

1 **Wolf – human interactions in a shared landscape: spatio-temporal distribution and visitors'**
2 **perception in The Hoge Veluwe National Park**

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3943 **ABSTRACT**

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4144 Large carnivores are increasingly recolonizing human-dominated landscapes, yet the mechanisms
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4445 enabling their persistence in intensively used landscapes and how this shapes risk perception and
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4646 tolerance remain insufficiently understood. In particular, few studies have integrated fine-scale
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4947 ecological data with on-site assessments of visitor perceptions from the same recreational area.

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5148 Using the Hoge Veluwe National Park as a case study, we combined camera-trap monitoring with a
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5349 visitor survey to examine wolf (*Canis lupus*) spatio-temporal behavior, human–wolf overlap, and
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5650 recreationists' attitudes toward wolf presence in a highly frequented recreational landscape.

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5851 Analysis on the activity patterns at trail crossings showed temporal segregation (overlap coefficient
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6152 = 0-0.31), with wolves primarily nocturnal and visitor activity peaking at midday. In contrast, and
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53 contrary to expectations, camera-trap data revealed a constant spatial distribution of wolf capture
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24 rates in forest and open habitats away from trails, with a frequent use of the latter during daylight
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55 hours. These findings suggest that wolves rely on behavioral flexibility, making spatial and
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76 temporal adjustments according to predictable patterns of human disturbance in order to persist in
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107 highly used recreational landscapes. The availability of spatial refuges and nocturnal windows of
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128 minimal human activity likely facilitates this coexistence dynamic. Survey responses indicated
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159 generally neutral-to-positive attitudes toward wolves in our sample with broad support for
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1760 coexistence and limited evidence that wolf presence would reduce future visitation even though
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2061 some expressed concerns regarding public safety and reduced ungulate visibility. Together, the
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2262 ecological and social findings point to a system characterized by structured human mobility, limited
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2463 encounter risk, and pragmatic tolerance.
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31 **KEY WORDS**

32 activity patterns, camera trapping, *Canis lupus*, human–wildlife conflict, recreational disturbance,
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3467 survey.
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41 **INTRODUCTION**

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4471 Since the mid-20th century, large carnivore populations show an increasing size trend in Europe (Di
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4672 Bernardi et al., 2025). After centuries of persecution, factors such as land abandonment, forest
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4973 recovery, legal protection, increased wild prey availability and urbanization have allowed large
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5174 carnivores to progressively expand from confined refuges to regions from where they had been
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5475 extirpated (Cimatti et al., 2021). The Grey Wolf (*Canis lupus*), in particular, went from remnant
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5676 populations in Italy, Poland, Russia and the Balkans to establish populations in France, Switzerland,
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5877 Germany and Scandinavia. In 2023, wolves were reported in 24 European countries (Blanco &
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6178 Sundseth, 2023; Di Bernardi et al., 2025).
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While this return represents a conservation success, it has reignited long-standing conflicts with humans (Pettersson et al., 2021). Wolf occurrence is now unfolding within a markedly different ecological context characterized by growing human population density, expanding infrastructure networks and intensified recreational use of anthropogenic landscapes (Zanni et al., 2023). Under these new conditions, traditional sources of conflict, such as livestock depredation and social mistrust persist, while new tensions arise: the shared landscape use by wolves and humans increases the likelihood of close encounters (Brogi et al., 2025), vehicle collisions and negative interactions with pets, including predation events (Martins et al., 2020; Linnell & Lescureux, 2014). Consequently, wolves had to enter a novel ecosystem (Kuijper et al., 2024) and adapt to the pervasive presence of humans and human-related features in the fragmented landscapes by taking on elevated levels of risk (Oriol-Cotterill et al., 2015). Literature reports coping strategies such as prioritizing prey capture over human avoidance in areas with low prey availability (Barker et al., 2023), scavenging livestock carcasses, exploiting garbage dumps (Ciucci et al., 2020; Mohammadi et al., 2019) and highlights wolves' ecological plasticity and ability to settle in and survive despite strong anthropogenic pressures. Nonetheless, wolves are embedded in antagonistic meanings and are widely framed as a symbol of wilderness, distance from human settlements, and nature beyond human control, shaping how their presence is perceived (Almarcha et al., 2023). As a result, sightings in urban and peri-urban areas trigger public concern among citizens, reflecting a perceived decrease in personal safety (Brogi et al., 2025), generating emotions such as fear, frustration and loss of trust in management measures (Johansson et al., 2012). This raises skepticism about whether wolves can effectively fulfill their ecological role in densely human-dominated countries, which is heavily debated (Breyne et al., 2021).

The Netherlands provides an interesting context for studying wolf dynamics in human-dominated environments, given the country's second-highest population density in Europe (541

105 inhabitants/km²; United Nations, 2024). The Dutch landscape is characterized by a dense matrix of
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inhabitants/km²; United Nations, 2024). The Dutch landscape is characterized by a dense matrix of discrete land use: urban areas, intensive agriculture and natural areas that also function as recreational areas. Wolves recolonized the Netherlands through natural dispersal from Germany in 2015, with the first reproduction recorded in the Veluwe in 2019. Since then, wolf sightings have increased with nine packs and thirty-nine pups recorded at the end of December 2023 (Blanco & Sundseth, 2023). Within this context, understanding how wolves and humans move at fine spatial and temporal scales becomes particularly relevant, as recreational sites represent locations where wildlife and human presence overlap, potentially intensifying the likelihood of interactions between wolves and recreationists. However, most available information on wolves in the Netherlands is derived from national-scale assessments (e.g., Wolf Plan 2025; Association Interprovincial Consultation [IPO], 2025), which provide limited insight into fine-scale spatio-temporal dynamics of wolves and humans within specific recreational areas. Yet, to the best of our knowledge, no study to date has combined monitoring of wolf and human spatio-temporal use and surveys within the same area.

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We aim to investigate how wolves and humans share space within a heavily used recreational landscape in this densely populated country, shedding light on spatial overlap and visitors' perceptions. The Hoge Veluwe National Park provides an ideal case study to address this question, as it concentrates high daily visitor numbers within a relatively small area that also hosts resident wolves, creating a setting where wildlife and recreation exist in proximity. Such an integrated approach broadens the understanding of how wolves respond to humans and how their presence is perceived by visitors, linking two relevant elements of wolf-human space sharing. The insights obtained are crucial for park and board managers, as wolf presence may affect the visitor experience, altering ungulates' visibility and public safety, ultimately influencing the site's touristic appeal.

130 Given the park's high daily visitor load and the absence of visitors at night due to park closure, we
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131 tested the following predictions: (i) wolves exhibit predominantly nocturnal activity patterns,
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132 minimizing activities during the day to reduce the likelihood of encounters with humans; (ii)
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133 capture rates are lower in open areas compared to forested areas during opening hours, as wolves
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134 may prefer to move in areas offering more cover from exposure to recreationists; and (iii) there is
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135 low temporal overlap between wolves and human activity as a response to visitor disturbance.
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136 These predictions were assessed using spatio-temporal data from camera traps set both on and off
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137 trails. Lastly, an explorative survey complemented the ecological data, providing a comprehensive
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138 understanding of the human dimensions of the conflict in the same recreational site.
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140 MATERIALS AND METHODS

141 Study area

242 The study was conducted in the Hoge Veluwe National Park (54 km², 52.1° N, 5.8° E, Gelderland,
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143 Netherlands; Fig. 1), a privately managed, fenced game reserve in the southern part of the Veluwe
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144 region. The Park is a popular destination in the Netherlands, attracting more than half a million
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145 visitors annually (576,000 visitors in 2024; Stichting Het Nationale Park de Hoge Veluwe). Access
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146 by car is allowed on the main asphalt roads only.
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4147 Habitat types include dry heathlands (28% of the park area), drift sands (18% of the park area),
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148 forests (53% of the park area) of Scots pine (*Pinus sylvestris*), oak (*Quercus robur*), Douglas-fir
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149 (*Pseudotsuga menziesii*), beech (*Fagus sylvatica*) and Japanese larch (*Larix kaempferi*), and game
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150 meadows (<1% of the park area). The Park supports populations of red deer (*Cervus elaphus*), wild
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151 boar (*Sus scrofa*), and roe deer (*Capreolus capreolus*) that are monitored (Dijkhuis, L. et al., 2023)
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152 and managed through gamekeeping plans (target population size at the end of 2021: 180 red deer,
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153 50 wild boar, and 160 roe deer). The mouflon (*Ovis aries musimon*) population reached apical
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154 numbers in 2021 with 220 individuals but collapsed after the settlement of the wolf. All remaining
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155 individuals are now confined to an electrified enclosure and therefore do not functionally contribute
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156 to the mammal community in the park. Other common mammal species include red fox (*Vulpes*
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157 *vulpes*), brown hare (*Lepus europaeus*), pine marten (*Martes martes*) and badger (*Meles meles*).
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158 The first wolf sighting occurred in May 2021, when an adult female was spotted within the Park
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159 boundaries. A second wolf, an adult male, was observed later that year in November. By spring
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160 2022, the pair had mated and given birth to five pups, of which three survived to the following year.
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161 In May 2023, one cub was born, but it died before the end of the summer. In 2024, the pack
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162 consisted of five wolves: the original breeding pair and three yearlings of the first litter. The Park is
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163 also occasionally used by wolves from the neighboring areas that jump over the fence.
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164 **Camera trap data**

165 *Data collection*

166 Between May and September 2024, nine camera traps (Fig. 1, blue dots)—four Seissiger (Seissiger
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167 Pro-Cam LTE, Germany) and five Bushnell (Bushnell Core DS-4K, USA)—were deployed on
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168 recreational trail crossings with previously documented wolf presence (scat records). These cameras
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169 were set opportunistically on selected points and continuously operated to measure the temporal
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170 overlap in the activity patterns between wolves and recreational users. Footage was manually
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171 examined by a trained operator. Each detection event was classified by species (wolf, human), date,
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172 clock time and camera location. To avoid the risk of double counting, detection events for the two
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173 species were defined as follows: for humans, since individuals were easily distinguishable by
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174 visible features, each event corresponded either to a single individual or a group moving through the
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175 camera's field of view. For wolves, if individual or group differentiation was not possible from the
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176 footage, detection events were considered independent if they were within three minutes of each
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177 other, following the default independence threshold implemented in Agouti (Casaer et al., 2019).
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178 All records were compiled into a Microsoft Excel spreadsheet, which was subsequently imported
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179 into RStudio (R Core Team, 2024) for statistical analysis. For each camera location, the wolf-to-
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180 visitor ratio per week and the capture rates were calculated, considering cameras' operation time.
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182 For comparison with trail activity, we used data from a permanent wildlife monitoring network in
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For comparison with trail activity, we used data from a permanent wildlife monitoring network in the same area, established in 2013. This includes 48 cameras (Reconyx Hyperfire HC500; Reconyx, USA) at locations generated in ArcGIS (Fig. 1, red dots), with the constraint that each camera be placed at least 25 m from the nearest path (including trails, bike lanes, and asphalt roads). The camera points are distributed across the six major habitat types following a stratified random design—with eight cameras per habitat type—to ensure balanced sampling across habitat categories rather than being proportional to the area. Moreover, within each habitat, half of the cameras were installed in (former) restricted areas ($n = 24$) and half in (former) publicly accessible areas ($n = 24$). This distinction disappeared in January 2016, when off-trail hiking became prohibited. Upon each trigger, ten photographs are taken at a rate of ~ 1 per second. Images were saved on SDHC memory cards and uploaded to Agouti.eu (Casaer et al., 2019), an online platform for processing and archiving. Two events are considered independent if the time elapsed between triggers is longer than 3 minutes. Species identification was partly done using AI; hence, cryptic or unclear appearances of wolves may have been missed. All wolf detections were checked and validated.

Data analysis

All analyses were conducted using R and RStudio (Posit team, 2024; R Core Team, 2024). For both on- and off-trail analysis, clock time was standardized to solar time, accounting for variation in day length during the study period (Vazquez et al., 2019). The overlap in activity patterns of wolves and visitors was calculated from cameras on trails fitting circular Kernel Density Estimators (KDEs) using the `overlap` package in R (Ridout & Linkie, 2009). This nonparametric method calculates the overlap coefficient (Δ) between wolf and human activity distributions ranging from 0 (no overlap) to 1 (complete overlap). As defined in previous studies, the overlap is categorized as high ($\Delta > 0.75$), intermediate ($0.50 < \Delta \leq 0.75$), or low ($\Delta \leq 0.50$) (Carter et al.,

205 2012; Petridou et al., 2023). The capture number was adjusted, accounting for variations in
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206 sampling effort—the period during which each camera was active.

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207 To assess spatio-temporal variation in wolf activity patterns in relation to human access, we compared
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208 capture rates between forested and open areas using the data from the permanent, habitat-stratified
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209 camera network. The off-trail dataset was subsetting to the period from May to September 2024 to
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210 match the temporal window of the on-trail camera network. Different habitat types were grouped into
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211 forest (53% of the park area) and open (meadows, heathland and drift sands, 47%) areas and further
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212 classified according to access status (formerly restricted or not). The issue of imbalanced sampling,
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213 due to an underrepresentation of habitat types in respect to their availability in the landscape, was
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214 addressed using a novel technique developed by Rowcliffe et al. (2026), which allows estimating
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215 activity patterns of population distribution across different habitats over time uncovering diurnal
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216 migration, spatial segregation and habitat preference. Habitat-specific densities were weighted by
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217 habitat area and effort (i.e., camera activity time) and used to fit a kernel density estimation.
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32 33 34 35 **Survey data**

36 37 *Data collection*

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40 To explore visitors' perceptions of wolf presence, a face-to-face survey was conducted with 203
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42 participants between the 15th of June and the 15th of July 2024. The survey consisted of twenty-five
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45 questions and was divided into two sections: the first, used as an icebreaker, focused on the visitor's
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48 use of the park with questions on movement patterns, frequency and the drivers of the visits, while
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51 the second targeted people's personal knowledge, experience and opinion on wolves' presence. The
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54 sociodemographic variables collected included gender, age and country of origin. Participants were
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57 selected using convenience sampling with binary gender quotas. Given the time and logistical
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60 constraints, this approach represented the most feasible option to collect a preliminary overview of
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63 visitors' perceptions. Due to the non-probabilistic sampling method design, results are best interpreted
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66 as exploratory insights specific to the sampled respondents rather than as generalizable inferences

231 about the entire Hoge Veluwe visitors population. The full questionnaire is available in
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232 Supplementary Data S1.

233 *Data analysis*

234 Survey responses were analyzed using a combination of qualitative and quantitative statistics, with
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235 percentages computed and interpreted to reveal overarching patterns. A chi-squared test was applied
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11 to identify significant relationships between sociodemographic and response variables within the
1236 dataset. A generalized linear model (GLM) was used to quantify the influence of explanatory
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14 variables on the likelihood of a “success” outcome in the survey. Odds ratios were calculated to
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16 evaluate the relative effect of a specific category compared to a reference category for each
1238 explanatory variable.
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242 **RESULTS**

243 **Camera trap data**

244 The nine camera traps placed on trails from May to September 2024 yielded 2680 detections. The
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32 monthly capture rate ranged from 0 to 0.80 for wolves and 0.10 to 12.08 for recreationists. The highest
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245 number of detections occurred in the month of June, with 63 and 696 recorded events for wolves and
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35 visitors respectively. As capture-time distributions reflect information on daily activity patterns at the
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37 population level (Rowcliffe et al., 2014), density plots across all sampling locations indicated that,
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39 on trails, wolves were predominantly nocturnal with peaks around 5:00 and 20:00-21:00 in contrast
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41 with visitor activity, which increased after park opening and decreased before closure, peaking around
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43 midday. The overlap coefficient values ranged from 0 to 0.31 (see Table 1; Fig. 2) across the nine
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45 locations.
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53 In contrast, off-trail activity captured by the 48 cameras in the permanent wildlife monitoring network
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55 between May and September 2024 followed a relatively constant spatio-temporal distribution with
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57 no strong temporal shifts (Fig. 3a) or spatial shifts between open and forested habitats (Fig. 3b)
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59 throughout the 24-hour cycle. Minor peaks appeared in the activity curve (n = 91), but these likely
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257 reflect low sample size and side effects of the habitat-weighting procedure rather than true activity
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258 surges (Fig. 3a). The daily distribution over habitat type revealed a rather constant proportional use
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259 of forest and open habitat (Fig. 3b). The available habitat in the study area consisted of 53.3% forest
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260 and 46.7% heathland; accordingly, the observed occupancy closely mirrored these proportions, with
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261 53.7% forested and 46.3% open area use recorded.

262 263 **Survey data**

264 An initial overview of visitation patterns indicates that the majority of respondents reported infrequent
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265 visits, with 60.1% visiting for the first time and 22.66% less than once a year. Primary visit drivers
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266 were predominantly cycling (30.9%) and museum visits (26.56%) among interviewees. Regarding
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267 mobility choices within the park, 28.14% of the respondents moved on foot along designated paths,
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268 while most relied either on private cars or on the free bicycles provided by the park. Almost half of
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269 the participants (44%) were traveling in groups of more than two people while 8% reported visits
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270 with their dog.

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Turning to media representation, most respondents (60%) perceived the media coverage on wolves
in their countries as predominantly negative, whereas 32.5% described it as positive. However, this
pattern was not uniform between compatriots: 63.33% of Dutch respondents reported negative
mediatic coverage, yet their perception of the wolf did not seem directly affected by it (26.11%
reported a negative impact, 24.63% a positive impact). Overall, wolf presence was more frequently
perceived as positive (41%) than negative (34%). Gender differences were minimal, although women
expressed slightly more positive views. Age and nationality emerged as more salient factors, with
respondents over 65 years old perceiving the wolf's impact as predominantly negative, in contrast
with younger groups. Dutch citizens (62%, n=126/203) focused slightly more on the negative
impacts, whereas non-Dutch citizens (38%, n=77/203) reported the opposite. Despite these trends, no
strong correlation was found between the selected variables and variations in perceptions of the wolf's

282 impact in the recreational area. Dutch nationality was the best predictor among those considered,
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283 though only marginally significant ($p=0.064$).
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284 Most respondents recognized that the wolf could add value to the park, aesthetically and ecologically.
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285 Opinions on the aesthetic value were significantly influenced by age ($\chi^2=14.654$, $df=3$, $p=0.002$) and
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286 nationality (Dutch vs non-Dutch; $\chi^2=8.830$, $df=1$, $p=0.003$). The final model included both ‘age’ and
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1287 ‘Dutch nationality’ as explanatory variables (AIC = 546.798). Compared to respondents under 25
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288 years old, those aged 25–50 were 40% more likely to agree with the wolf’s added value, whereas
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1289 respondents aged 50–65 and >65 exhibited 47% and 63% lower odds, respectively. Dutch
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290 respondents showed 56.3% lower odds of recognizing the wolf’s additional value compared to
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291 visitors of other nationalities. Fear responses were also analyzed, showing that fear was significantly
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292 associated with the Dutch nationality ($\chi^2 = 6.904$, $df = 1$, $p = 0.009$; AIC = 515.618). Again, Dutch
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293 respondents showed 52.3% lower odds of expressing fear in comparison to non-Dutch visitors.
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295 When asked whether wolves belonged to the park, responses tended towards neutrality, particularly
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308 presence, while older respondents (50–65 and over 65 years old) had 57% and 45% lower
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309 probabilities, respectively. Dutch interviewees were 54% less likely than non-Dutch to report an
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310 increase in visitation frequency due to the wolf presence.
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DISCUSSION

Wolves have increasingly recolonized human-dominated landscapes, yet the mechanisms underlying human-wolf dynamics remain poorly understood, especially those regarding wolves' persistence in recreational areas with high visitor load. Our study provides a fine-scale assessment of wolf movements and visitor perceptions from the same study area, linking together social and ecological aspects. Building on our results, wolves exhibited evenly distributed activity patterns across the 24-hour cycle in the off-trail camera data set, suggesting limited spatio-temporal behavioral adjustment in response to human presence. In particular, the consistently high proportional use during daylight hours suggests that wolf habitat use in this park was not constrained by human activity, neither in forests nor in open areas. These findings align with growing evidence that wolves can persist in human-dominated landscapes by exhibiting behavioral plasticity and tolerance towards human presence (Barker et al., 2023). An alternative explanation may be related to prey displacement towards public-access areas to decrease the likelihood of predation (Berger, 2007).

Despite this high relative proportion of habitat use during daytime hours indicating potential spatial overlap with recreationists, activity patterns of wolves and visitors on trail crossings revealed high temporal segregation throughout the study period. In these specific locations, wolves were primarily nocturnal and largely inactive during midday hours when human activity peaked, suggesting that spatial overlap does not necessarily lead to an elevated encounter risk. Daytime detections and direct encounters were rare and only occurred on trails with low absolute human frequency or with dense forest cover. Human disturbance is negatively correlated with wildlife detection probability (Oberosler et al., 2017), often leading to more elusive behaviors (Suraci et al., 2019) and adjustments of species' spatial and temporal activity patterns in response to human presence, increasing

334 nocturnality (Gaynor et al., 2018) or strictly avoiding anthropogenic features such as buildings and
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335 roads (Kuijper et al., 2024). Such spatio-temporal segregation is also common in protected areas
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336 where visitor activity is intense (Oberosler et al., 2017).
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337 However, in the Hoge Veluwe, the availability of spatial refuges (e.g., off-path restrictions and dense
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338 forest cover with limited visibility) together with predictable spatially concentrated disturbance along
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339 trails, bike lanes, museums and restaurants channel visitor flows away from remote areas. This setting
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340 gives wolves the possibility to adjust their time-energy budgets and remain active during the day
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341 without requiring strong spatial displacements (Linnell et al., 2016). Moreover, nocturnal windows
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342 of minimal human activity due to park closure to the public (Lewis et al., 2021; Gaynor et al., 2018)
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343 allow wolves to allocate energy toward demanding behaviors such as hunting and territorial defense
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344 when human disturbance is at its lowest.
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346 The socio-ecological evidence of limited encounter risk aligns with the generally neutral-to-positive
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347 attitudes expressed by visitors, suggesting that current wolf presence does not substantially undermine
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348 recreational experiences. Knowledge about wolves' conservation status and population trends
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349 appeared robust, with the presence of packs and human-wolf conflicts in respondents' areas playing
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350 a role in this awareness. Judgments were strongly shaped by both direct and indirect experiences of
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351 conflict faced by respondents or members of their social circle, whereas media coverage had a
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352 comparatively smaller influence due to emotional distance and reduced risk perception. By contrast,
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353 the lack of previous experiences often led to ambivalence, with opinions shaped by the prevailing
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354 local media narrative or by preconceptions rather than by objectivity. Pro-wolf narratives appeared
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355 more effective in catalysing public opinion, whereas coverage emphasizing human-wolf conflicts
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356 created more division. This aligns with earlier findings suggesting that sensational media coverage
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357 has the power to leave lasting impressions (Bombieri et al., 2018), which make people overestimate
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358 the likelihood and the consequences of encounters, ultimately reducing tolerance (Pohja-Mykrä &
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359 Kurki, 2014), hampering conservation efforts and fueling poaching (Suutarinen & Kojola, 2017).
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360 Notably, these effects do not occur in isolation but get shaped by multiple social factors, including
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361 management procedures, institutional efficiency and the time elapsed since wolf recolonization
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362 (Pettersson et al., 2021). In general terms, visitors had a positive view of the wolf impact with a
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363 prevailing proactive approach towards coexistence rather than towards systematic population control.
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364 However, respondents less favorable to wolf presence tended to support coexistence only under the
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365 condition that systematic population control is implemented and clear thresholds are established.
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366 Active population management is often considered an essential strategy to embrace a land-sharing
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367 perspective, as it enhances the perception of institutional oversight and control (Pettersson et al.,
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368 2021; Pettersson and Von Essen, 2025). Geographical and cultural background further shaped
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369 perceptions. Visitors from highly urbanized regions such as the Randstad region expressed support
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370 for the presence of the wolf, while residents from other Dutch provinces had a more reluctant attitude.
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371 A predominantly positive stance among urban residents may generate friction with rural communities,
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372 which may interpret wolf recovery as an urban-imposed vision of nature that overlooks the practical
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373 and social challenges of coexistence (Drenthen, 2021; Keuning, 2022). The dominant trend obtained
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374 from the European nationalities in the sample revealed a prevailing positive evaluation of the wolf in
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375 rural areas too, even though mixed feelings of resignation were reported within some communities.
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376 Compared to Dutch, visitors from other countries expressed more consistently positive attitudes,
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377 possibly reflecting longer coexistence histories in their countries of origin, where local communities
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378 consider wolves a component of the ecosystem and an opportunity for local tourism rather than as
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379 incompatible intruders in the system (Houston et al., 2010; López-Bao et al., 2017). In densely
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380 populated countries such as the Netherlands, characterized by high human and livestock densities
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381 (Eurostat 2020), land fragmentation and extensive infrastructure, the perception of limited spatial
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382 capacity may amplify concerns about carnivore recolonization, especially when this requires a sudden
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383 change in people habits. Even though visitors may not be afraid, the unease that can arise when
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384 walking in wolf areas, coupled with the need to reconsider expectations on the use of recreational
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385 spaces and ungulate visibility, could reduce the likelihood of future visits. Feelings of “lack of space”
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386 or reduced control can shape resistance to adaptation, even in the absence of direct fear. However, as
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387 found by Breyne (2020), people would rather increase or keep the frequency of their visits unchanged
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388 than decrease it.
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390 While providing an integrated ecological and social assessment, several limitations should be
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11 acknowledged. First, this study was conducted within a single protected area over a limited temporal
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13 window. Wolf behavior and human perceptions vary in response to seasonal prey dynamics, prey
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15 abundance, day lengths, park opening times, fluctuations in visitor numbers and episodic conflict
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17 events. Second, the survey component relied on voluntary participation; thus, individuals with a pre-
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19 existing interest in wildlife or conservation topics may have been more willing to participate,
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21 potentially resulting in more optimistic attitudes toward wolves than those present in the broader
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23 visitor population. Furthermore, the sample included a substantial proportion of tourists and first-time
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25 visitors, which underrepresent the perspectives of local residents who experience more sustained
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27 exposure to wolf presence.
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3400 35 36 **CONCLUSIONS** 37

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39 In conclusion, our findings indicate that, within a highly structured recreational landscape, wolves
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41 show high behavioral flexibility, adapting to high levels of human disturbance. However, the spatial
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43 overlap with humans did not prevent high temporal segregation on trail points, reducing the
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45 opportunities for conflicts. Predictable and spatially concentrated patterns of human disturbance and
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47 restrictions to tourists' use of the area allow wolves to remain active during the day without being
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49 seen, as shown by the off-trail camera network. Conversely, visitor perceptions reveal a generally
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51 neutral to positive coexistence-oriented attitude and limited evidence that wolf presence undermines
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53 their recreational expectation or future visit likelihood. Together, these ecological and social patterns
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55 suggest that space sharing in intensively used protected areas may be facilitated by the combination
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57 of controlled human mobility, spatial refuges for wildlife and park's closure times rather than strict
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412 segregation. Integrated approaches can help produce results that balance conservation practices with
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413 recreational use while providing a more accurate understanding of risk perception while engaging
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414 recreationists in the process.
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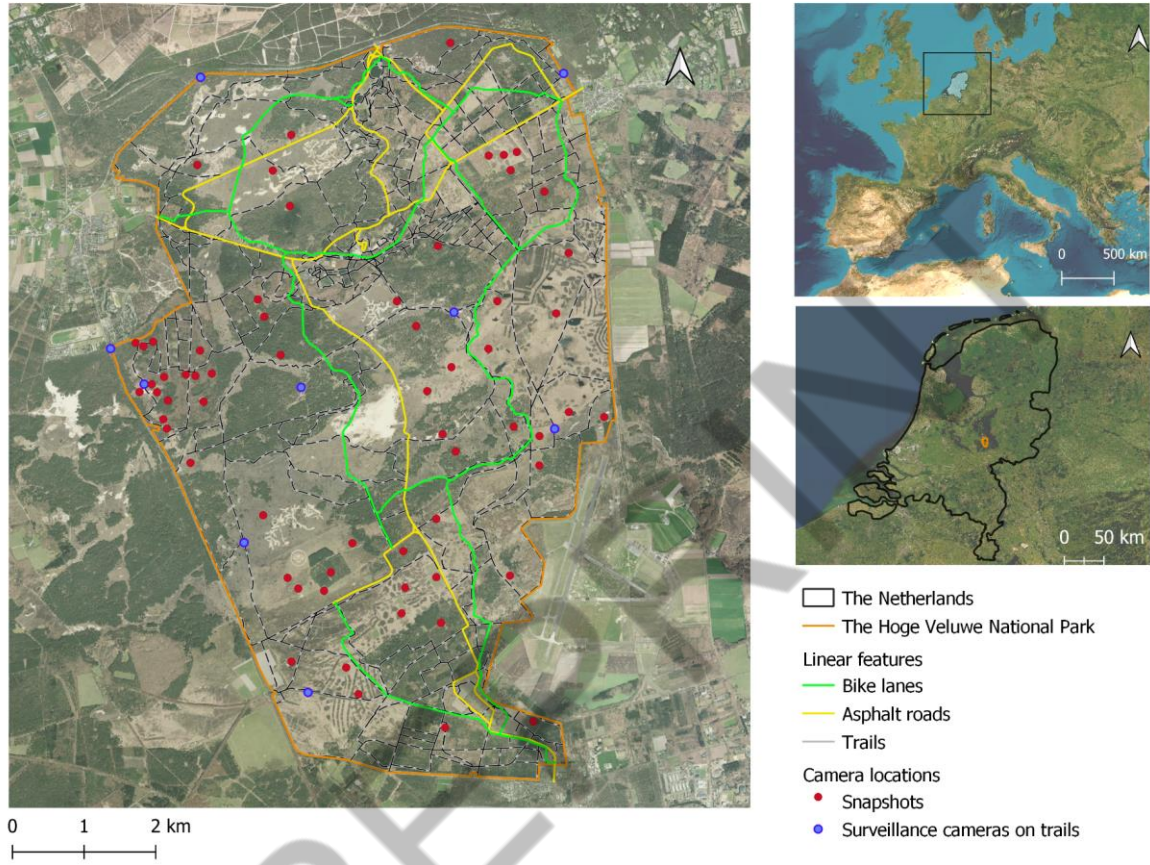
566 **Table 1.** Records from camera trap locations on trails. For each of the nine locations, the number of
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 567 wolves and visitors and the camera activity period were used to calculate the capture rate for the
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 568 two species. The coefficients of overlap are also reported.
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Location	Activity period	Number of wolves	Number of visitors	Wolf-visitor ratio	Overlap	Capture rate wolves	Capture rate visitors
Otterlo forest	111	89	56	1.59	0.11	0.80	0.50
Driftsands Otterlo	123	92	83	1.11	0.15	0.75	0.67
Pleijmen corridor	97	18	62	0.29	0.12	0.18	0.64
Old rest area	46	8	170	0.05	0.05	0.17	3.69
Genieweg	154	29	16	1.81	0.22	0.19	0.10
Siberie	89	8	1075	0.01	0.31	0.09	12.08
Koeverbos corridor	124	34	342	0.10	0.18	0.27	2.76
Deelense start	101	9	171	0.05	0.13	0.09	1.69
Mouflon fence	73	0	417	0	0	0	5.71

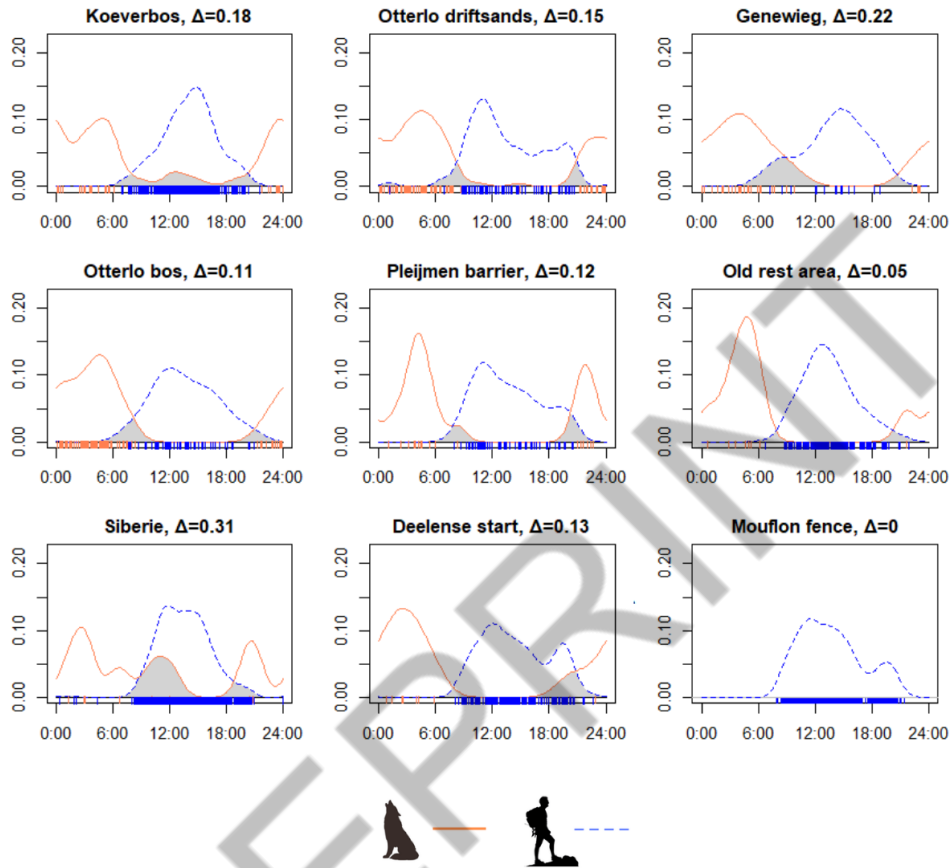
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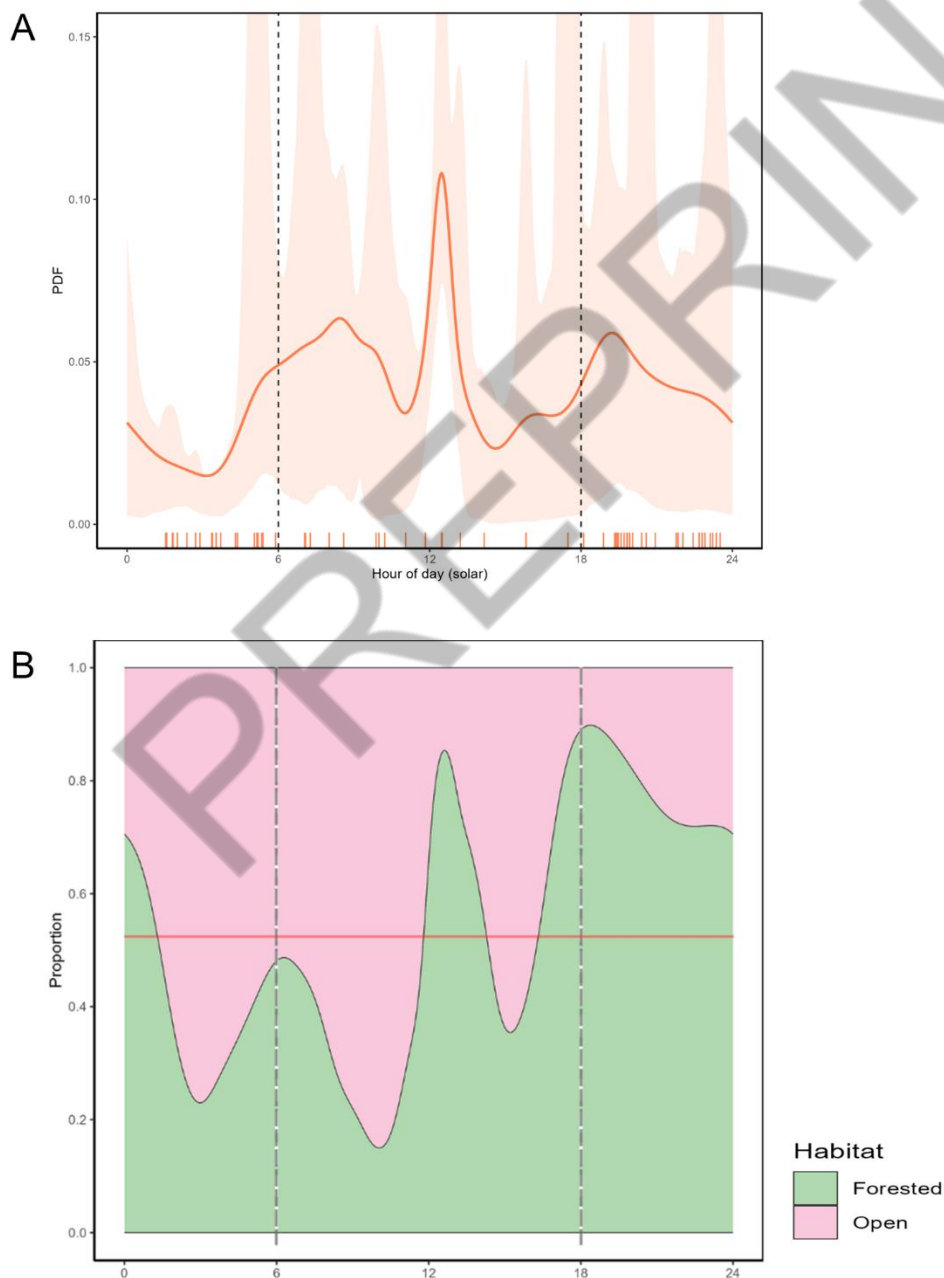
Figure 1. Map of Hoge Veluwe National Park (54 km², 52.1° N, 5.8° E, Netherlands) and the camera trap locations.



584 **Figure 2.** Activity patterns of humans (blue dotted line) and wolves (orange line) at the different
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585 locations. The overlap coefficient ranges from 0 to 0.31 and is shown by the shadow area.
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588 **Figure 3.** Wolf activity and habitat use in Hoge Veluwe National Park during 2024, estimated from
1 captures on camera traps. (A) Smoothed circular density of wolf detections (solid line) from May to
589 September 2024 (n=91), with a 95% bootstrap confidence envelope (shaded). Red ticks represent
590 raw observations. (B) Proportional daily distribution of detections in forest (green) and open (pink)
591 habitat. The red dashed line represents the expected proportion based on habitat availability (53.3%
592 for forest and 46.7% for open habitat, respectively). Time was standardized to solar time but shown
593 in hours for readability; dashed lines indicate sunrise and sunset.



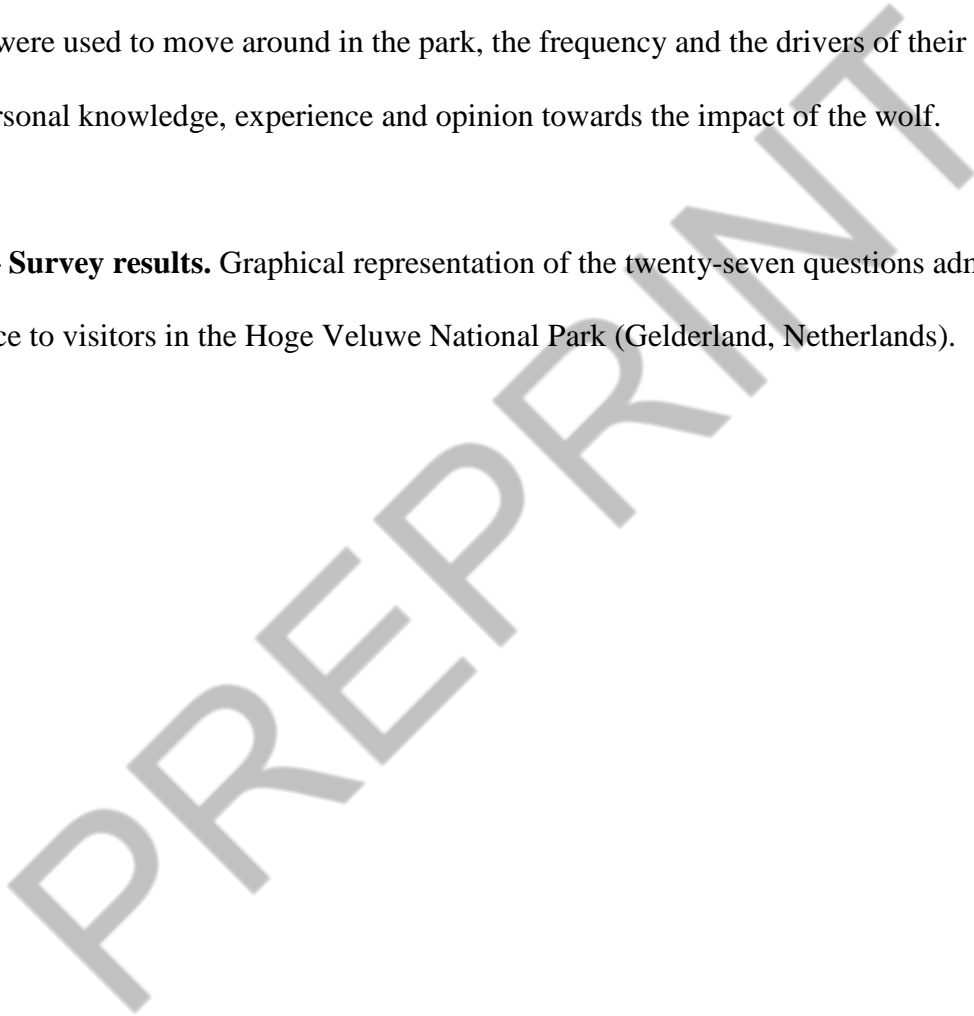
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596 **Supporting Information – Online Resources**

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Data S1 - Survey. Questions administered face to face to visitors in the Hoge Veluwe National Park (Gelderland, Netherlands). The data collection for the survey was done from the 15th of June to the 15th of July, involving 203 participants. The survey had twenty-seven questions, and it was divided in two sections: 1) Icebreaker, focused on the visitor's use of the park with questions on the way they were used to move around in the park, the frequency and the drivers of their visits; 2) people personal knowledge, experience and opinion towards the impact of the wolf.

Data S2 – Survey results. Graphical representation of the twenty-seven questions administered face-to-face to visitors in the Hoge Veluwe National Park (Gelderland, Netherlands).



608 **Declarations**

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609 *Ethics approval and consent to participate*

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610 The study complies with all relevant national and regional laws, and with the ethical standards of
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611 scholarly research.

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Availability of data and materials

614 All data generated or analysed during this study are included in this paper and in its supplementary
615 information files, or available upon request.

617 *Competing interests*

618 The authors declare that they have no competing interests.

620 *Funding*

621 This research did not receive any specific grant from funding agencies in the public, commercial, or
622 not-for-profit sectors.

625 **CRedit authorship contribution statement:**

1
26 **Zambotto G.:** Writing – review & editing, Writing – original draft, Data curation, Formal analysis,
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27 Conceptualization. **Chirichella R.:** Writing – review & editing, Data curation, Methodology,
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28 Conceptualization. **Jansen P. A.:** Writing – review & editing, Methodology, Conceptualization,
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29 Supervision. **Dijkhuis L .R.:** Data curation, Writing - review and editing. **Liefting Y.:** Data
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30 curation, Software. **Leidekker J.:** Writing – review & editing, Conceptualization. **Apollonio M.:**
12
13
31 Writing – review & editing, Conceptualization, Supervision.
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27 Mission 4 Component 2 Investment 1.4.
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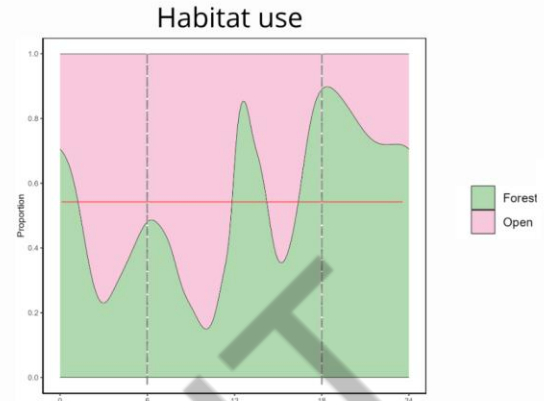
641 **Highlights**

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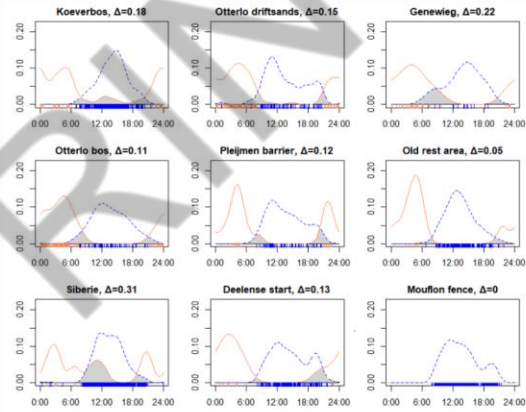
- Constant spatio-temporal distribution of capture events off trail over the 24-hour cycle in both forest and open areas.
- Low overlap ($\Delta = 0-0.31$) between wolf and human activity patterns on trail points.
- Visitors expressed a general neutral to positive attitude towards wolf presence.

PREPRINT

Wolf-human interaction in the Hoge Veluwe National Park

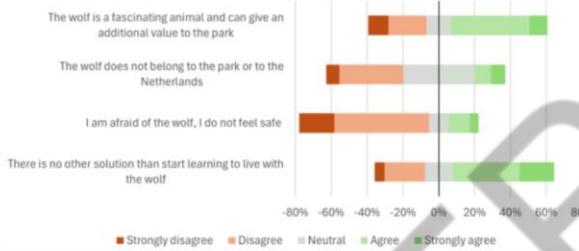


Overlap in daily activity patterns



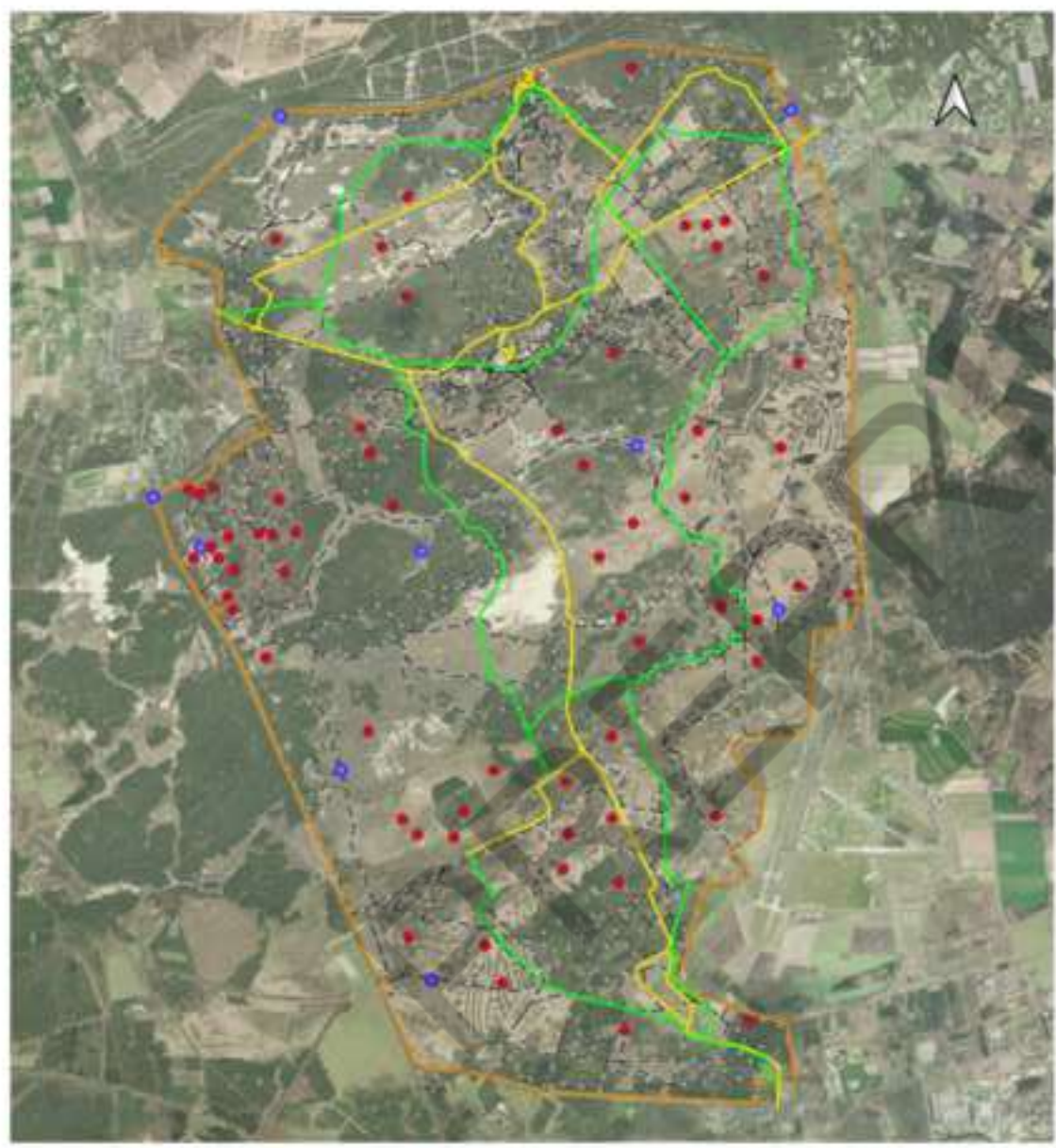
Insights on visitors' perception

How do you feel about the following statements?



PREPRINT

Figure 1



-  The Netherlands
-  The Hoge Veluwe National Park
- Linear features
 -  Bike lanes
 -  Asphalt roads
 -  Trails
- Camera locations
 -  Snapshots
 -  Surveillance cameras on trails

