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Physiological correlates of social and anthropogenic stressors in mountain gorillas *(Gorilla beringei beringei)*

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ABSTRACT: Protected areas are a cornerstone of conservation, yet are often embedded within densely populated human landscapes. As a result, wildlife within their borders remains vulnerable to anthropogenic disturbance, in addition to density-dependent challenges due to population crowding. Both processes can elevate physiological stress, with potential consequences for individual health, fitness, and survival, as well as population persistence. Endangered mountain gorillas *(Gorilla beringei beringei)* in Volcanoes National Park, Rwanda, exemplify these pressures. They are at risk of entrapment in snares set by proximal human communities hunting other species for subsistence, and are experiencing more frequent intergroup encounters as their population grows within a confined habitat. Using non-invasive monitoring of faecal glucocorticoid metabolites (fGCMs), we investigated how snare and intergroup encounters influence stress physiology in mountain gorillas. Between 2022-2024, we collected 2,059 faecal samples from adult individuals across eight social groups and quantified fGCM concentrations using cortisol enzyme-linked immunosorbent assays. We then applied generalised linear mixed models to compare fGCM concentrations following encounters to baseline values. We found that intergroup encounters were associated with greater fGCMs among each adult age-sex class. Specifically, silverbacks exhibited a baseline fGCM concentration of 4.71 ± 2.41ng/g, which increased to 7.22 ± 4.07ng/g following IGEs (χ^2=35.98, df=1, p<0.001). Adult females had slightly higher baseline concentrations, at 4.85 ± 2.38ng/g, which similarly increased to 7.34 ± 4.58ng/g (χ^2=50.18, df=1, p<0.001), and although blackback fGCMs rose from the baseline of 4.51 ± 2.20ng/g to 6.44 ± 4.59ng/g following encounters, this effect was weaker and only approached statistical significance (χ^2=3.35, df=1, p=0.07). Conversely, snare encounters were only associated with elevated fGCM concentrations among silverbacks, increasing from the baseline concentration of 5.43 ± 2.70ng/g to 7.02 ± 3.22ng/g post-event (χ^2=11.81, df=1, p<0.001). Although blackback fGCMs also increased in response to snare encounters, from 5.21 ± 2.57ng/g to 7.90 ± 4.33ng/g, we did not detect a significant change (χ^2=0.41, df=1, p=0.52). Finally, adult female fGCMs were slightly lower following snare encounters: 5.40 ± 2.40ng/g compared to baseline: 5.44 ± 2.58ng/g, albeit not significantly (χ^2=2.21, df=1, p=0.14). These findings suggest that both snare and intergroup encounters can activate the physiological stress response in mountain gorillas. These events likely represent acute stressors, and are associated with threats including injuries and mortality. Therefore, heightened physiological stress may be adaptive, facilitating changes that improve chances of survival, including enhancing vigilance and rapidly mobilising energy needed to cope with snares or compete against other groups. Elevated fGCMs may further reflect the greater energetic demands

associated with subsequence avoidance behaviours. Given the rapid pace and scale of anthropogenic change, this study highlights the value of non-invasive hormonal monitoring for understanding how different stressors affect threatened populations. Our results can also inform conservation strategies to safeguard mountain gorilla health and survival. Integrating physiological monitoring with indicators of fitness and health, alongside efforts that reduce community reliance on park resources and expand available habitat, will be critical for the long-term conservation of this population.

1. INTRODUCTION

Human activities are driving rapid, large-scale, and unpredictable environmental changes that are increasingly affecting primates, including the Virunga population of mountain gorillas *(Gorilla beringei beringei)* in Volcanoes National Park (VNP), Rwanda[1-3]. Mountain gorillas are exposed to substantial pressures arising from high-density human populations surrounding VNP who hunting using snares for subsistence[4]. Although intended for other species, the indiscriminate nature of snares poses a threat to gorillas which can suffer injuries and mortality due to accidental entrapment[5]. Furthermore, the space-restricted growth of the Virunga population within the confines of VNP is exacerbating social stressors, and has led to a sixfold increase in the frequency of intergroup encounters (IGEs)[6-8]. In mountain gorillas, IGEs are predominantly driven by mate-defence and are often aggressive, resulting in severe injuries or death of silverbacks and dependent infants[9,10].

Understanding how anthropogenic pressures shape physiological stress has become increasingly important[11]. The physiological stress response is a proximate mechanism by which exposure to unpredictable and aversive stimuli activates the hypothalamic-pituitary-adrenal (HPA) axis and triggers a neuroendocrine cascade that culminates in the secretion and systemic elevation of glucocorticoids (GCs)[12,13]. GCs are a group of steroid hormones, including cortisol, that elicit a suite of behavioural and physiological changes promoting survival[11,12]. Although this response is normally adaptive, chronically elevated GCs may lead to HPA dysregulation, ultimately compromising the fitness and survival of wild species[12].

Methodological advances in measuring faecal GC metabolites (fGCMs) have enabled researchers to quantify physiological stress in wild primates[13,14]. Studies have shown that human activities including logging[15], hunting[15,16], direct disturbance[17,18], exposure to domestic animals[16], human-primate conflicts[19,20], and inhabiting fragmented or unprotected landscapes[17,19-21] are associated with elevated fGCMs. Furthermore, by intensifying competition over limited space and resources, and enhancing the rate of IGEs, habitat modification can amplify physiological stress indirectly[22-25]. However, some species show greater sensitivity and others greater tolerance to human activities[15] and IGEs[26], underscoring the need for context and species-specific studies.

The prevalence of both snare and intergroup encounters is increasing within VNP[4,7]. Therefore, the main goal of this study was to assess how these anthropogenic and social pressures impact stress physiology in mountain gorillas. Given that detrimental human activities including hunting are associated with physiological stress in other primates[14-16], we predicted that snare encounters would elevate fGCM concentrations *(P1).* As IGEs can be highly aggressive, unpredictable, and result in reproductive challenges, injuries, or mortality[9,10] we predicted that IGEs would also increase fGCM concentrations *(P2).* Monitoring the physiology of mountain gorillas will shed light on their ability to cope with increasingly complex challenges and inform conservation strategies.

2. METHODS

2.1 Study Site and Subjects

We conducted our study in VNP, Rwanda, a 160km^2 area that spans a steep altitudinal gradient (2,400-4,500m) with distinct vegetation zones including bamboo forest (<2,800m), Afromontane forest (2,800-3,300m), and Afroalpine vegetation (>3,300m)[6,7,27]. VNP experiences moderate temperatures (4-32°C), and receives 1,500-2,500mm of bimodally distributed rainfall annually[28]. We studied eight groups of the research subpopulation of habituated Virunga mountain gorillas in VNP (1°210-1°350S, 29°22-29°440E), that have been studied by the Dian Fossey Gorilla Fund (hereafter, Fossey Fund) since 1967.

2.2 Data Collection

All data and samples were collected between January 2022 and August 2024 by Fossey Fund field staff and authors LWJ, DI, and WE. Research activities in VNP were typically conducted between 7:00 to 14:00, in compliance with government regulations aimed at minimising anthropogenic disturbance.

2.2.1 Stressor Data Collection: We collected data on stressors systematically during group observation and tracking. For IGEs, we recorded both auditory and visual encounters between groups and between groups and solitary silverbacks (N=49). Although the majority of IGEs were observed directly (N=41), interactions inferred from indirect but reliable field evidence (including interaction sites containing trampled vegetation and biological materials such as hair, blood, or diarrhoea) were also incorporated into the analyses (N=8).

Snare encounters (N=23) were confirmed when behaviours performed by gorillas indicated detection, including inspection or dismantling of the snare, aggression, displays, or vocalisations directed towards conspecifics in the vicinity of the snare, and abrupt changes in travel direction. Most snare encounters were also observed directly while following groups (N=16), although we inferred unobserved encounters when snares were set within 10m of the group's trail (N=7).

2.2.2 Faecal Sample Collection: All samples were collected non-invasively following established protocols[8,29]. Upon defecation, we waited for the individual to move away before retrieving uncontaminated samples using a glove. We labelled each sample with the date, time of collection, and the individual's identification and group code, and transported them to Fossey Fund's endocrinology laboratory at the Ellen DeGeneres Campus in Rwanda, where they were stored at -20°C. We collected all samples from involved individuals for five consecutive days following intergroup (N=265) and snare (N=122) encounters. To establish baseline fGCM concentrations, we aimed to collect one sample per individual per week when no known stressful event had occurred, which we defined as the period before an intergroup or snare encounter and ≥6 days after (N=1,672). To control for potential stressful events that we did not observe, we applied an iterative process in which baseline samples exceeding the mean + 1.5 standard deviation (SD) were excluded for each individual, and repeated until all remaining samples were equal to or less than the mean + 1.5 SD[29]. This process resulted in N=1,186 baseline samples used in the analyses.

2.3 Hormone Extraction and Laboratory Analysis

All sample processing and analyses were conducted at Fossey Fund's endocrinology laboratory. Hormone extractions were performed by trained technicians (authors RU and CU) ~2-3 months after samples were collected using an ethanol-based protocol[29]. Following extraction, samples were dried down, capped, and stored at -20°C until being reconstituted in assay buffer following established protocols[29] prior to analysis. Trained personnel (including authors RU, CU, SR, and LWJ) then quantified fGCM concentrations using a commercially available cortisol enzyme-linked immunosorbent assay (ELISA; ISWE Cortisol, Arbor Assays, Ann Arbor, MI) previously validated for use in the Virunga population[30].

2.4 Statistical Analysis

2.4.1 Model Design and Validation: We analysed the effects of snare and intergroup encounters on mountain gorilla physiology by constructing generalised linear mixed models (GLMMs) implemented in R[31]. We fitted each model with a gamma family and log link, and included a range of covariates known to influence mountain gorilla fGCMs, including age, season, habitat type, weather, group size, and female reproductive stage[8]. We assessed the significance of predictor variables by comparing the full model to a reduced model that excluded only the fixed effect of interest using likelihood ratio tests, and visually inspected residual plots to ensure model assumptions were not violated.

2.4.2 Model Implementation: To test the effect of snare encounters on physiology, we fitted GLMMs for silverbacks (Model 1), adult females (Model 2), and blackbacks (Model 3), with fGCM concentration as the response variable and sample type *(baseline* or *snare)* as a fixed categorical effect. We also included group (N=6) and individual (N=46) identity as random effects to account for repeated sampling of the same study groups and gorillas. To examine the effect of IGEs, we fitted GLMMs with fGCM concentration as the response variable and sample type *(baseline* or *IGE)* as a fixed categorical effect. We also constructed separate models for silverbacks (Model 4), adult females (Model 5), and blackbacks (Model 6), and included group (N=8) and individual (N=65) identity as random effects.

3. RESULTS

3.1 Changes in fGCMs Following Snare Encounters (Models 1-3)

Snare encounters were only associated with elevated fGCM concentrations among silverbacks. Across all groups and individuals, fGCMs increased slightly from the mean ± SD baseline concentration of 5.41 ± 2.62ng/g to 6.16 ± 3.34ng/g following snare encounters. fGCMs in silverbacks significantly increased from the baseline concentration of 5.43 ± 2.70ng/g to 7.02 ± 3.22ng/g following encounters (χ^2=11.81, df=1, p<0.001), and although blackback fGCMs also increased in response to these events, from 5.21 ± 2.57ng/g to 7.90 ± 4.33ng/g, a significant change was not detected (χ^2=0.41, df=1, p=0.52). Adult female fGCMs were slightly lower following snare encounters: 5.40 ± 2.40ng/g compared to baseline: 5.44 ± 2.58ng/g, albeit not significantly (χ^2=2.21, df=1, p=0.14).

3.2 Changes in fGCMs Following IGEs (Models 4-6)

IGEs were also associated with elevated fGCM concentrations. Among all groups and individuals, fGCMs increased from the mean ± SD baseline concentration of 4.77 ± 2.37ng/g to 7.24 ± 4.41ng/g following IGEs, and this relationship remained consistent across age-sex classes. Silverbacks exhibited a baseline fGCM concentration of 4.71 ± 2.41ng/g, which increased to 7.22 ± 4.07ng/g following IGEs (χ^2=35.98, df=1, p<0.001). Adult females had slightly higher baseline concentrations, at 4.85 ± 2.38ng/g, which similarly increased to 7.34 ± 4.58ng/g in response to IGEs (χ^2=50.18, df=1, p<0.001). Blackback fGCMs likewise rose from the baseline of 4.51 ± 2.20ng/g to 6.44 ± 4.59ng/g following encounters, although this effect was weaker and only approached statistical significance (χ^2=3.35, df=1, p=0.07).

4. DISCUSSION

4.1 Snares and Physiological Stress

We found partial support for snare encounters resulting in physiological stress *(P1)* because silverbacks, but not adult females, exhibited greater fGCM concentrations following these events. Blackbacks also had greater fGCMs which, although not statistically significant, may be biologically meaningful, nonetheless. Snare encounters may constitute an acute stressor because gorillas recognise the dangers they pose, including entrapment and injuries[32]. The stress response may be enhanced in silverbacks who often display behaviours which may heighten psychological and energetic demands, including dismantling snares and alerting other gorillas to their presence through warning vocalisations or aggressive displays[32]. The absence of an analogous relationship in females may reflect several factors. Firstly, despite our efforts, it was not possible to collect samples from all individuals for five consecutive days after encounters, and greater sampling coverage may be necessary to detect a signal. Secondly, encounters may not trigger the physiological stress response, either because gorillas do not consider them a major threat, or they have become habituated to their stimulus. Finally, groups avoid areas affected by snaring[33] which may be sufficient to deal with anthropogenic stressors such that mounting a stress response is not warranted. To our knowledge, no other studies have tested the effects of snare encounters on physiological stress, limiting direct comparisons. However, direct and indirect hunting is a major driver of physiological stress in primates[15,16] and other mammals[34,35] because GC secretion may mobilise energy and enhance vigilance, allowing individuals to survive the associated lethal and unpredictable threats[14,35].

4.2 IGEs and Physiological Stress

Social stressors also affected physiological stress, and silverbacks, adult females, and blackbacks had greater fGCM concentrations following IGEs, supporting *P2.* Our findings align with studies on other primates which demonstrate comparable GC increases in response to IGEs[22-25,29]. IGEs likely elicit physiological stress via multiple mechanisms. First, elevated GC secretion is adaptive during intergroup conflict, enhancing vigilance and facilitating the rapid production of energy needed to compete[22,25]. This response is particularly important among silverbacks, the main participating demographic, who can incur substantial costs including severe injuries and fatality, or loss of current (through infanticide) or future (through loss of intragroup females to extragroup males) reproductive opportunities[9,10,29]. In addition, IGEs can be energetically demanding, especially if they involve physical fights and threat displays, and the resulting metabolic load could also elevate fGCMs[24]. Consistent with an energetic explanation, groups have longer daily travel distances following interactions[36], and the associated physical exertion could contribute to heightened fGCMs not only in silverbacks, but also adult females and blackbacks, who rarely engage directly in IGEs[10].

4.3 Conclusions

Understanding how anthropogenic stressors and associated impacts on social dynamics affect the physiology of wildlife is critical as human activities and habitat modification intensifies worldwide[1-3]. Although more data are needed to draw firm conclusions, our findings indicate that both intergroup and snare encounters are associated with physiological stress in mountain gorillas, with responses varying across age-sex classes. This study highlights the value of non-invasive hormonal monitoring for understanding how different stressors affect threatened populations. It also informs potential conservation strategies to safeguard population health and viability[8,29]; as population recovery[7] and illegal activities[4] increase within VNP, prolonged and cumulative exposure to stressors may impact the reproduction, health, and ultimately survival of mountain gorillas[8]. Therefore, integrating stress physiology monitoring with direct or proxy indicators of fitness is essential for assessing the long-term effects of stressor exposure[12,14]. Monitoring additional biomarkers, including thyroid hormones, will further enhance our understanding of the energetic consequences of intergroup and snare encounters, and remains an ongoing component of our research. Equally important is addressing the needs of communities bordering VNP to reduce their reliance on protected park resources[4], and expanding VNP to facilitate the viable growth of this space-restricted population.

5. BUDGET

We used the PSGB Research Grant funds (£1,247.40) to partially cover the costs of the laboratory hormone analyses. Specifically, we purchased supplies for the cortisol ELISA, including an ISWE cortisol mini-kit from Arbor Assays (catalogue no. ISWE002; Ann Arbor, MI) for $499.50 (£372.55). We used the remaining funds, $1,172.98 (£874.85) to purchase approximately 23 goat anti-rabbit IgC coated 96 well plates from Arbor Assays (catalogue no. X016-1EA; Ann Arbor, MI, $52.32 per plate). Together, these supplies enabled us to measure the fGCM concentrations of approximately 897 faecal samples.

6. REFERENCES

1. Almeida-Rocha, J. M. D., Peres, C. A., & Oliveira, L. C. (2017). Primate responses to Anthropogenic habitat disturbance: A pantropical meta-analysis. *Biological Conservation*, *215*, 30–38. https://doi.org/10.1016/j.biocon.2017.08.018
2. Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K. A.-I., Nijman, V., Heymann, E. W., Lambert, J. E., Rovero, F., Barelli, C., Setchell, J. M., Gillespie, T. R., Mittermeier, R. A., Arregoitia, L. V., De Guinea, M., Gouveia, S., Dobrovolski, R., … Li, B. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1), e1600946. https://doi.org/10.1126/sciadv.1600946
3. Torres-Romero, E. J., Nijman, V., Fernández, D., & Eppley, T. M. (2023). Human-modified landscapes driving the global primate extinction crisis. *Global Change Biology*, 29, 5775–5787. https://doi.org/10.1111/gcb.16902
4. Tolbert, S., Munyarugero, I., Uwingeli, P., & Ndagijimana, F. (2023). Assessing the drivers of illegal resource use to improve wildlife conservation interventions. *Biological Conservation*, *281*, 109983. https://doi.org/10.1016/j.biocon.2023.109983
5. Haggblade, M. K., Smith, W. A., Noheri, J. B., Usanase, C., Mudakikwa, A., Cranfield, M. R., & Gilardi, K. V. K. (2019). Outcomes of snare-related injuries to endangered mountain gorillas *(Gorilla beringei beringei)* in Rwanda. *Journal of wildlife diseases*, *55*(2), 298–303. https://doi.org/10.7589/2018-01-008
6. Caillaud, D., Ndagijimana, F., Giarrusso, A. J., Vecellio, V., & Stoinski, T. S. (2014). Mountain gorilla ranging patterns: Influence of group size and group dynamics. *American Journal of Primatology*, *76*(8), 730–746. https://doi.org/10.1002/ajp.22265
7. Caillaud, D., Eckardt, W., Vecellio, V., Ndagijimana, F., Mucyo, J.-P., Hirwa, J.-P., & Stoinski, T. (2020). Violent encounters between social units hinder the growth of a high-density mountain gorilla population. *Science Advances*, *6*(45), eaba0724. https://doi.org/10.1126/sciadv.aba0724
8. Eckardt, W., Stoinski, T. S., Rosenbaum, S., & Santymire, R. (2019). Social and ecological factors alter stress physiology of Virunga mountain gorillas *(Gorilla beringei beringei)*. *Ecology and Evolution*, *9*(9), 5248–5259. https://doi.org/10.1002/ece3.5115
9. Robbins, M. M., & Sawyer, S. C. (2007). Intergroup Encounters in Mountain Gorillas of Bwindi Impenetrable National Park, Uganda. *Behaviour*, *144*(12,), 1497–1519.
10. Rosenbaum, S., Vecellio, V., & Stoinski, T. (2016). Observations of severe and lethal coalitionary attacks in wild mountain gorillas. *Scientific Reports*, *6*(1), 37018. https://doi.org/10.1038/srep37018
11. Mirante, D., Santini, L., Costantini, D., & Benítez-López, A. (2025). Glucocorticoid responses of wildlife to anthropogenic stressors are influenced by disturbance type and species traits. *Functional Ecology*, *39*(3), 681–697. https://doi.org/10.1111/1365-2435.14741
12. Beehner, J. C., & Bergman, T. J. (2017). The next step for stress research in primates: To identify relationships between glucocorticoid secretion and fitness. *Hormones and Behavior*, *91*, 68–83. https://doi.org/10.1016/j.yhbeh.2017.03.003
13. Behringer, V., & Deschner, T. (2017). Non-invasive monitoring of physiological markers in primates. *Hormones and Behavior*, *91*, 3–18. https://doi.org/10.1016/j.yhbeh.2017.02.001
14. Kaisin, O., Fuzessy, L., Poncin, P., Brotcorne, F., & Culot, L. (2021). A meta-analysis of anthropogenic impacts on physiological stress in wild primates. *Conservation Biology*, *35*(1), 101–114. https://doi.org/10.1111/cobi.13656

15. Rimbach, R., Link, A., Heistermann, M., Gomez-Posada, C., Galvis, N., & Heymann, E. W. (2013). Effects of logging, hunting, and forest fragment size on physiological stress levels of two sympatric ateline primates in Colombia. *Conservation Physiology*, *1*(1), cot031–cot031. https://doi.org/10.1093/conphys/cot031
16. Rangel-Negrín, A., Coyohua-Fuentes, A., Chavira, R., Canales-Espinosa, D., & Dias, P. A. D. (2014). Primates Living Outside Protected Habitats Are More Stressed: The Case of Black Howler Monkeys in the Yucatán Peninsula. *PLoS ONE*, *9*(11), e112329. https://doi.org/10.1371/journal.pone.0112329
17. Vanlangendonck, N., Nuñez, G., Chaves, A., and Gutiérrez-Espeleta, G.A. (2015). New Route of Investigation for Understanding the Impact of Human Activities on the Physiology of Non-Human Primates. *Journal of Primatology*, *04*(01). https://doi.org/10.4172/2167-6801.1000123
18. Cañadas Santiago, S., Dias, P. A. D., Garau, S., Coyohua Fuentes, A., Chavira Ramírez, D. R., Canales Espinosa, D., & Rangel Negrín, A. (2020). Behavioral and physiological stress responses to local spatial disturbance and human activities by howler monkeys at Los Tuxtlas, Mexico. *Animal Conservation*, *23*(3), 297–306. https://doi.org/10.1111/acv.12541
19. Carlitz, E. H. D., Miller, R., Kirschbaum, C., Gao, W., Hänni, D. C., & Van Schaik, C. P. (2016). Measuring Hair Cortisol Concentrations to Assess the Effect of Anthropogenic Impacts on Wild Chimpanzees *(Pan troglodytes)*. *PLOS ONE*, *11*(4), e0151870. https://doi.org/10.1371/journal.pone.0151870
20. McLennan, M. R., Howell, C. P., Bardi, M., & Heistermann, M. (2019). Are human-dominated landscapes stressful for wild chimpanzees *(Pan troglodytes)? Biological Conservation*, *233*, 73–82. https://doi.org/10.1016/j.biocon.2019.02.028
21. Kaisin, O., Amaral, R. G., Bufalo, F., Sabino, G. P., Palme, R., Poncin, P., Rezende, G. C., Brotcorne, F., & Culot, L. (2025). Lower Habitat Quality Increases Physiological Stress in an Endangered Neotropical Primate. *Animal Conservation*, *28*(5), 619–630. https://doi.org/10.1111/acv.70003
22. Schoof, V. A. M., & Jack, K. M. (2013). The Association of Intergroup Encounters, Dominance Status, and Fecal Androgen and Glucocorticoid Profiles in Wild Male White-Faced Capuchins *(Cebus capucinus)*. *American Journal of Primatology*, *75*(2), 107–115. https://doi.org/10.1002/ajp.22089
23. Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Deschner, T., & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nature Communications*, *7*(1), 13361. https://doi.org/10.1038/ncomms13361
24. Jaeggi, A. V., Trumble, B. C., & Brown, M. (2018). Group-level competition influences urinary steroid hormones among wild red–tailed monkeys, indicating energetic costs. *American Journal of Primatology*, *80*(5), e22757. https://doi.org/10.1002/ajp.22757
25. Samuni, L., Preis, A., Deschner, T., Wittig, R. M., & Crockford, C. (2019). Cortisol and oxytocin show independent activity during chimpanzee intergroup conflict. *Psychoneuroendocrinology*, *104*, 165–173. https://doi.org/10.1016/j.psyneuen.2019.02.007
26. Huck, M., Löttker, P., Heymann, E. W., & Heistermann, M. (2005). Characterization and Social Correlates of Fecal Testosterone and Cortisol Excretion in Wild Male Saguinus mystax. *International Journal of Primatology*, *26*(1), 159–179. https://doi.org/10.1007/s10764-005-0728-8
27. McNeilage A. (2001) Diet and habitat use of two mountain gorilla groups in contrasting habitats in the Virungas. In: Robbins MM, Sicotte P, Stewart KJ, editors. Mountain gorillas: three decades of research at Karisoke. Cambridge: Cambridge University

Press; 2001. p. 265–92.
28. Grueter, C. C., Deschner, T., Behringer, V., Fawcett, K., & Robbins, M. M. (2014). Socioecological correlates of energy balance using urinary C-peptide measurements in wild female mountain gorillas. *Physiology & Behavior*, *127*, 13–19. https://doi.org/10.1016/j.physbeh.2014.01.009
29. Eckardt, W., Stoinski, T. S., Rosenbaum, S., Umuhoza, M. R., and Santymire, R. (2016). Validating faecal glucocorticoid metabolite analysis in the Virunga mountain gorilla using a natural biological stressor. *Conservation Physiology*, *4*(1), cow029. https://doi.org/10.1093/conphys/cow029
30. Grebe, N. M., Eckardt, W., Stoinski, T. S., Umuhoza, R., Santymire, R. M., & Rosenbaum, S. (2023). An empirical comparison of several commercial enzyme immunoassays for the non-invasive assessment of adrenocortical and gonadal function in mountain gorillas. *General and Comparative Endocrinology*, *342*, 114351. https://doi.org/10.1016/j.ygcen.2023.114351
31. R Core Team (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/
32. Williamson, E. A. (2005). *Snare Aware Mountain Gorillas*. Gorilla Gazette, 18(1), p. 8.
33. Wiseman-Jones, L. M., Ishimwe, D., Eckardt, W., Stoinski, T. S., & Milich, K. M. (2026). Flexible changes in mountain gorilla *(Gorilla beringei beringei)* ranging patterns in response to snare encounters. *Global Ecology and Conservation*, *65*, e04046. https://doi.org/10.1016/j.gecco.2025.e04046
34. Gobush, K. S., Mutayoba, B. M., & Wasser, S. K. (2008). Long-Term Impacts of Poaching on Relatedness, Stress Physiology, and Reproductive Output of Adult Female African Elephants. *Conservation Biology*, *22*(6), 1590–1599. https://doi.org/10.1111/j.1523-1739.2008.01035.x
35. Bryan, H. M., Smits, J. E. G., Koren, L., Paquet, P. C., Wynne-Edwards, K. E., & Musiani, M. (2015). Heavily hunted wolves have higher stress and reproductive steroids than wolves with lower hunting pressure. *Functional Ecology*, *29*(3), 347–356. https://doi.org/10.1111/1365-2435.12354
36. Wiseman-Jones *et al.* in preparation.