

First camera survey in Burkina Faso and Niger reveals human pressures on mammal communities within the largest protected area complex in West Africa

RT: Human pressures on mammals in West Africa

Nyeema C. Harris¹, Kirby L. Mills^{1,2}, Yahou Harissou³, Emmanuel M. Hema^{4,5}, Isaac T. Gnoumou⁶, Jenna VanZoeren¹, Yayé I. Abdel-Nasser³, and Benoit Doamba⁶

¹Applied Wildlife Ecology Lab, Ecology and Evolutionary Biology Department, University of Michigan, Ann Arbor MI 48106, USA

²School for Environment and Sustainability, University of Michigan, Ann Arbor MI 48106, USA

³Parc W- Niger, Direction Générale Des Eaux et Forêts, Ministère de l'Environnement de la Salubrité Urbaine et du Développement Durable

⁴UFR/Sciences Appliquées et Technologiques, Université de Dédougou, Dédougou, Burkina Faso

⁵Laboratoire de Biologie et Ecologie Animales, Université Ouaga I Professeur Joseph Ki-Zerbo, 09 B.P. 848 Ouaga 09 Ouagadougou, Burkina Faso

⁶Direction de la Faune et des Ressources Cynégétiques, Ministère de l'Environnement, l'Economie Verte et du Changement Climatique 03 BP 7044 Ouagadougou 03, Burkina Faso

KEYWORDS: anthropogenic, carnivore, coexistence, conflict, coupled human-natural, ecosystem services, effectiveness, management, pastoralism, production

ARTICLE TYPE: Letters

WORDS: 150 (Abstract); 2974 (Total - Abstract through Acknowledgements)

REFERENCES: 40

FIGURES/TABLES: 5; SUPPLEMENT: 7

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/conl.12667](https://doi.org/10.1111/conl.12667).

This article is protected by copyright. All rights reserved.

CORRESPONDENCE: Nyeema C. Harris, Applied Wildlife Ecology Lab, Ecology and Evolutionary Biology, University of Michigan, 1101 N University Ave, Ann Arbor Michigan, 48109 nyeema@umich.edu

AUTHOR CONTRIBUTIONS: NCH designed and led project, wrote and analyzed data. NCH, YH, HE, IG, YIA completed data collection and assisted with field logistics. NCH, KLM, JV processed images. BD and YH secured access to study areas and permits, and coordinated field support. All authors reviewed and edited manuscript.

Abstract

The dearth of ecological data from protected areas at relevant scales challenges conservation practice in West Africa. We conducted the first camera survey for Burkina Faso and Niger to elucidate interactions between resource users and mammals in the largest protected area complex in West Africa (W-Arly-Pendjari, WAP). We differentiated direct (e.g., poaching) and indirect (e.g., domestic animals) human activities to determine their effects on species richness, composition, and behavior. Livestock was the dominant human pressure while gathering was the most prevalent direct human activity. Human pressure did not influence species richness or composition, but reduced mammal activity with greater consequences from indirect activities. We also found distinct differences among guilds in their behavioral responses to human pressures as wild ungulates exhibited the greatest sensitivities to livestock presence. Our findings, that aggregated socio-ecological data, transition the WAP complex from the singular mandate of nature conservation to a dynamic coupled human-natural ecosystem.

1 | INTRODUCTION

Protected areas remain the most pervasive conservation strategy to safeguard biodiversity and ecosystem services (Watson, Dudley, Segan, & Hockings, 2014). Venter *et al.* (2014) reported that 83% of threatened vertebrates have a portion of their range within the boundaries of protected areas. Mammals in particular garner conservation benefits and security from protected areas (Schipper *et al.*, 2008; Hoffmann *et al.*, 2010). Conservation efforts including protected areas slowed the decline of more than half of the world's 235 wild ungulates (Hoffmann *et al.*, 2015). Climate models further highlight the importance of protected areas based on species turnover predicted for mammals in West Africa (Baker *et al.*, 2015). However, gains gleaned from occupancy within protected areas may be circumvented by human threats sprawled across 52% of ranges for mammals of conservation concern (Allan *et al.*, 2019).

Despite global declarations of expansion and reinforcement, protected areas are under intense human pressure including many in West Africa, with natural resource utilization and poaching being amongst the top threats (Venter *et al.*, 2014; Jones *et al.*, 2018; Schulze *et al.*, 2018). A global analysis revealed that bushmeat hunting jeopardizes over 300 mammal species (Ripple *et al.*, 2016). Particularly for developing nations, protected areas contribute to human well-being and provide societal benefits through provisioning services (Naughton-Treves, Holland, & Brandon, 2005; Palomo *et al.*, 2014; Naidoo *et al.*, 2019). Resource use operating across scales, combined with transnational trade in wildlife products, underscore the urgency to reconcile social benefits with the increasingly complex requirements of effective conservation.

West Africa simultaneously harbors high levels of biodiversity and faces a myriad of environmental challenges (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Schipper et al., 2008; Luiselli et al., 2019). Agricultural expansion and demands for energy fuel high rates of deforestation throughout the region (Schipper et al., 2008; Mayaux et al., 2013). Future habitat loss expected from urban development will endanger the Guinean forest of West Africa, a biodiversity hotspot (Seto, Guneralp, & Hutyra, 2012). Climate projections predict biome shifts with contractions in the distribution of savanna and loss of tree cover in coastal areas (Heubes et al., 2011). Asefi-Najafabady & Saatchi (2013) reported weather anomalies over the last decade causing water deficits and droughts particularly in forests near savannas in West Africa. These perturbations of habitat loss and climate change operate within and beyond protected areas, and act synergistically and non-additively to threaten biodiversity throughout West Africa (Mantyka-pringle, Martin, & Rhodes, 2012; Luiselli et al., 2019).

Existing broad scale assessments of human pressure in protected areas, though dramatic and compelling, have diminutive application for decision-making at a local scale (Geldmann, Joppa, & Burgess, 2014; Jones et al., 2018). Furthermore, these studies apply the human footprint index comprised of direct and indirect pressures to understand effects on natural systems (Geldmann, Joppa, & Burgess, 2014; Venter et al., 2016). This aggregated metric assumes additive effects and static relative contributions across locations for human pressures. Such limitations complicate our understanding of species vulnerability and mitigation strategies at a scale relevant for management.

Camera surveys are an effective approach to obtain social and ecological data that aids decision-making, given indiscriminate detections of human activities and animals alike (Hossain et al., 2016; Buxton, Lendrum, Crooks, & Wittemyer, 2018). Although West Africa

is undergoing severe environmental changes making protected areas increasingly more vulnerable, few camera surveys have been conducted to monitor biodiversity or threats to biodiversity (Agha et al., 2018). Here, we conduct the first camera survey for Burkina Faso and Niger in W-Arly-Pendjari (WAP) parks, the largest transboundary protected area complex in West Africa. We obtain fine-scale data to concurrently discern human activities and assess their effects on mammal communities by examining three questions. Do direct (e.g., poaching) activities exceed indirect activities (e.g., domestic animals) across national parks? Do these human pressures influence species diversity, composition or behavior within mammal communities? Which taxonomic group exhibits the greatest sensitivity to human pressure? We predict that: 1) direct activities detected in our camera survey will exceed indirect activities; 2) human pressures will have the greatest consequence on mammal behavior; and 3) carnivores will suffer the most from human activities. Ultimately, obtaining socio-ecological data and discriminating human activities from camera surveys can promote coexistence between social and conservation agendas within protected areas of West Africa.

2 | METHODS

2.1 | Study area

We assessed human pressure and interactions with mammal communities within the W-Arly-Pendjari (WAP) transboundary protected area complex (0.514-3.224°E, 10.62-12.817°N). WAP, a UNESCO World Heritage site, is the largest protected area complex in West Africa comprised of national parks, faunal reserves, and hunting concessions spanning 27,167 km² throughout Benin, Burkina Faso, and Niger (Figure 1). Our study occurred in three national parks established in 1954 that have stricter regulations than other designations within WAP: Arly National Park (ARL; 2,228 km²), Park W-Burkina Faso (WBK; 2,344 km²) and Park W-Niger (WNI; 2,226 km²). Though area and ecological features are

comparable, we present results separately for each survey because differences in management infrastructure (e.g., law enforcement, adjacency to hunting concessions) could influence human pressures and faunal responses (Miller, Minn, & Sinsin, 2015; Barnes, Craigie, Dudley, & Hockings, 2017). Surveys in our study included: WBK₂₀₁₆, WBK₂₀₁₇, WNI₂₀₁₇, ARL₂₀₁₇, and ARL₂₀₁₈.

2.2 | Camera survey

We surveyed the mammal community non-invasively using remotely-triggered cameras during the dry season (January-May) from 2016-2018. We divided the study area into 10 x 10 km grid cells and systematically deployed cameras (Reconyx© PC800, PC850, PC900) within 2 km of the centroid in each grid (Figure 1, Supplementary Methods). The Applied Wildlife Ecology (AWE) Lab at University of Michigan used double observers to validate images for species identification. We aggregated species to compare human pressure across taxonomic groups: carnivore (CARN), primate (PRIM), ungulate (UNG), and small mammal (ROD+). For human images, consultation occurred with field teams in Burkina Faso and Niger to ensure accurate interpretation of the local context. We identified specific human activities (Supplementary Methods), and then categorized activities as direct (e.g., gathering, herding/pastoralism, poaching, and transiting/recreation) or indirect (e.g., cattle, goat, donkey, and dog; Figure 2).

2.3 | Data analysis

Before assessing effects of human pressure on community attributes, we first determined differences in activities across surveys. We evaluated whether particular activities occurred more or less than expected using Chi-square statistics and associated residuals.

We distinguished among sampling units (i.e., camera locations) based on three human pressure categories to assess impacts on species diversity: no detection of humans, detection of direct, and detection of indirect human activities. A single camera could be assigned to both human pressure categories. We then calculated the Shannon-Wiener index at the camera-level and averaged across human categories for each survey. We tested for differences in pairwise combinations between human categories using Mann-Whitney tests with the Hochberg correction of significance levels. We evaluated sampling effort using species accumulation curves for each park (Figure S1). We also calculated trap success (TS) for every mammal species and human activity category as the number of independent event triggers divided by total number of trap nights multiplied by 1000.

We also determined how human pressure influenced community structure and whether such perturbations altered species composition and community similarity. From presence-absence species matrices with a binary human detection designation to camera locations, we calculated Bray-Curtis indices to obtain dissimilarity distances and applied non-metric multidimensional scaling (NMDS) with $k=3$ to visualize differences between groups. Analytically, we tested for significant differences in community composition between locations with and without human pressure using an analysis of similarity (ANOSIM). Because ANOSIM only determines mean differences between groups, we also calculated average distances from the median to determine effects of human pressure on dispersion of community dissimilarity.

Lastly, we evaluated the response of mammal behavior to human pressure within each survey using trigger activity per species. We implemented a 30-minute quiet period between triggers to create independent records of species detections in all analyses. If species were sensitive to human presence, we expect avoidance behavior spatially as evident by less time

spent (i.e., fewer triggers) at locations sympatric with human activities. We aggregated the number of triggers per species to compare differences in activity between direct vs. human absent, and indirect vs. human absent categories. By comparing human presence categories to when humans are absent, negative values indicate lower species activity in the presence of associated human pressures. We used Kruskal-Wallis rank sum tests to determine if there were differences in activity among groups. If significant results emerged, we then used Mann-Whitney tests with the Hochberg correction of significance level adjustments to evaluate where differences occurred in pairwise combinations between human categories. We repeated this analysis at the taxonomic-level, expecting greatest consequences on carnivores. We also extended beyond the binary consideration of human pressure to evaluate whether intensity influenced mammal activity using mixed effects models (Supplementary Methods). All analyses were completed with packages ‘camtrapR’, ‘vegan’, ‘corrplot’, ‘ggpubr’, ‘nlme’, and ‘MuMIn’ in Program R.

3 | RESULTS

In the first camera survey for Burkina Faso and Niger, we recorded 8,506 independent detections of at least 36 wild mammal species across 13,223 trap nights (Table S1-S2). Ungulates and carnivores represented 72-85% and 7-17% of all mammal detections across surveys, respectively. Cheetah (*Acinonyx jubatus hecti*) was the rarest species in our survey. We documented an additional seven (sub)species of conservation concern including the critically endangered West African lion (*Panthera leo*) (Henschel et al., 2014, Table S3). Cheetah, leopard (*Panthera pardus*), and hippopotamus (*Hippopotamus amphibius*) were only detected at ARL and 95% of red-fronted gazelle (*Eudorcas rufifrons*) detections occurred at WNI.

We recorded 427 independent triggers of human and domestic animals (Figure 2, Table S1). Human pressure did vary across surveys with the highest occurring in WBK where 47% of cameras documented human activities ($\chi^2 = 199.3$, $df = 24$, $p < 0.0001$; Table S1, Figure S2). Theft represented another form of human pressure with 8% ($n = 12$ cameras) lost during our survey (ARL= 5, WBK = 3; WNI = 4). Consistent with our expectation, overall direct activities exceeded indirect within WAP (Trap success, TS =18.46 vs. 13.85; Figure 2, S2). However, the single most dominant human pressure was the indirect activity of production animals, livestock grazing and traversing (TS=12.33). Poaching (TS=3.63) was the least common direct activity while the most pervasive was gathering of forest products (TS=6.88).

Despite differences among human pressures, overall species diversity for mammals was not significantly reduced from either direct or indirect activities (Figure 3a). Similarly, community composition between human absent and present categories only differed for ARL₂₀₁₈ survey (Figure. 3b; ANOSIM R : 0.314, $p = 0.005$). We documented little evidence of dispersion when comparing variances with dissimilarity matrices between human absent and present groups across sites (Mean difference in median = 0.019, SE = 0.005). However, we observed the most pronounced effects of human pressures on avoidance behavior (Figure 3c). Overall, indirect activities corresponded to on average 17x fewer triggers when compared to direct activities (Table S3). Direct activities significantly reduced mammal activities only at ARL₂₀₁₇ (Mann-Whitney $U = 801.5$; $p < 0.001$); and at several sites, species activity was actually higher in comparison to locations where humans were not detected, suggesting some degree of coexistence (Table S3). Contrary to other surveys, all species exhibited reduced activity due to overall human pressure at ARL₂₀₁₇ (Figure S3).

General trends across taxonomic groups were consistent with reductions in activity due to human pressure from both direct and indirect activities (Figure 4). Surprisingly, ungulates were most sensitive to human pressure with on average 10x fewer triggers in association with indirect in comparison to direct activities. On average, carnivores had 5x fewer triggers at locations with indirect in comparison to direct activities. We also evaluated the effects of human intensity on mammal activity using a linear mixed-effort modeling approach (Supplementary Results, Table S4). The top model included the effects of direct activities (DIR_c) and taxonomy (TAX) on the behavior of mammals in our survey (Table 1). The effect of direct activities on species activity was small, slightly positive, and significant ($\beta = 0.0065$; $p\text{-value} < 0.00$). Activity for primates ($\beta = 0.743$; $p\text{-value} = 0.0231$) and ungulates ($\beta = 0.608$; $p\text{-value} = 0.0023$) was significantly higher in comparison to carnivores.

4 | DISCUSSION

Threats from hunting and agriculture continue to endanger mammals (Hoffmann et al., 2010). Benitez-Lopez et al. (2017) found that mammal abundances declined from hunting pressures inside protected areas in a global analysis. In Tanzania, hunting pressure best predicted mammal species richness (Jones, Hawes, Norton, & Hawkins, 2019). However, hunting pressure did not influence occupancy for carnivores in Ghana (Burton, Sam, Balangtaa, & Brashares, 2012). Despite poaching, gathering, herding and recreation accounting for 57% of human-related triggers in our survey, we documented little consequence for diversity, community composition, and behavior of mammals in WAP. Reliance on forest products was evident with the gathering of firewood, grasses, medicinal and edible plants, flowers, and fruits being the dominant direct activity (Figure 2, S2). As such, management practices that promote sustainable use of forest products and integrate

inclusive monitoring of socio-ecological processes will improve effectiveness of protected areas across beneficiaries and scales.

We found that indirect activities, namely livestock presence, were most influential on the activity of mammals. Conflict between food production and conservation has become of growing concern in securing a sustainable future due to land scarcity and increasing human demands (Crist, Mora, & Engelman, 2017). On private lands, the integration of livestock production and wildlife tourism seems feasible with positive implications of disease management and vegetation (Keesing et al., 2018). However, livestock grazing in protected areas may not harvest these benefits due to competition with wild ungulates (Odadi, Karachi, Abdulrazak, & Young, 2011). The significant reduction of triggers in ungulate species associated namely with indirect activities questions how effective protected areas will be at reducing threats to maintain ungulate populations in WAP in the future (Hoffmann et al., 2015). Furthermore, examining effects of livestock on predators is also necessary, given the displacement of natural prey can result in depredation and human-wildlife conflict (e.g., Kuiper et al., 2015).

We postulate that the variation observed in behavioral responses to human pressures across parks is due to some populations becoming more acclimated to increased human presence (Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015; Santini et al., 2019). Mammals at ARL₂₀₁₇, the least disturbed site (i.e., lowest % of triggers with humans), exhibited the greatest negative response to human pressure with lower activity observed across all 33 (sub) species detected. Interestingly, Arly National Park occurs in the western region of the complex surrounded by more hunting concessions and is geographically divided from the other national parks in our study. Among the most vulnerable, we expected carnivores to experience the greatest consequences from human pressure due to their trophic

level, low abundances and long gestation periods (Cardillo et al., 2004). We found that mesocarnivores such as jackal (*Canis* sp.) and civet (*Civettictis civetta*) were the most negatively affected by overall human activities as opposed to large-bodied carnivores species (Figure S3). However, we found that ungulates were the most sensitive group with all species negatively affected by human pressure, particularly indirect human activities (Table S3). We attribute this finding to the high prevalence of livestock pressure resulting in competitive exclusions. Given the multiple points of entry for herdsmen to traverse livestock across WAP, regulating impacts from livestock and mitigating detriment to wild mammals requires community engagement and transboundary cooperation across management authorities.

Our collaborative research leverages socio-ecological data garnered from a common monitoring technique to enhance management capacity, identify resource user agendas, and fill critical information gaps to promote coexistence and conservation practice at scale. As the first camera study in Burkina Faso and Niger, we documented extensive human activities with social benefits co-occurring within the fragile mammal community of West Africa. Human pressures varied across space and time; justifying annual monitoring, an integrative, adaptive management framework, and transboundary coordination. We were only able to capture consequences induced from livestock by discerning specific activities from our camera survey, which stresses the need to incorporate livestock husbandry in protected area management and the utility of aggregated approaches in decision-making and policy intervention (Ogada, Woodroffe, Oguge, & Frank, 2003; e.g., Galvez et al., 2018). Our findings constitute a crucial step in shifting the WAP complex from the singular and arguably outdated mandate of nature conservation to a more dynamic coupled human-natural ecosystem approach of sustainable, integrated management (Palomo et al., 2014).

ACKNOWLEDGEMENTS

We thank the AWE Lab especially R. Malhotra, S. Boerger, M. Lyons, S. Gamez, and G. Gadsden for image identification and data management as well as R. Hardin for comments on manuscript drafts. We extend our appreciation to the field staff and park managers that assisted with data collection and logistical support. We thank administrators in Ministries of Environment in Burkina Faso (OFINAP & DGEF) and Niger as well as private concessionaires throughout WAP for wildlife management efforts. We acknowledge University of Michigan (UM) African Studies Center- STEM initiative, UM Office of Research, and the Detroit Zoo for financial support.

REFERENCES

- Agha M., Batter T., Bolas E.C., Collins A.C., Gomes da Rocha D., Monteza-Moreno C.M., . . . Sollmann R. (2018). A review of wildlife camera trapping trends across Africa *African Journal of Ecology*, 56(694-701)
- Allan J.R., Watson J.E.M., Di Marco M., O'Bryan C.J., Possingham H.P., Atkinson S.C., & Venter O. (2019). Hotspots of human impact on threatened terrestrial vertebrates. *PLoS Biology*, 17(3), e3000158
- Asefi-Najafabady S., & Saatchi S. (2013). Response of African humid tropical forests to recent rainfall anomalies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1625)
- Baker D.J., Hartley A.J., Burgess N.D., Butchart S.H.M., Carr J.A., Smith R.J., . . . Willis S.G. (2015). Assessing climate change impacts for vertebrate fauna across the West African protected area network using regionally appropriate climate projections. *Diversity and Distributions*, 21(9), 991-1003
- Barnes M.D., Craigie I.D., Dudley N., & Hockings M. (2017). Understanding local-scale drivers of biodiversity outcomes in terrestrial protected areas *Annals of the New York Academy of Sciences*, 1399(42-60)
- Benitez-Lopez A., Alkemade R., Schipper A.M., Ingram D.J., Verweij P.A., Eikelboom J.A.J., & Huijbregts M.A.J. (2017). The impact of hunting on tropical mammal and bird populations. *Science*, 356(6334), 180-183
- Burton A.C., Sam M.K., Balangtaa C., & Brashares J.S. (2012). Hierarchical Multi-Species Modeling of Carnivore Responses to Hunting, Habitat and Prey in a West African Protected Area. *PLOS ONE*, 7(5)
- Buxton R.T., Lendrum P.E., Crooks K.R., & Wittemyer G. (2018). Pairing camera traps and acoustic recorders to monitor the ecological impact of human disturbance. *Global Ecology and Conservation*, 16(
- Cardillo M., Purvis A., Sechrest W., Gittleman J.L., Bielby J., & Mace G.M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biology*, 2(7), 909-914
- Crist E., Mora C., & Engelman R. (2017). The interaction of human population, food production, and biodiversity protection. *Science*, 356(6335), 260-264
- Galvez N., Guillera-Arroita G., St John F.A.V., Schuttler E., Macdonald D.W., & Davies Z.G. (2018). A spatially integrated framework for assessing socioecological drivers of carnivore decline. *Journal of Applied Ecology*, 55(3), 1393-1405
- Geldmann J., Joppa L.N., & Burgess N.D. (2014). Mapping Change in Human Pressure Globally on Land and within Protected Areas. *Conservation Biology*, 28(6), 1604-1616

- Henschel P., Coad L., Burton C., Chataigner B., Dunn A., MacDonald D., . . . Hunter L.T.B. (2014). The Lion in West Africa Is Critically Endangered. *PLOS ONE*, *9*(1), e83500
- Heubes J., Kühn I., König K., Wittig R., Zizka G., & Hahn K. (2011). Modelling biome shifts and tree cover change for 2050 in West Africa. *Journal of Biogeography*, *38*(12), 2248-2258
- Hoffmann M., Duckworth J.W., Holmes K., Mallon D.P., Rodrigues A.S.L., & Stuart S.N. (2015). The difference conservation makes to extinction risk of the world's ungulates. *Conservation Biology*, *29*(5), 1303-1313
- Hoffmann M., Hilton-Taylor C., Angulo A., Bohm M., Brooks T.M., Butchart S.H.M., . . . Stuart S.N. (2010). The Impact of Conservation on the Status of the World's Vertebrates. *Science*, *330*(6010), 1503-1509
- Hossain A.N.M., Barlow A., Barlow C.G., Lynam A.J., Chakma S., & Savini T. (2016). Assessing the efficacy of camera trapping as a tool for increasing detection rates of wildlife crime in tropical protected areas. *Biological Conservation*, *201*(314-319)
- Jones K.R., Venter O., Fuller R.A., Allan J.R., Maxwell S.L., Negret P.J., & Watson J.E.M. (2018). One-third of global protected land is under intense human pressure. *Science*, *360*(6390), 788-+
- Jones T., Hawes J.E., Norton G.W., & Hawkins D.M. (2019). Effect of protection status on mammal richness and abundance in Afromontane forests of the Udzungwa Mountains, Tanzania. *Biological Conservation*, *229*(78-84)
- Keesing F., Ostfeld R.S., Okanga S., Hockett S., Bayles B.R., Chaplin-Kramer R., . . . Allan B.F. (2018). Consequences of integrating livestock and wildlife in an African savanna. *Nature Sustainability*, *1*(10), 566-573
- Kuiper T.R., Loveridge A.J., Parker D.M., Johnson P.J., Hunt J.E., Stapelkamp B., . . . Macdonald D.W. (2015). Seasonal herding practices influence predation on domestic stock by African lions along a protected area boundary. *Biological Conservation*, *191*(546-554)
- Luiselli L., Dendi D., Eniang E.A., Fakae B.B., Akani G.C., & Fa J.E. (2019). State of knowledge of research in the Guinean forests of West Africa region. *Acta Oecologica-International Journal of Ecology*, *94*(3-11)
- Mantyka-pringle C.S., Martin T.G., & Rhodes J.R. (2012). Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, *18*(4), 1239-1252
- Mayaux P., Pekel J.-F., Desclée B., Donnay F., Lupi A., Achard F., . . . Belward A. (2013). State and evolution of the African rainforests between 1990 and 2010. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1625)
- Miller D.C., Minn M., & Sinsin B. (2015). The importance of national political context to the impacts of international conservation aid: evidence from the W National Parks of Benin and Niger. *Environmental Research Letters*, *10*(11), 115001
- Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B., & Kent J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853-858
- Naidoo R., Gerkey D., Hole D., Pfaff A., Ellis A.M., Golden C.D., . . . Fisher B. (2019). Evaluating the impacts of protected areas on human well-being across the developing world. *Science Advances*, *5*(4), eaav3006
- Naughton-Treves L., Holland M.B., & Brandon K. (2005). The role of protected areas in conserving biodiversity and sustaining local livelihoods *Annual Review of Environment and Resources*, *30*(1), 219-252
- Odadi W.O., Karachi M.K., Abdulrazak S.A., & Young T.P. (2011). African Wild Ungulates Compete with or Facilitate Cattle Depending on Season. *Science*, *333*(6050), 1753-1755
- Ogada M.O., Woodroffe R., Oguge N.O., & Frank L.G. (2003). Limiting Depredation by African Carnivores: the Role of Livestock Husbandry. *Conservation Biology*, *17*(6), 1521-1530

- Palomo I., Montes C., Martín-López B., González J.A., García-Llorente M., Alcorlo P., & Mora M.R.G. (2014). Incorporating the Social–Ecological Approach in Protected Areas in the Anthropocene. *Bioscience*, 64(3), 181-191
- Ripple W.J., Abernethy K., Betts M.G., Chapron G., Dirzo R., Galetti M., . . . Young H. (2016). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*, 3(10), 160498
- Samia D.S.M., Nakagawa S., Nomura F., Rangel T.F., & Blumstein D.T. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications*, 6(8877)
- Santini L., González-Suárez M., Russo D., Gonzalez-Voyer A., von Hardenberg A., & Ancillotto L. (2019). One strategy does not fit all: determinants of urban adaptation in mammals. *Ecology Letters*, 22(2), 365-376
- Schipper J., Chanson J.S., Chiozza F., Cox N.A., Hoffmann M., Katariya V., . . . Young B.E. (2008). The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science*, 322(5899), 225-230
- Schulze K., Knights K., Coad L., Geldmann J., Leverington F., Eassom A., . . . Burgess N.D. (2018). An assessment of threats to terrestrial protected areas. *Conservation Letters*, 11(3)
- Seto K.C., Guneralp B., & Hutyra L.R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences of the United States of America*, 109(40), 16083-16088
- Venter O., Fuller R.A., Segan D.B., Carwardine J., Brooks T., Butchart S.H.M., . . . Watson J.E.M. (2014). Targeting Global Protected Area Expansion for Imperiled Biodiversity. *PLoS Biology*, 12(6), e1001891
- Venter O., Sanderson E.W., Magrach A., Allan J.R., Beher J., Jones K.R., . . . Watson J.E.M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, 7(12558)
- Watson J.E.M., Dudley N., Segan D.B., & Hockings M. (2014). The performance and potential of protected areas. *Nature*, 515(7525), 67-73

Table 1 Parameter estimates of top model from linear mixed effect models to determine factors influencing mammal activity, as the log of mammal triggers in WAP complex, West Africa (Table S4). DIR_c = total triggers of direct human activities; and TAX = taxonomy as a factor variable including CARN = carnivores, PRIM = primates, ROD+ = small mammals, and UNG = ungulates.

Parameter	Estimate	SE	df	t-value	p
Intercept	0.8033	0.1383	122	5.8068	<0.0001
DIR_c	0.0065	0.0018	122	3.6904	0.0003
TAX_PRIM	0.7434	0.3111	31	2.3902	0.0231
TAX_ROD+	-0.1293	0.3136	31	-0.4122	0.6830
TAX_UNG	0.6081	0.1831	31	3.3216	0.0023

Figure Legends

Figure 1 W-Arly-Pendjari (WAP), the largest transboundary protected area complex in West Africa. Study area included: Arly National Park, Park W- Burkina Faso, and Park W- Niger with camera locations depicting survey design for 2017 (see Supplementary Methods).

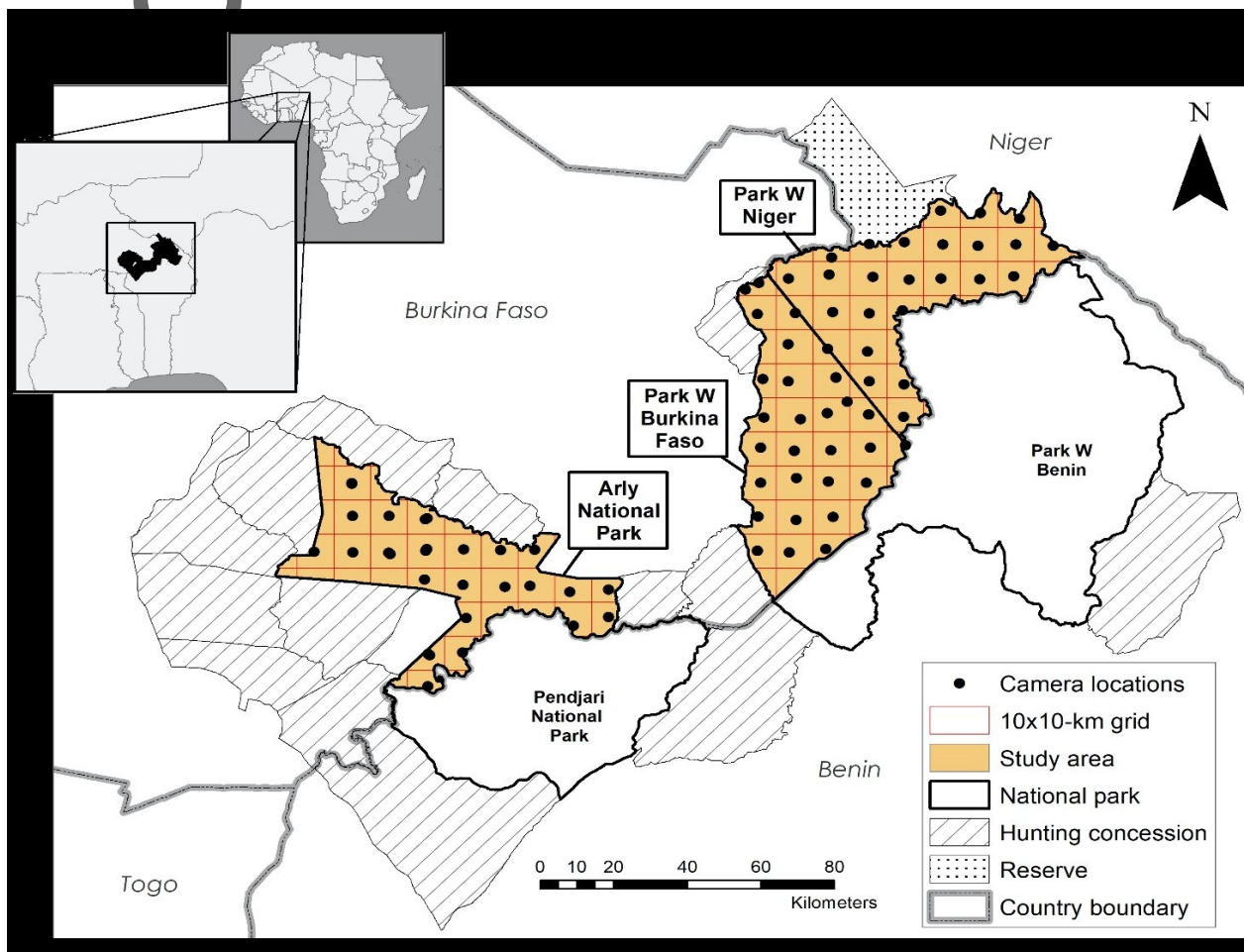
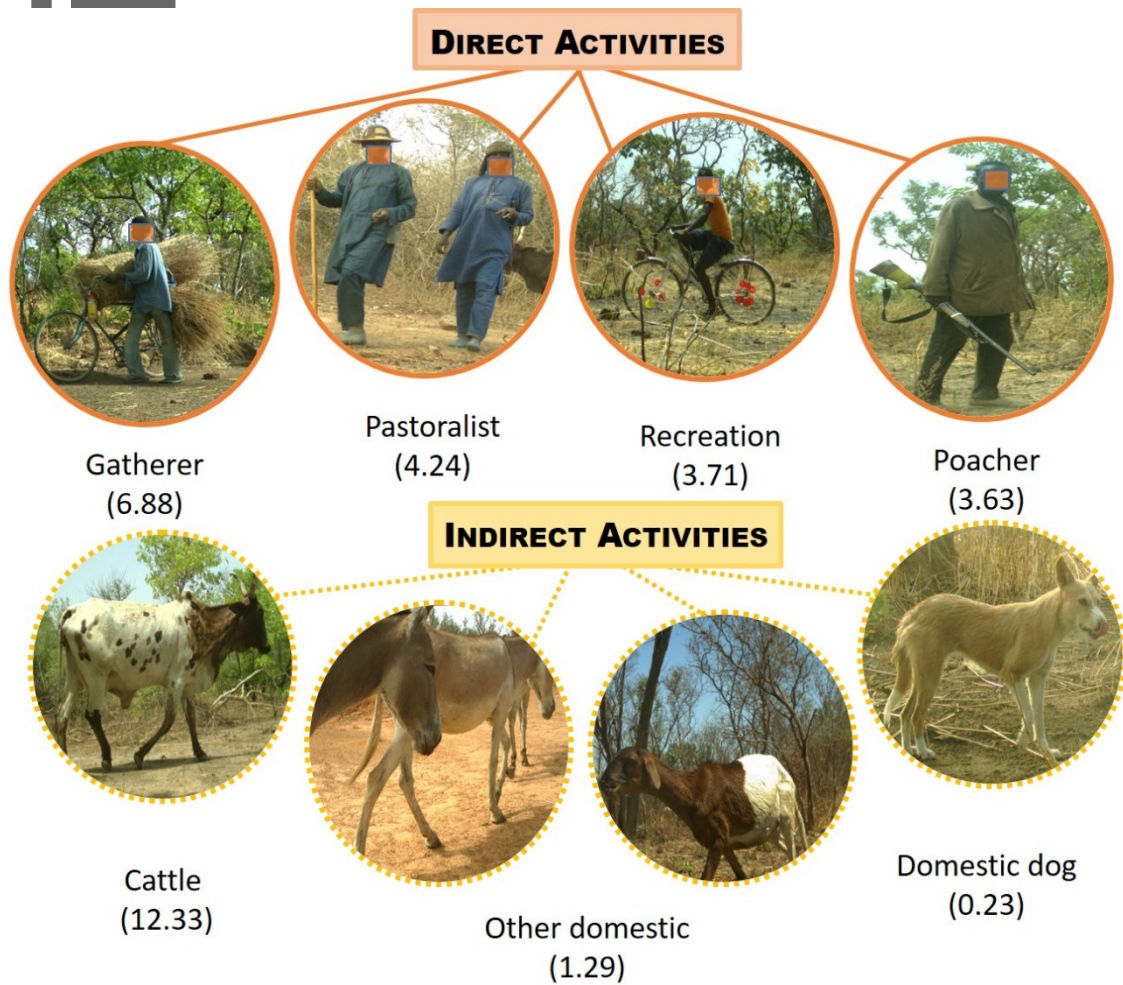


Figure 2 Human pressures detected in WAP complex during 2016-2018 camera survey including direct and indirect activities. Trap success provided in parenthesis based on 13,223 trap nights.



Auth

Figure 3 Effects of human pressures categories (absent, direct activities, and indirect activities) on mammal community metrics in WAP complex. **A)** Species diversity – sample size too small for error bar in ARL18 survey. **B)** Community composition – distinction in community similarity between sites with and without humans detected. ARL17 is representative of other surveys not shown. **C)** Species behavior – triggers with a 30-minute quiet period to index activity. Mann-Whitney test for pairwise comparisons between human categories with significance codes: ‘****’ < 0.0001 ‘***’ < 0.001 ‘**’ < 0.01 ‘*’ < 0.05. Error bars represent SE.

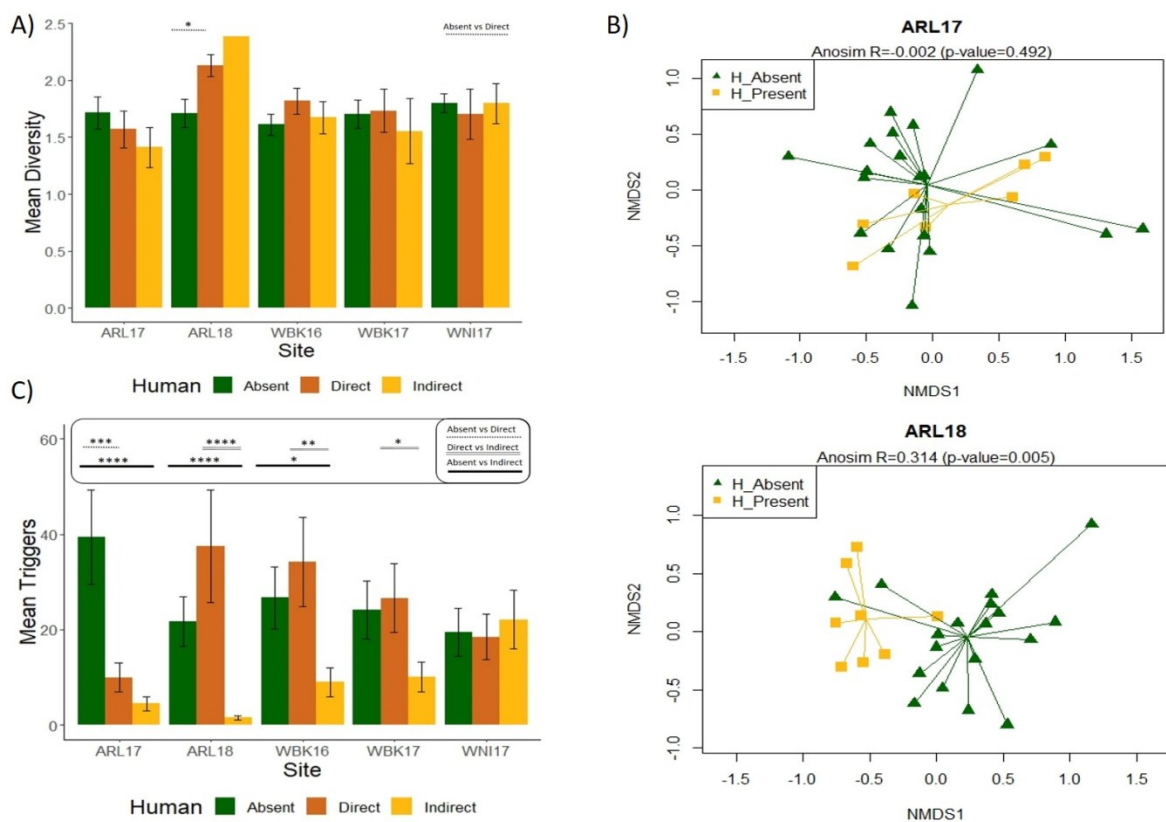


Figure 4 Variation in mammal activity by taxonomic groups for indirect (IND) and direct (DIR) human activities compared to locations where humans were not detected across surveys in WAP complex (ARL: Arly National Park, Burkina Faso; WBK: Park W-Burkina Faso; WNI: Park W- Niger). Activity defined as species triggers with a 30-minute quiet period obtained from camera survey in 2016-2018. Negative values indicate reduced activity in association with human pressure. Asterisks indicate significant differences between categories using Mann Whitney U tests ($p < 0.05$).

