Insights from a 30-year study demonstrate an inverse correlation between recreational activities and red deer fecundity, with bodyweight as a mediator

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Abstract

Human activity is omnipresent in our landscapes. Animals can perceive risk from humans similar to predation risk, which could affect their fitness. We assessed the influence of recreation on bodyweight and pregnancy rates of red deer (Cervus elaphus) between 1985 and 2015. We hypothesized that stress, as a result of recreational activities, affects pregnancy rates of red deer directly and indirectly via a reduction in bodyweight. Furthermore, we expected non-motorized recreational activities to have a larger negative effect on both bodyweight and fecundity, compared to motorized recreational activities. The intensity of recreational activities was recorded through visual observations. We obtained pregnancy data from female red deer that were shot during the regular hunting season. Additionally, age and bodyweight were determined through post-mortem examination. We used two Generalized-Linear-Mixed Models (GLMM) to test the effect of different types of recreation on 1) pregnancy rates and 2) bodyweight of red deer. Recreation had a direct negative correlation with the fecundity of red deer, with bodyweight as a mediator as expected. Besides, we found a negative effect of non-motorized recreation on fecundity and bodyweight and no significant effect of motorized recreation. Our results support the concept of humans as a 'super predator' affecting wild animal populations at a population level and plead to regulate recreational activities in protected areas that are sensitive. The fear humans induce in large-bodied herbivores and its consequences for fitness may have strong implications for animal populations and the regeneration, structure and composition of forests and related fauna.

Materials and methods

Study site

The Veluwe area (1250 km^2) is designated as a protected area (i.e., Natura 2000) in the Netherlands (52° 5' N, 5deg 48' E) (Fig. 2). It has a temperate maritime climate and its geology mainly consists of ice-pushed ridges, fluvioglacial deposits and wind-blown sands. The area is elevated 50-100m above sea-level, holding a large freshwater aquifer. Dry coniferous forest (i.e., mainly Scots pine (*Pinus silvestris*)), deciduous forest (i.e., mainly oak (*Quercus sp.*) and beech (*Fagus sp.*)) make up the majority of the habitat, interspersed with dry to moist heathland, containing common heather (*Calluna vulgaris*) and grasses (Ten Houte de Lange, 1977). Apart from red deer, three other ungulate species occur on the Veluwe, namely: wild boar (*Sus scrofa*), fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*) (Broekhuizen et al., 2016). Hunting levels in the Veluwe area can be up to 9.48 ind.km-2.year-1 (Ramirez et al., 2021).

Data collection and preparation

We performed a quantitative study using a correlational research design to test our hypotheses. In order to do this, we collated data of recreational activities and red deer bodyweight and fecundity between 1985 and

2015 (Fig. 3). We quantified fecundity as a pregnancy rate.

Recreational activities

Between 1985 and 2015, intensity of recreational activities was recorded by a single observer (R. Bijlsma) with the aim to assess their effect on ground-breeding bird ecology (see Bijlsma, 2006). The recreational activities were visually observed in Mosselse zand and Otterlose zand, for a mean time (+-SD) of 19.7 (+-13.4) hours (range: 2-61 hours) spread across an average (+-SD) of 8.9 (+-5.4) days per year (range: 2-23 days) (Fig. 2). Recreationists in the area were counted whilst walking without a fixed route, but with complete visual coverage of the whole area. They were divided into six different categories, namely: hikers, horse riders, vehicles (cars and quads), dogs (off-leash) and cyclists (including All Terrain Bikes, ATBs). Using this data, we calculated the annual number of recreationists for each type, taking into account the time spent observing.

Red deer characteristics

During the regular hunting season between 1985 until 2015, hunters culled female red deer (n = 488) between October and June in assigned locations, within the area of the Game Management Unit (GMU)(Fig. 2). The GMUs predetermine the number of animals to cull in each age class before the hunt, to reduce population numbers and promote tree regeneration. Age and bodyweight are known to affect fecundity (Borowik et al., 2016). During that period, data on the age and bodyweight were collected by Han ten Seldam and Dirk Lieftink for no specific purpose but to serve as baseline of red deer demographic data. Age was defined through post-mortem examination. For red deer younger than 2.5 years, age was determined through incisor and molar changes. Age of older individuals was estimated from the wear of the teeth in the lower jaw (Lowe, 1967). After evisceration, female red deer were weighed (n = 261) and the presence or absence of a foetus was recorded.

Characteristics of the study area

We collated data of population variables, to control for their effects on bodyweight and fecundity. Red deer bodyweight and pregnancy rates can be influenced by the density of red deer (Putman, et al., 2019; Carpio et al., 2021), and the density of competitor ungulates (Barrios-Garcia and Ballari, 2012; Borowik et al., 2016). Therefore, we collated data on red deer density (t_{-3}, t_{-2}, t_{-1} and t_0) and wild boar density estimated by hunters and game managers (Hušek et al., 2021), using a yearly census according to a fixed protocol (see Supplementary Materials I) (Game Management Unit Gelderland, 2019). Census of red deer took place in March and April at count sites (1 per 400 ha) within fixed subareas (Fig. 2), when animals got active and vegetation cover did not limit visibility. Wild boar were counted between May and June at fixed locations (1 per 200 ha) within the area of the GMU, using bait. Furthermore, we collated data on the densities of semi-domesticated herds of Sayaguesa and Scottish Highland cattle that were present and monitored in the area since 2002. Moreover, we collated culling data from the Game Management Unit (GMU), to account for their effect on chronic stress (Vilela et al., 2020) and red deer density (Carpio et al., 2021), and therefore bodyweight and fecundity (Putman et al., 2019; Bötsch et al., 2020).

Additionally, we collated environmental variables that were known to affect bodyweight and fecundity via food availability (Borowik et al., 2016), such as habitat availability, the presence of supplementary feeding sites, and mean annual temperature and precipitation (Rodriguez-Hidalgo et al., 2010). We assessed changes in habitat availability (Stankowich, 2008) using ArcMap (10.7.1) and LGN1 – LGN7 Landsat images (WUR-Alterra, 1980-2012). We quantified the available habitat for red deer by including habitat types related to foraging (i.e., grasslands, deciduous forest, coniferous forest, mixed forest and heath; Gebert and Verheyden-Tixier, 2001) (Fig. 4). In addition, we recorded the presence and absence of supplementary feeding sites in the area. Moreover, we collected mean annual temperatures and precipitation from the nearest weather station (i.e., Deelen at 8.4 km from the study site), as it can affect energy expenditure, bodyweight and the production of biomass (i.e., food) (Rodriguez-Hidalgo et al., 2010).

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Data analysis

Data has been explored in SPSS (IBM SPSS statistics 28) following the protocol by Zuur et al. (2010). Because the different types of recreation were strongly correlated, we used a Principal Component Analysis with a varimax rotation to extract two components (96.9% of the total variance) with an eigenvalue larger than 1. We characterized the first component as a 'non-motorized' axis, due to its strong correlation with the number of dogs, hikers, cyclists (including ATBs) and horse riders (Table 1). The second component was characterized as a 'motorized' axis based on its strong correlation with the number of vehicles (including quads). Since the vehicle data contained a lot of zeros (60.9%), we transformed it to a presence-absence variable.

We took into account the following control variables: age, available habitat, presence of feeding sites, red deer density (t_{-3}, t_{-2}, t_{-1} and t_0), wild boar density, cattle density, mean annual temperature and precipitation and the annual number of red deer culled. The density of red deer and densities of wild boar and cattle were square-root transformed to reduce skewness. The continuous independent variables were standardized and assessed for multicollinearity ($r > 0.7$; Dormann et al., 2013). Correlation between categorical and continuous variables was visually assessed through overlap in boxplots. Multicollinearity was assumed in absence of overlap and therefore one of the variables was not included in the initial model. After selection, the following control variables remained: age, density red deer (t_{-3} and t_0), available habitat, mean annual precipitation and mean annual temperature.

We constructed two Generalized Linear Mixed Models (GLMMs) in R (v.4.2.1.) to assess the direct and indirect effect via bodyweight of two recreational components, motorized and non-motorized, on red deer pregnancy rates. For the direct effect of recreation on pregnancy rates, we used a Binomial GLMM with a log-link function with the glmmTMB package (v.1.1.4; Brooks et al., 2017). In addition to the control variables mentioned above, bodyweight was included as an independent variable. Age was square-root transformed to reduce skewness. To obtain odds ratios and 95% Confidence Intervals the model parameters function (parameters package, version 0.18.2; Lüdecke et al., 2020) was used. To assess the effect of recreation on bodyweight we used a Gaussian GLMM, which included the linear- and quadratic term of age (Putman et al., 2019) in addition to the control variables mentioned above and the random factor year.

We used the "drop1" protocol of Zuur et al. (2009) to select the models with the lowest value for Akaike Information Criterion with a correction for small sample sizes (Table 3). We then assessed the fit of both final models using residual diagnostics and tested the pregnancy model for overdispersion and zero inflation using the DHARMA package (v.0.4.6; Hartig and Lohse, 2022). Finally, we used piecewise Structural Equation Modelling in R (Lefcheck, 2016) to perform a pathway analysis. We assessed the direct effects of recreation intensity on bodyweight and pregnancy rates, and the indirect and total effect of recreation intensity on pregnancy rates, with bodyweight as a mediator.

Results

In total 228 red deer out of 261 were pregnant (mean = 79.3 ($\pm$ 26.5%) pregnant per year) with an average bodyweight of 61 kg (SD = 8; range: 41-83 kg) (Table 2). The relative density of red deer in the area was on average 2.4 deer.km-2 (SD = 0.4 ; range: 1.8-3.5). Between 1985 and 2015, red deer pregnancy rate decreased by 10.2%, while average female bodyweight decreased with 8 kg.

In the final models, non-motorized recreation had a strong direct negative effect on red deer pregnancy rates (Fig. 5a, Table 4) ($\beta = -0.59$), and an even stronger negative effect on bodyweight (Fig. 5b) ($\beta = -1.69$). Motorized recreation did not affect pregnancy rates and bodyweight. Bodyweight had the strongest relative (positive) effect on pregnancy rates (Fig. 5c) ($\beta = 1.24$). Except age, none of the other control variables, density red deer (t_{-3} and t_0), available habitat, mean annual precipitation and mean annual temperature, affected red deer pregnancy rates and body weight.

Based on a pathway analysis with standardized beta's (Fig. 6), the indirect effect of non-motorized recreation on pregnancy rates, with bodyweight as a mediator was 29% of the total effect (-0.27). Therefore, the direct

effect of non-motorized recreation on red deer pregnancy rates (-0.19) is much larger than the indirect effect via bodyweight (-0.08).

Discussion

Our study investigated the effect of fear of humans on the fitness of a large-bodied ungulate over a 30-year period. It is important to understand the fitness consequences of the fear of humans as a 'super predator' on other species for the management and conservation of these species (Darimont et al., 2015; Larson et al., 2016; Naidoo and Burton, 2020). In particular, it enhances our understanding of the mechanisms that can result in trophic cascades (Chitwood et al., 2022), because large-bodied ungulates can structure landscapes such as forests (Ramirez et al., 2018; 2023), affecting forest-related plant and animal species (Svenning et al., 2015). Even though it is known that predators can affect the fitness of small-bodied prey species (Weterings et al., 2022a), large-bodied ungulates may be expected to fear humans more strongly than other (apex) predators, such as wolves, thereby exhibiting strong responses to humans (see Ciuti et al., 2012; Zbyryt et al., 2018; Crawford et al., 2022), especially hunters (Cromsigt et al., 2013). However, compared to hunting, species responses to recreation are generally considered less strong (Gundersen et al., 2021), in particular if recreation is restricted to trails (Reimers and Colman, 2006). Besides, repeated exposure to humans can also lead to habituation to fear (Blumstein, 2016). Nevertheless, in line with our first hypothesis, we found a direct negative correlation between the intensity of non-motorized recreation and the pregnancy rates of red deer. Besides, recreation correlated negatively with bodyweight, whilst bodyweight was strongly positively related with the pregnancy rates of red deer (e.g. Creel et al., 2014; Borowik et al., 2016; Creel, 2018; Putman et al., 2019). This substantiates our second hypothesis that recreational activities can have an indirect effect on pregnancy rates with bodyweight as a mediator. Even though we assumed that repeated recreation could lead to chronic stress, ultimately affecting the pregnancy rate of red deer, we did not measure chronic stress. Boonstra (2013) suggested that chronic activation of the stress axis is an evolved adaptive response to variation in risk. Red deer possibly adapted to the recent increase (i.e., last couple of decades) in disturbance by recreational activities, as adaptive evolution can operate on a generation-to-generation time scale (Bonnet et al., 2022). Nevertheless, both Boonstra (2013) and Creel (2018) argue that acute (unpredictable) stressors (e.g., a risky encounter) can have stress-mediated costs, in particular if they would impact an animal's stress physiology for a longer duration. It is therefore probable that frequent encounters with recreational activities could result in chronic stress in red deer in the Veluwe (see also Zbyryt et al., 2018).

Even though recreational activities can affect the fecundity of species (Larson et al., 2016; Bötsch et al., 2020), the knowledge about the mechanisms that affect the responses of ungulates to human activities like recreation is far from complete. Recent studies suggest that the responses of ungulates to non-risky cues of recreationists could have consequences on the population level if ungulates incorrectly perceive these cues as risky (i.e., over-response) (see assessment mismatch hypothesis; Smith et al., 2021). Habitat characteristics can modify risk or affect risk assessment of ungulates (Weterings et al., 2022b). Especially in open habitats like the heathland areas in the Veluwe animals have ample visibility and show increased perceptions of risk when disturbed compared to closed habitats (Stankowich, 2008). Next to this, population dynamics are suggested to be driven by a response mismatch (Smith et al., 2021) if ungulates display a generalized antipredator response to all non-risky cues initiated by humans. This could be the case when ungulates associate humans with the potential presence of a dog or hunting activities (Stankowich, 2008), which can both be associated with increased levels of risk (Cromsigt et al., 2013; Darimont et al., 2015).

Our results showed standardized effect sizes ranging from small to medium (Cohen, 1992), which corroborates Stankowich and Blumstein (2005). Possibly, these effect sizes are relatively high because of the presence of hunting in the Veluwe, which could exacerbate species' responses to recreation (Thiel et al., 2007) especially in areas with a high level of disturbance (Ciuti et al., 2012). Moreover, hunting in the Veluwe is also done with high-powered rifles that is more difficult to associate with a predictable cue (Cromsigt et al., 2013; Ramirez et al., 2021). Besides, recreation in protected areas can be more substantial than recreation in areas that are not protected, because areas that are protected attract visitors (Reinius and Fredman, 2007). This

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is also seen happening in protected areas around the world where recreation has increased to great numbers (Vallecillo et al., 2019). As a result, recreation in protected areas with a high intensity of use can have a strong impact on species ecology (see e.g. Sundersen et al., 2021). While zonation of recreationists in less-sensitive areas, could be used to manage ungulate populations (Widén et al., 2022), our results primarily emphasise the importance of regulating recreational activities in sensitive locations such as protected areas. In addition to animals, this could also benefit vegetation and soils, as recreation is an important source of pressure on the environment (Ballantyne and Pickering, 2013). Notably, visitors should be more actively informed by protected area managers about the effects of recreation on wild animal populations and their surroundings, as most visitors are unaware about the consequences of their activities (Gruas et al., 2020). This requires protected-area management to be knowledge driven, evidence based, site specific and effective (Pressey et al., 2015), especially when related to management of recreational pressure and its corresponding effects on nature values.

Corroborating our third hypothesis, motorized recreation showed less effect on red deer fecundity than non-motorized recreation. On the one hand, this could apply to other species as well (Stankowich, 2008; Larson et al., 2016). For example, coyote (*Canis latrans*), bobcat (*Lynx rufus*) (George and Crooks, 2006) and wolverine (*Gulo gulo*) (Krebs et al., 2007) showed no responses to motorized recreation as opposed to non-motorized recreation. On the other hand, non-motorized recreation can affect species ecology in many ways (Papouchis et al., 2001; Newsome et al., 2004; Stankowich, 2008; Larson et al., 2016).

Besides recreation, we took various variables into account to control for their effect on fecundity and body-weight (see Tarlow and Blumstein, 2007), in particular, mean annual temperature and precipitation, food supplementation, available habitat and population density. However, we did not find an effect of the mean annual temperature and precipitation. Possibly, this is because in different periods throughout the year temperature and precipitation have a different effect on the quality and availability of food, red deer bodyweight and fecundity (Schmidt et al., 2001) that could be negated at a large temporal scale. Additionally, we did not find density-dependent effects on fecundity and bodyweight. Possibly density dependence in red deer reproduction and body condition operates only in resource restricted areas (Putman et al., 2019), in contrast to our Veluwe area (Ramirez et al., 2021). Moreover, density dependence is not shown in populations at equilibrium (Clutton-Brock et al., 1985). The relative densities of our population did not vary that much between 1985 and 2015 and fluctuated around an 'equilibrium' of 2.4 deer.km^{-2}, making it more difficult to detect density dependence. Similarly, the low variation in available habitat made effects of this variable on fecundity and body weight difficult to detect.

In conclusion, recreational intensity was negatively correlated with fecundity and body weight of red deer. Our results support the regulation of the number of recreationists in sensitive nature areas, especially non-motorized recreationists such as hikers, horse riders and dog-walkers.

Acknowledgements

Competing interests Statement

The authors declare that they have no conflict of interest.

Ethics approval

Red deer were culled and made available by hunters. Not being part of an animal experiment as referred to in the Dutch Act on Animal Experiments, an ethical assessment was not needed. Besides, for this type of

retrospective study formal consent is not required.

Data Accessibility Statement

During submission the data base and R scripts will be provided as supplementary data files. After acceptance, the data base and R scripts will be deposited in the Dryad Digital Repository under the reference number [identifier number].

Author Contributions

MW originally formulated the idea. MW, EE, BS, HK designed the study. GJS collated and contributed culling data, data on competitor density and the number of road kills. EE, BS and HK performed statistical analyses. MW, EE, BS and HK wrote the manuscript, while GJS provided editorial advice. All authors reviewed the manuscript.

Literature cited

Ballantyne M, Pickering CM (2013) Tourism and recreation: a common threat to IUCN red-listed vascular plants in Europe Biodiversity Conservation. 22: 3027-3044

Banks PB, Bryant JV (2007) Four-legged friend or foe? Dog walking displaces native birds from natural areas. Biological Letters 3: 611–613

Barrios-Garcia MN, Ballari SA (2012) Impact of wild boar (Sus scrofa) in its introduced and native range: a review. Biological Invasions 14(11): 2283-2300

Bijlsma RG (2006) Effecten van menselijke verstoring op grondbroedende vogels van Planken Wambuis. De Levende Natuur 107(5): 191-198

Blumstein DT (2016) Habituation and sensitization: new thoughts about old ideas. Animal Behaviour 120: 255-262

Boonstra R (2013) Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. Functional Ecology 27(1): 11-13

Bonnet T, Morrissey MB, de Villemereuil P, Alberts SC, Arcese P, Bailey LD, Boutin S, Brekke P, Brent LJN, Camenisch G, Charmantier A, Clutton-Brock TH, Cockburn A, Coltman DW, Courtiol A, Davidian E, Evans SR, Ewen JG, Festa-Bianchet M, de Franceschi C, Gustafsson L, Höner OP, Houslay TM, Keller LF, Manser M, McAdam AG, McLean E, Nietlisbach P, Osmond HL, Pemberton JM, Postma E, Reid JM, Rutschmann A, Santure AW, Sheldon BC, Slate J, Teplitsky C, Visser ME, Wachter B, Kruuk LEB (2022) Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals. Science 376: 1012-1016

Borowik T, Wawrzyniak P, Jedrzejewska B (2016) Red deer (Cervus elaphus) fertility and survival of young in a low-density population subject to predation and hunting. Journal of Mammalogy 97(6): 1671-1681

Bötsch Y, Tablado Z, Almasi B, Jenni L (2020) Human recreation decreases antibody titre in bird nestlings: an overlooked transgenerational effect of disturbance. Journal of Experimental Biology 223(8): jeb210930

Broekhuizen S, Spoelstra K, Thissen JBM, Canters KJ Buys JC (eds) 2016 Atlas van de Nederlandse zoogdieren. Naturalis Biodiversity Center & EIS Kenniscentrum insecten en andere ongewervelden Leiden

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9(2): 378–400

Caro T (2005) Antipredator Defenses in Birds and Mammals. University of Chicago Press Chicago USA.

Carpio AJ, Apollonio M, Acevedo P (2021) Wild ungulate overabundance in Europe: Contexts causes monitoring and management recommendations. Mammal Review 51(1): 95-108

Chitwood MC, Baruzzi C, Lashley MA, (2022) "Ecology of fear" in ungulates: Opportunities for improving conservation. Ecology and Evolution 12: e8657

Ciuti S, Northrup JM, Muhly TB, Simi S, Musiani M, Pitt JA, Boyce MS (2012) Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLoS ONE 7(11): e50611

Clutton-Brock TH, Major M, Guinness FE (1985) Population regulation in male and female red deer. Journal of Animal Ecology 54: 831-846

Cohen J (1992) A power primer. Psychological Bulletin 112(1): 155-159

Cooper Jr WE, Blumstein DT (eds) (2018) Escaping from predators: an integrative view of escape decisions. Cambridge University Press, Cambridge, UK.

Cordell HK (2008) The latest trends in nature-based outdoor recreation. Forest History Today Spring 2008.

Crawford DA, Conner LM, Clinchy M, Zanette LY, Cherry MJ (2022) Prey tells large herbivores fear the human 'super predator'. Oecologia 198: 91-98

Creel S, Schuette P, Christianson D (2014) Effects of predation risk on group size vigilance and foraging behavior in an African ungulate community. Behavioral Ecology 25(4): 773-784

Creel S (2018) The control of risk hypothesis: Reactive vs proactive antipredator responses and stress-mediated vs food-mediated costs of response. Ecology Letters 21(7): 947-956

Cromsigt JP, Kuijper DP, Adam M, Beschta RL, Churski M, Eycott A, Kerley GIH, Mysterud A, Schmidt K, West K (2013) Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology 50(3): 544-549

Darimont CT, Fox CH, Bryan HM, Reimchen TE (2015) The unique ecology of human predators. Science 349(6250): 858-860

Dormann CF, Elith J, Bacher S, et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36: 27–46

Fauna Registration System (2022) WBE gebieden [internet] Retrieved on June 21 2022 from: https://wwwfaunaregistratienl/Public/InfoOpenbaaraspx

Frid A, Dill L (2002) Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1): 11.

Game Management Unit Gelderland (2019) Faunabeheerplan Grote Hoefdieren FBE Gelderland 2019 2025 FBE Gelderland [internet] Retrieved on April 26 2022 from: https://wwwfaunabeheereenheidnl/gelderland/PUBLICATIES

Gebert C, Verheyden-Tixier H (2001) Variations of diet composition of red deer (Cervus elaphus L) in Europe. Mammal Review 31(3-4): 189-201

George SL, Crooks KR (2006) Recreation and large mammal activity in an urban nature reserve. Biological Conservation 133(1): 107-117

Gruas L, Perrin-Malterre C, Loison A (2020) Aware or not aware ? A literature review reveals the dearth of evidence on recreationists awareness of wildlife disturbance. Wildlife Biology 4: 00713

Gundersen V, Myrvold KM, Rauset GR, Selvaag SK, Strand O (2021) Spatiotemporal tourism pattern in a large reindeer (Rangifer tarandus tarandus) range as an important factor in disturbance research and management. Journal of Sustainable Tourism 29(1): 21-39

Hartig F, Lohse L (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 046 https://CRANR-projectorg/package=DHARMa

Hušek J, Boudreau MR, Panek M (2021) Hunter estimates of game density as a simple and efficient source of information for population monitoring: A comparison to targeted survey methods. PLoS ONE 16(8): e0256580

Jayakody S, Sibbald AM, Gordon IJ, Lambin X (2008) Red deer Cervus elaphus vigilance behaviour differs with habitat and type of human disturbance. Wildlife Biology 14: 81-91

Krebs J, Lofroth EC, Parfitt IAN (2007) Multiscale habitat use by wolverines in British Columbia Canada. The Journal of Wildlife Management 71(7): 2180-2192

Kuiters AT, Bruinderink GW, Lammertsma DR (2005) Facilitative and competitive interactions between sympatric cattle red deer and wild boar in Dutch woodland pastures. Acta Theriologica 50(2): 241-252

Larson CL, Reed SE, Merenlender AM, Crooks KR (2016) Effects of recreation on animals revealed as widespread through a global systematic review. PloS one 11(12): e0167259

Lefcheck JS (2016) piecewiseSEM: Piecewise structural equation modelling in r for ecology evolution and systematics. Methods in Ecology and Evolution 7(5): 573-579

Lowe VPW (1967) Teeth as indicators of age with special reference to red deer (Cervus elaphus) of known age from Rhum. Journal of Zoology 152(2): 137-153

Lüdecke D, Ben-Shachar M, Patil I, Makowski D (2020) Extracting Computing and Exploring the Parameters of Statistical Models using R. Journal of Open Source Software 5(53): 2445

Naidoo R, Burton AC (2020) Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. Conservation Science and Practice 2(10): e271

Newsome D, Cole DN, Marion JL (2004) Environmental impacts associated with recreational horse-riding. Environmental Impacts of Ecotourism 61-82

Papouchis CM, Singer FJ, Sloan WB (2001) Responses of desert bighorn sheep to increased human recreation. Journal of Wildlife Management 65: 573–582

Pemberton JM, Kruuk LEB, Clutton-Brock T (2022) Long-term studies of individuals: the example of the Isle of Rum red deer project. The Annual Review of Ecology Evolution and Systematics 53: 327-351

Pressey RL, Visconti P, Ferraro PJ (2015) Making Parks make a difference: poor alignment of policy planning and management with protected-area impact and ways forward. Philosophical Transactions of the Royal Society B 370: 2140280

Putman R, Nelli L, Matthiopoulos J (2019) Changes in bodyweight and productivity in resource-restricted populations of red deer (Cervus elaphus) in response to deliberate reductions in density. European Journal of Wildlife Research 65(1): 1-13

Ramirez JI, Jansen PA, Poorter L (2018) Effects of wild ungulates on the regeneration structure and functioning of temperate forests: A semi-quantitative review. Forest Ecology and Management 424: 406-419

Ramirez JI, Zwerts JA, van Kuijk M, Iacobelli P, Li X, Herdoiza N, Jansen PA (2021) Density dependence of daily activity in three ungulate species. Ecology and Evolution 11: 7390-7398

Ramirez JI, Poorter L, Jansen PA, den Ouden J, Siewert M, Olofsson J (2023) Top-down and bottom-up forces explain patch utilization by two deer species and forest recruitment. Oecologia 201: 229-240

Reimers E, Colman JE (2006) Reindeer and caribou (Rangifer tarandus) response towards human activities. Rangifer 26(2): 55–71

Reinius SW, Fredman P (2007) Protected areas as attractions. Annuals of Tourism Research 34: 839-854

Rodriguez-Hidalgo P, Gortazar C, Tortosa FS, Rodriguez-Vigal C, Fierro Y, Vicente J (2010) Effects of density climate and supplementary forage on body mass and pregnancy rates of female red deer in Spain. Oecologia 164(2): 389-398

Schmidt KT, Stien A, Albon SD, Guinness FE (2001) Antler length of yearling red deer is

determined by population density weather and early life-history. Oecologia 127: 191-197

Smith JA, Gaynor KM, Suraci JP (2021) Mismatch between risk and response may amplify lethal and non-lethal effects of humans on wild animal populations. Frontiers in Ecology and Evolution 9: 604973

Stankowich T, Blumstein DT (2005) Fear in animals: a meta-analysis and review of risk assessment. Proceedings of the Royal Society B 272: 2627-2634

Stankowich T (2008) Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141(9): 2159-2173

Svenning J-C, Pedersen PB, Donlan CJ, Ejrnaes R, Faurby S, Galetti M, Hansen DM, Sandel B, Sandom CJ, Terborgh JW (2015) Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. Proceedings of the National Academy of Sciences of the United States of America 113(4): 898-906

Tarlow EM, Blumstein DT (2007) Evaluating methods to quantify anthropogenic stressors on wild animals. Applied Animal Behaviour Science 102: 429-451

Ten Houte de Lange SM (ed) (1977) Rapport van het Veluwe-onderzoek: Een onderzoek van natuur landschap en cultuurhistorie van de ruimtelijke ordening en het recreatiebeleid. Pudoc Wageningen, Wageningen, the Netherlands.

Thiel D, Menoni E, Brenot J-F, Jenni L (2007) Effects of recreations and hunting on flushing distance of capercaillie. Journal of Wildlife Management 71(6): 1784-1792

Vallecillo S, La Notte A, Zulian G, Ferrini S, Maes J (2019) Ecosystem services accounts: Valuing the actual flow of nature-based recreation from ecosystems to people. Ecological Modelling 392: 196-211

Vilela S, Alves da Silva A, Palme R, Ruckstuhl KE, Sousa JP, Alves J (2020) Physiological stress reactions in red deer induced by hunting activities. Animals 10(6): 1003

Weterings MJA, Losekoot S, Kuipers HJ, Prins HHT, van Langevelde F, van Wieren SE (2022a) Chronic exposure to high predation risk by multiple predators decreases body condition and fecundity of prey. Ecology & Evolution 12: e8442

Weterings MJA, Meister N, Fey K, van Langevelde F, Jansen PA, Kuipers HJ (2022b) Context-dependent responses of naive ungulates to wolf-sound playback in a human-dominated landscape. Animal Behaviour 185: 9-20

Whirledge S, Cidlowski JA (2010) Glucocorticoids stress and fertility. Minerva Endocrinologica 35(2): 109

Widen A, Clinchy M, Felton AM, Hofmeester TR, Kuijper DP, Singh NJ, Widemo F, Zanette LY, Cromsigt JP (2022) Playbacks of predator vocalizations reduce crop damage by ungulates. Agriculture Ecosystems & Environment 328: 107853

Zanette LY, White AF, Allen MC, Clinchy M (2011) Perceived predation risk reduces the number of offspring songbirds produce per year. Science 334(6061): 1398-1401

Zbyryt A, Bubnicki JW, Kuijper DP, Dehnhard M, Churski M, Schmidt K (2018) Do wild ungulates experience higher stress with humans than with large carnivores? Behavioral Ecology 29(1): 19-30

Zuur AF, Leno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. (Vol 574) New York Springer, New York, USA.

Zuur AF, Leno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1(1): 3-14

Tables

Table 1 : Principal Component scores and eigenvalues of five types of recreational activities in the Veluwe nature area.

Type of recreational activity	Principal component 1	Principal component 2
Dog walking	**0.97**	0.01
Hiking	**0.95**	-0.01
Cycling	**0.90**	0.27
Horse riding	**0.78**	0.37
Vehicle driving	0.1	**0.98**
Eigenvalues (%)	3.44 (68.8)	1.00 (20.01)

The main structuring variables relative to each axis are indicated in bold.

Table 2: Characteristics (mean $\pm$ SD (Range)) of recreational activities red deer and the study area in three periods of 10-years.

	1985-1994	1995-2004	2005-2015
Recreational activities			
Non-motorized recreation [a]	$898 \pm 310.4 \ (487 - 1500)$	$3619 \pm 1476.6 \ (2451 - 6039)$	$6890 \pm 1988.2 \ (4526 - 10950)$
Motorized recreation [b]	$10 \pm 20.7 \ (0 - 56)$	$87 \pm 83.2 \ (0 - 244)$	$24 \pm 42.8 \ (0 - 104)$
Red deer (n/year)	$(n = 6 - 22)$	$(n = 2 - 15)$	$(n = 1 - 6)$
Age (year)	$4 \pm 3.4 \ (1 - 12)$	$5 \pm 4.9 \ (1 - 16)$	$2 \pm 1.6 \ (1 - 6)$
Bodyweight (kg)	$63 \pm 4.3 \ (56 - 70)$	$62 \pm 6 \ (55 - 72)$	$55 \pm 6 \ (50 - 67)$
Red deer pregnancy rate (%)	$91 \pm 11.1 \ (67 - 100)$	$81 \pm 15.1 \ (50 - 100)$	$67 \pm 38.8 \ (67 - 100)$
Study area			
Number of red deer shot	$93 \pm 24.1 \ (62.5 - 122)$	$74 \pm 27 \ (38 - 123)$	$93 \pm 41.2 \ (31 - 145)$
Density red deer (red deer.km-2)	$3 \pm 0.2 \ (2 - 3.7)$	$2 \pm 0.3 \ (1.8 - 2.9)$	$3 \pm 0.4 \ (2 - 3.5)$
Available habitat (km2)	$68 \pm 1.6 \ (66.7 - 69.8)$	$66 \pm 0.2 \ (65.8 - 66.2)$	$65 \pm (62 - 68.1)$

[a] Total number of dogs hikers cyclists (including ATBs) and horse riders; [b] Total number of vehicles (including quads)

Table 3: Model selection red deer pregnancy rate and bodyweight model

Pregnancy rate model [1]	AICc [2]	ΔAICc	w [3]
PR ~ SQRT(A) + BW + MR + NMR	173.83	0.0	0.41
PR ~ SQRT(A) + BW + MR + NMR + HA	174.24	0.4	0.33
PR ~ SQRT(A) + BW + MR + NMR + HA + P	175.61	1.8	0.17
PR ~ SQRT(A) + BW + MR + NMR + HA + P + T	177.65	3.8	0.06
PR ~ SQRT(A) + BW + MR + NMR + HA + P + T + SQRT(D_0)	179.72	5.9	0.02
PR ~ SQRT(A) + BW + MR + NMR + HA + P + T + SQRT(D_0) + SQRT(D_{-3})	181.87	8.0	0.01
Bodyweight model	AICc	ΔAICc	w
BW ~ A + A^2 + MR + NMR + P + (1|Year)	1731.42	0.0	0.30
BW ~ A + A^2 + MR + NMR + P + HA + (1|Year)	1731.53	0.1	0.28
BW ~ A + A^2 + MR + NMR + P + HA + SQRT(D_{-3}) + (1|Year)	1732.01	0.6	0.22

Pregnancy rate model [1]	AICc [2]	ΔAICc	w [3]
BW ~ A + A^2 + MR + NMR + P + HA + SQRT(D$_{-3}$) + SQRT(D$_0$) + (1|Year)	1732.99	1.6	0.14
BW ~ A + A^2 + MR + NMR + P + HA + SQRT(D$_{-3}$) + SQRT(D$_0$) + T + (1|Year)	1734.92	3.5	0.05

1 A = age, BW = bodyweight, D$_0$ = density t$_0$, D$_{-3}$ = density t$_{-3}$, HA = habitat availability, MR = motorized recreation, NMR = non-motorized recreation, P = mean annual precipitation, T = mean annual temperature; [2] AICc = Akaike Information Criterion corrected for small sample sizes; [3] w = model weight

Pregnancy rate model [a]
(Intercept)
sqrt(age)
bodyweight
motorized recreation [d]
non-motorized recreation
Bodyweight model [e]
(Intercept)
age
age^2
motorized recreation [d]
non-motorized recreation

[a] Pregnancy rate ~ sqrt(age) + bodyweight + motorized recreation + non-motorized recreation (the predictors of the pregn

Table 4: Summary of final model results with the effect of age bodyweight motorized recreation and non-motorized recreation on pregnancy rates and bodyweight of female red deer (n = 261) between 1985 and 2015.

Figure Legends

Fig. 1 Conceptual representation of the effect of recreation on bodyweight and fecundity. Dotted box represents stress mechanism that can affect animal fecundity via two pathways.

Fig. 2 Overview of the study area with sampling locations (see data collection and preparation). Delineated in black: boundaries of the area of the Game Management Unit (GMU) (79.88 km2). Circles: monitoring locations of red deer. Triangle: sample location of recreational activities. Hatched surface: culling area of red deer. Inset: boundaries of the Veluwe including the study area. Data from Province of Gelderland (2021) and the Fauna registration system (2022).

Fig. 3 Conceptual model of the effects of recreation intensity on ungulate bodyweight and pregnancy rates. Recreation intensity includes dogs cyclists hikers horse riders and vehicles. Focus variables are indicated in white and control variables are indicated in grey. + = positive effect; - = negative effect; ? = effect is unclear; + - = effect could be both positive and negative. 1) Borowik et al. 2016; 2) Putman et al. 2019; 3) Papouchis et al. 2001; 4) Newsome et al. 2004; 5) Larson et al. 2016; 6) Carpio et al. 2021; 7) Rodriguez-Hidalgo et al. 2010; 8) Bötsch et al. 2020) 9) Vilela et al. 2020; 10) Barrios-Garcia and Ballari 2012; 11) Kuiters and Lammertsma 2005; 12) Jayakody 2008; Stankowich 2008.

Fig. 4 Available habitat for red deer in the Veluwe area between 1984 and 2015.

Fig. 5 Effects of non-motorized recreation on (a) pregnancy rates and (b) bodyweight and the effect of bodyweight on pregnancy rates of female red deer (n = 261) between 1985 and 2015.The component non-motorized recreation is extracted from a principal component analysis of dogs hikers cyclists (including ATBs) and horse riders.

Fig. 6 Final model structure and path coefficients (i.e. standardized regression coefficients) that show the direct effect of non-motorized recreation on pregnancy rates and bodyweight and the direct effect of bodyweight on pregnancy rates. Effect size path coefficients (Cohen 1992): large effect = 0.50 medium effect = 0.30 small effect = 0.10.
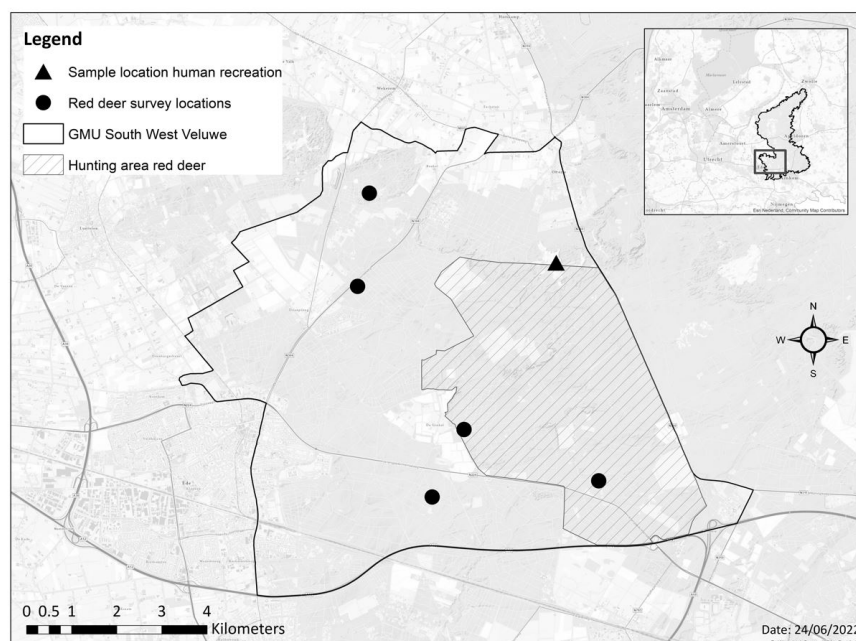
Figures

[Fig. 1]

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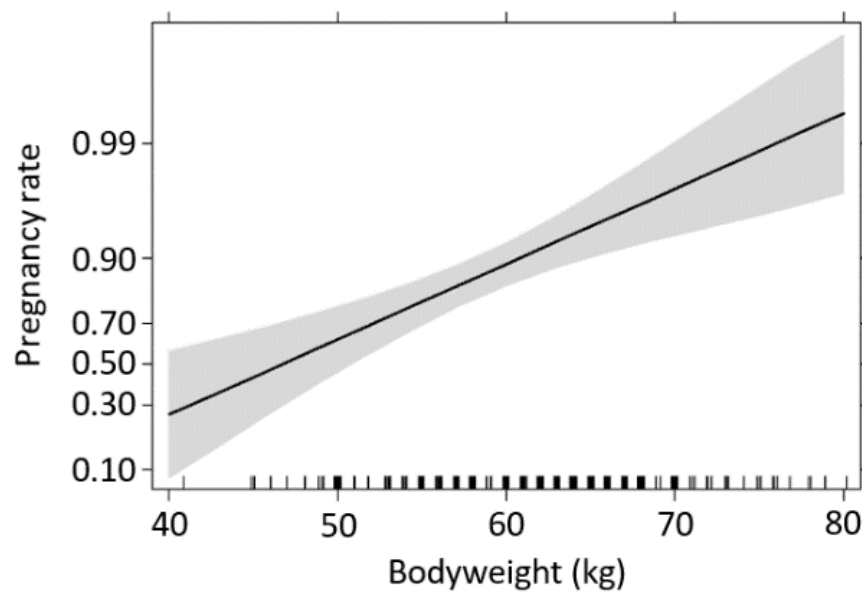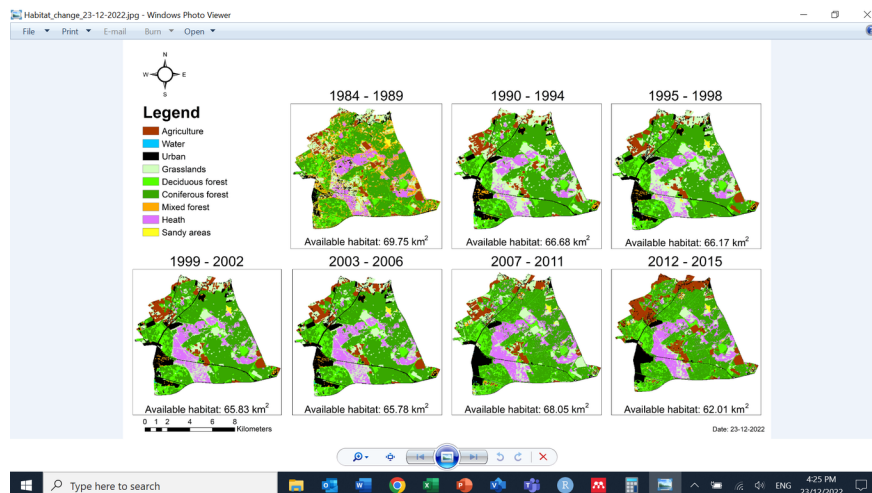
[Fig. 2]

[Fig. 3]

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[Fig. 4]

[Fig. 5] [Fig. 6]

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