design (grid size range: 9 to 143 km^2).

We compiled presence and absence data on 31 known chimpanzee behaviors (table S1) from these 46 chimpanzee communities and complemented the dataset 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 dataset (Fig. 1 and data file S1). We recorded observations on these behaviors by (i) extensive camera trapping; (ii) fecal samples that provided evidence of ingestion of insects, algae, and honey, resources often exploited with the aid of tools; and (iii) artifacts of tool use identified during reconnaissance, line, and strip transect surveys. We selected behaviors that were detectable through 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*, *12*) (table S1). 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*, *2*, *4*, *5*, *13*). Moreover, many behaviors included here have already been classified as cultural (*1*).

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 1-km-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 (*12*). We controlled for observation effort in number of months, spatial autocorrelation, and chimpanzee subspecies in the analyses (*12*) (tables S2 to S6 and figs. S1 to S5).

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 and S4 and 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 and 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 (*10*). 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 (*7*). Third, climate change may play a role. For example, nut production is strongly dependent on weather conditions and a changing climate is causing greater interannual 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 (*9*). 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 (*9*), and one may ask whether the processes of behavioral

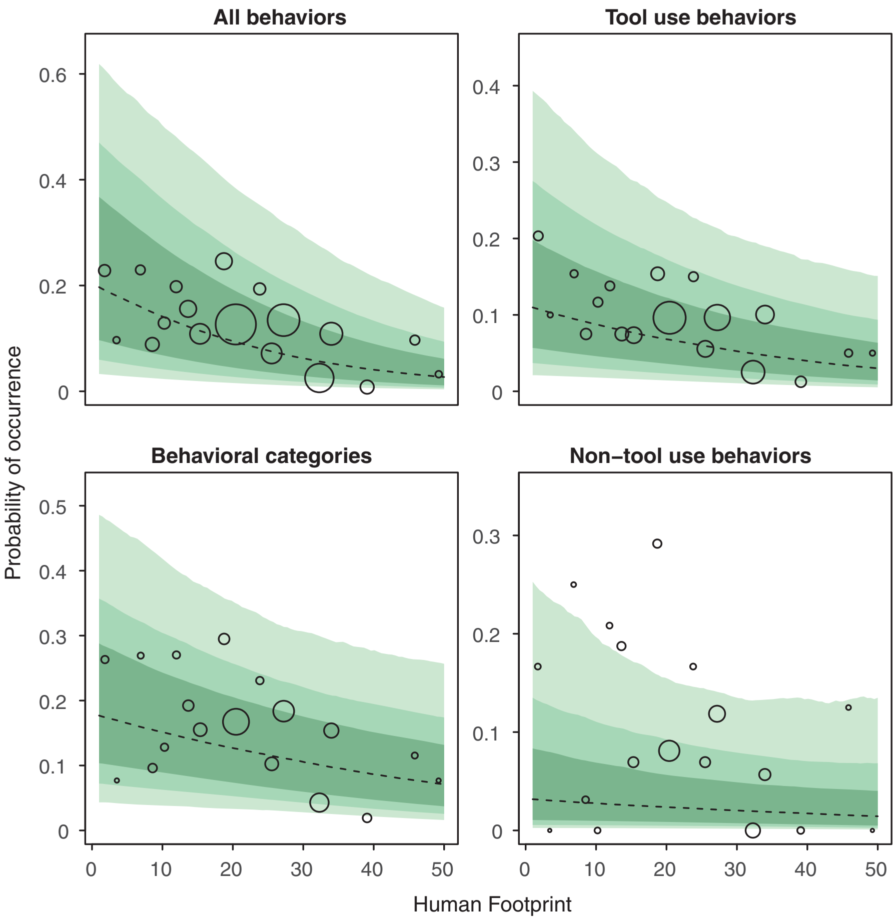

Fig. 2. The probability of occurrence of a behavior per chimpanzee community decreases with human impact. Human impact negatively affects the probability of occurrence of behaviors (top left), irrespective of grouping behaviors by category (bottom left), or by tool use and non–tool use behaviors (top and bottom right, respectively). The probability of occurrence across behaviors is depicted by 67, 87, and 97% credibility intervals (green areas) of the mean predicted posterior distribution (dashed line), 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 to 36 communities).

loss and innovation act on similar, or different, time scales, and at which point they might reach equilibrium (*7*).

We are currently witnessing a decline in great ape populations at a rate of 2.5 to 6% per year due to human impact (*10*, *19*). Our results suggest that chimpanzee populations are losing their characteristic sets of behavioral traits and that a number of as-yet undiscovered 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 that 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 (*6*) 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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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/363/6434/1453/suppl/DC1
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More than just numbers

We often frame negative human impacts on animal species in terms of numbers of individuals reduced or numbers of regions from which species are absent. However, human activities are likely affecting species in more complex ways than these figures can capture. Kühl *et al.* studied behavioral and cultural diversity in our closest relative, the chimpanzee. They found that human-mediated disturbance is reducing these complex traits. Human influence thus goes well beyond simple loss of populations or species, leading to behavioral change even where populations persist.

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