Individual variation in red deer responsiveness towards human disturbance: A prospect for wildlife viewing in Europe's national parks.

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Abstract

Animals adjust behavior to changes in perceived predation risk, their so called “landscape of fear”. However, individuals within populations can differ greatly in their plasticity towards perceived risk. In national parks, where animals are often protected from human hunting, wildlife may start losing their fear of humans and become more observable, a process that starts at the individual level. Here we aim to test whether ungulates in one of the only largely non-hunted populations in Europe show individual variation in behavioral plasticity towards gradients of human disturbance. We used random regression to dissolve the individual movement responses of 63 red deer (*Cervus elaphus*) to spatio-temporal variation in human recreation. We measured human disturbance as the number of recreationists on the closest trail on a given day. We quantified conditional repeatability, i.e., between-individual variation, along the perceived risk gradient. To avoid pseudoreplication, we fitted models to the hours of the day with peak activity or passivity. Diel activity patterns were conserved across individuals in our population, with peak activity in the early morning and late evening. When actively foraging during the morning, red deer responded to human disturbance with flight, i.e., longer hourly movement distances, while they reduced movement in response to disturbance when resting in the middle of the day. Between-individual variation increased with visitor frequentation, i.e., red deer behaved similarly when human disturbance was low, but with increasing human disturbance some deer adjusted movement while others responded little. Our results show that individuals varied greatly in their responsiveness towards human disturbance, with some resuming normal movement behavior. Flight responses are costly and may be selected against in non-hunted populations, leading to an increase in human-tolerant individuals over time. These are good news for national parks for which wildlife viewing is an effective tool to engage the public in conservation. Observing wildlife in Europe is difficult, likely due to a long persecution history and strong hunting pressure. Our results

demonstrate that large non-hunting zones may, over time, successfully reduce wildlife's extreme fear of humans.

Keywords: Landscape of fear, individual plasticity, animal personality, reaction norm, movement

Introduction

Animals make state-dependent decisions about when and where to move and dynamically adjust movement to the local environmental conditions (Nathan *et al.* 2008). For example, movement decisions differ when animals are foraging versus selecting resting sites and movements often slow down at steeper slopes and denser vegetation. When animals are active, their movement decisions are dominated by two main drivers: finding areas of high forage availability and avoiding predation risk. In particular for ungulates, foraging and risk avoidance (sometimes of multiple predator species (Lone *et al.* 2014)) lead to trade-offs as the highest quality food can often be found in open meadows where visibility and predation risk are higher (Mao *et al.* 2005).

How animals manage this trade-off has been at the heart of ecological research, referred to as the "landscape of fear". Landscapes of fear describe where and when prey perceive predation risk as high and adjust their behavior accordingly (Kohl *et al.* 2018; Gaynor *et al.* 2019). Recent advances indicate that prey responsiveness to perceived landscapes of fear, expressed for example as plastic adjustments of movements to increasing risk or infrastructure, may vary substantially among individuals (Dammhahn, Lange & Eccard 2022; Xu *et al.* 2023). Contrarily, comparative studies under controlled conditions suggest that high perceived predation risk may limit the expression of between-individual variation and force individuals to conform to a common behavioral phenotype, while behavioral variation can be expressed more freely under low perceived risk (Dingemanse *et al.* 2009). However, under controlled conditions, risk-benefit trade-offs are solely hypothetical as selection pressures are absent (i.e. no fitness benefits of higher resource acquisition and no mortality cost of risky behavior) and therefore laboratory findings may not apply in the wild (Moiron, Laskowski & Niemelä 2020).

Here we aim to test whether ungulates in the wild differ in behavioral plasticity towards gradients of perceived risk. We are particularly interested in whether fear promotes or restricts between-individual variation compared to contexts that are perceived as less risky. We use a model system of an ungulate prey, the red deer (*Cervus elaphus*), responding to spatio-temporal variation in human presence, their main predator. Red deer have been hunted to extinction throughout large parts of Central Europe, have since recovered in isolated populations and are nowadays again one of the top game species. At the same time, in national parks, nature tourism and wildlife viewing, are becoming important agents to increase the public's appreciation for protecting nature (Böhn 2021). Yet observing wildlife in Central Europe is difficult, even in national parks. The most likely reason is that, unlike in North America or Africa, game species are rarely protected from hunting in European national parks, the rationale being that populations need to be managed in absence of regulatory natural predation (van Beeck Calkoen *et al.* 2020). Our study area, the Bavarian Forest Nationalpark (BFNP) offers a unique situation of a no-hunting zone, which was first implemented 25 years ago in 1997, which represents approximately 5 red deer generations (Coulson *et al.* 1998). The non-hunting zone nowadays encompassed 75% (18,700 ha) of the park area. However, human disturbance is rife, with intense frequentation by visitors and recreationists over the summer months, and heavy hunting pressure in the management zone and outside of the park. The system, therefore offers a unique opportunity to study spatio-temporal dynamics of prey responses to perceived fear because we can track and model human presence at very fine resolutions: Human visitors are almost exclusively active during the daylight hours and on trails, are more abundant during weekends, vacations or when the weather is nice and are disproportionately more active on trails close to parking lots, huts or touristic points of interest. Visitors on trails have been counted with eco-counters and wildlife cameras originally deployed in the frame of a large carnivore monitoring along trails over the

course of one year, which formed the basis of a model predicting daily visitor load on every official trail in the park (Mitterwallner *et al.*). However, as suggested previously, spatial context is expected to modulate the impact of human disturbance on red deer behavior. For example, deer may be less responsive to humans when hidden in dense vegetation. The BFNP actively monitors its forests and fine scale Lidar scans provide the basis for a high-resolution shrub and visibility layer, allowing to control for the spatial context of concealing vegetation cover (Zong *et al.* 2021a). Our model system provides a natural experiment to test the synergetic effects of human disturbance and cover on the expression of between-individual variation in red deer movement behavior. Our main objective for this study was to determine whether human disturbance promotes or restricts individual variation in red deer movements. In the absence of hunting in large parts of the area, more risky individuals are not removed from the population. We therefore predicted that some individuals respond with flight to higher perceived risk, while others are more observable and less disturbed by humans. Such between-individual variation in responsiveness could over time lead to a less fearful and more observable red deer population in the BFNP.

Methods

Study area and species

The study took place in the Bavarian Forest National Park (BFNP, 49°3´19´´N; 13°12´9´´E, 254km^2), Germanys oldest national park. The forest has been largely unmanaged for the past 50 years creating, together with the Czech Sumava NP, the largest strictly protected forested area in Central Europe (Heurich *et al.* 2015). More than 60% of the area is covered by coniferous forest (mainly Norway spruce, *Picea abies*), 20% by mixed forests, and 14% by grasslands. The area is characterized by low to intermediate elevations (500 - 1453 m.a.sl). Nowadays the BFNP is a popular area for recreational activities with about 300 km of hiking

and 150 km of biking trails and approximately 1.3 million visitors annually. Several access points with designated parking areas provide access to a dense network of hiking trails. The park is home to a thriving red deer population (*Cervus elaphus*), which was formerly extinct in the area, alongside roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Natural predators are the Eurasian lynx (*Lynx lynx*) feeding mostly on calves (Belotti *et al.* 2015) and the Grey wolf (*Canis lupus*) that has been recolonizing the area since 2015 (Hulva *et al.*). The red deer population is partially migratory with 25 %, while the remaining 75% stay in their summer ranges (Peters *et al.* 2019). Hunting is strictly prohibited throughout most of the study area in the BFNP (75%). However, the red deer population is still closely managed. Annual quotas are determined based on counts, quotas in previous years and browsing damage. Hunting is allowed in the park's hunting zone, which is located along its borders as well as outside the park's boundaries from June to January and red deer are mainly hunted from high stands and culled in winter enclosures. These structures are feeding stations that are fenced, intending to reduce damages in managed forests near the border of the park (Möst *et al.* 2015).

Red deer movement data

Between 2018-2021 we captured and collared 63 mature female red deer in four winter enclosures. While most individuals were equipped with collars without chemical immobilization, some were immobilized via teleinjection, with the Hellabrunner mixture (Ketamin and Xylazine). Experimental procedures were approved by the Ethics Committee of the Government of Upper Bavaria (permit number: ROB-55.2-2532.Vet_02-19-130; ROB-55.2-2532.Vet_02-17-190). Red deer were fitted with Vertex Plus GPS collars from Vectronic Aerospace GmbH, scheduled to record a GPS location every hour. We removed positions resulting in unusually long displacements (> 4000 m) or unusually high speeds (>

4.17 m /s). We included locations from the beginning of May to the end of October, i.e., the period of the year when red deer are not in the winter enclosures. Most individuals were followed for more than one year (range 1 – 4 years) resulting in 104 monitoring years (deer-year). We constructed individual movement trajectories and calculated step-lengths using the R package amt (Signer, Fieberg & Avgar 2018). Step-length was calculated as the Euclidian distance between successive, hourly positions of an individual. We extracted spatial covariates for the leading GPS location of each step-length.

Spatial covariates

Human disturbance

From November 2020 – November 2021 61 wildlife cameras were distributed along the BFNP trail network in the frame of the large carnivore monitoring, providing additional information on human recreation activities on trails at any given day of the year. On a total of 24,461 camera days, we captured > 700,000 pictures. We attributed information about weather, weekend and holiday seasons and the location of the path relative to parking sites and huts, the density of parking sites and touristic points of interest in the area as well as information on the path access restrictions, to model the number of daily visitors on a given hiking trail and to predict spatio-temporally explicit trail use. Our models explained 44/47% of the variance in the number of daily visitors (Mitterwallner *et al.*). We extracted the closest path segment for each red deer GPS location and predicted the number of visitors expected on this path on the given day when the red deer GPS location was recorded.

Visibility at 140cm from LiDAR data

In June 2017, the entire national park was subject to airborne LiDAR scanning (ALS) from a helicopter using a Riegl LMSQ 680i instrument. Scans were conducted with a helicopter

from 550m flight altitude. The average point density was 30 points/m2 and the vertical and horizontal accuracy of the ALS data was 6 and 5 cm (Krzystek *et al.* 2020). We used fine scale terrestrial LiDAR scans at 93 forest sampling plots to build a random forest model that best predicted visibility. Using ALS sensed metrics of the five covariates best predicting visibility we then predicted visibility across the whole park. These five covariates were: 10th height percentiles of canopy returns, 70th height percentiles of understory returns, normalized relative point density (NRD), percentage of NRD and coefficient of variation of 99th height percentiles of understory returns. We specifically predicted habitat visibility at 140 cm height (equivalent to a standing height of red deer). The resulting visibility layer had a spatial resolution of 35m. Please refer to (Zong *et al.* 2021b; Zong *et al.* 2022) for methodological details.

Statistical analyses

The main aim of this study was to assess between-individual variation in plasticity towards human disturbance with random regression. Movement trajectories are a great source of data providing many repeated measures of an individual's behavior (here step length) along ecological gradients. However, movement data are inherently spatially and temporally autocorrelated, particularly when fix intervals are short, under limited movement activity (i.e., stationary behavior), or when the spatial resolution at which ecological covariates are measured is courser than the step length. To avoid pseudoreplication and, thereby upward bias of between-individual variation estimates (successive records of an individual reflecting the same behavior under the same conditions, Niemelä & Dingemanse 2017), we first determined red deer diel activity patterns to then select data at discrete times of day for further analyses, effectively ruling out any potential for temporal autocorrelation or pseudoreplication.

Diel activity patterns

We determined diel patterns of movement activity, measured as step length, by fitting a cubic spline over the time of day. We accounted for between-individual variation in activity patterns with a random intercept and slope for each deer-year. Because diel activity may shift over the summer due to changing daylight or disturbance, we fitted individual models for each month (May to October). We log-transformed step lengths as they were highly skewed towards shorter distances. We quantified and visually examined whether individual variation in diel activity patterns existed. We then inspected the population average diel activity profile and selected the month-specific hours of the day when activity peaked or was at its lowest for further analysis.

Random regression

Given a bimodal activity pattern, we fitted four models, one for the respective hours of the day when activity peaked or troughed. We modelled step length (log-transformed) as a function of human disturbance interacting with visibility at 140cm height. Red deer were mostly in close vicinity to the next trail where the disturbance was measured (median distance 155m, few positions up to 2km from the closest trail), owing to the high trail density in the park. We only included positions no farther than 300m from a trail (80% of all red deer positions in the original dataset), which we presumed to be within the perceptional range of red deer. We expected that visibility, i.e., cover, would moderate the effect of human disturbance on red deer behavior and therefore fitted an interaction between the two terms. We further accounted for known effects of elevation (nonlinear second-order polynomial) and canopy cover on movement behavior. Last, we fitted random intercepts for each deer-year and random slopes over human disturbance interacting with visibility to account for

between-individual variation in behavior plasticity. To interpret effects, we predicted red deer movements from low to high human disturbance (resp., 1 – 40 recreationists on the closest trail, Supplementary material Figure S2) and at low and high visibility (10th and 90th percentile of visibility distribution, Figure S1), while we assumed an average elevation and canopy cover.

Between-individual variation in plasticity

We assessed between-individual variation in plasticity using estimates of conditional repeatabilities along the gradients of human disturbance and visibility following (Schielzeth & Nakagawa 2022). Conditional repeatability is the ratio of between-individual variance to phenotypic variance (between-individual variance plus residual variance) at specific levels along the environmental, i.e., random slopes gradient. The index ranges from 0 to 1 with higher values indicating greater between-individual behavioral variability.

All random regression and diel activity models were fit with a Gaussian family on log transformed step length using the R package brms (Bürkner 2017). We ran four chains over 2000 iterations with a warmup of 1000 and a thinning interval of 2. The model inference was based on 2000 posterior samples and had satisfactory convergence diagnostics with $\hat{R} < 1.01$ and effective sample sizes > 1000. Posterior predictive checks recreated the underlying Gaussian distribution well.

Results

Pronounced crepuscular activity pattern with little between-individual variation

Red deer showed a crepuscular activity pattern over the entire summer, which shifted with changes in sunrise and sunset (**Fig 1**). Movement distances were longest during the morning

and evening twilight. Movement distances were shorter during the night and daylight hours with pronounced resting during midday. Although between-individual variation in movement distances were evident, we found little between-individual variation in the shape of the diel activity patterns, i.e., all individuals followed a bimodal activity pattern. We therefore proceeded to analyze between-individual variation in movement during the month-specific hours of highest and lowest activity (gray bars in **Fig 1**).

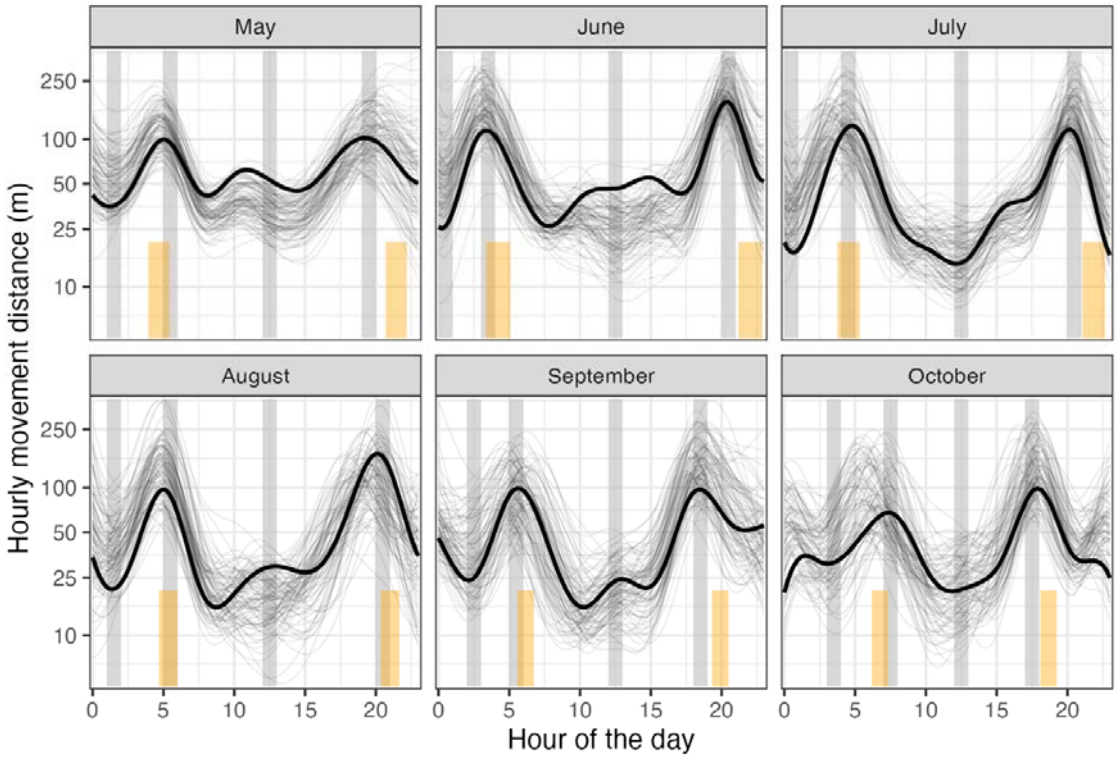

Fig. 1 Population (thick line) and individual level (thin lines) diel activity patterns of red deer monitored in the Bavarian Forest National Park from May to October. Orange bars indicate times of dusk and dawn (from nautical dawn until sunrise and from sunset to nautical dusk). Grey bars indicate hours of peak activity and lowest activity. We took forward daily movement distances recorded at hours of highest and lowest activity to model between-individual variation in red deer responsiveness towards human disturbance.

Population level responses to human disturbance and visibility

Selecting the month-specific hours of highest and lowest activity we fitted four behavior- and daytime-specific models, each based on around 12,000 GPS locations from 104 deer monitoring years: a night passive model (selecting step length at 12 – 3 am, depending on the month, see **Fig. 1**), morning active model (3 – 7 am, **Fig. 1**), midday passive model (centered at 12 pm, **Fig. 1**), and evening active model (6 – 8 pm, **Fig. 1**). Human disturbance on trails varied from 1 to 111 visitors per day but red deer mostly experienced low numbers of visitors per day (1st – 3rd quartile = 5 – 11, Figure S2), though almost all red deer were exposed to a moderate number of 20 visitors at some point (Figure S2). Red deer were primarily found in intermediately dense vegetation with moderately high visibility, except for the middle of the day when they were found in areas with lower visibility (Figure S1).

Behavioral responses of red deer to human disturbance were context and state depended, both at the population and the between-individual level (**Table 1, Fig 2**). On the population level, red deer responded to increasing numbers of recreationists during the daytime (morning active and midday passive) but not during the night (nights passive and evening active) (partial support for human disturbance term, **Table 1**). Red deer moved over longer step length in open than in dense vegetation at all times of day (support for visibility term, **Table 1**) and particularly during the morning active and midday passive bout. The effect of human disturbance on red deer movement was not moderated by the surrounding vegetation (no support for the interaction term, **Table 1**). Specifically, red deer responded most strongly to increasing human disturbance (from 1 – 40 recreationists) during the morning activity bout and increased movement distances from 140 to 190 m/hr, when in open vegetation (**Fig 2**). While, in line with their diel activity patterns, red deer generally moved very little during the middle of the day resting bout, they further reduced movement from an average of 48 m/hr to 10 m/hr on days when disturbance was high and when in open vegetation (**Fig 2**).

Between-individual variation in responsiveness to human disturbance

Red deer varied most strongly in their responsiveness towards human disturbance during the morning bout of activity (**Table 1**). For example, under high visibility the most responsive individual increased movement fourfold, from 200m/hr under low disturbance to 790m/hr under high disturbance (**Fig 2**), while the least responsive individual only increased movement by 60m/hr (from 190m/hr to 260m/hr). Individual variation in red deer movement were therefore mainly expressed when disturbance was high with individuals reacting differentially responsive to increases in perceived risk. There was no correlation between an individual's expression at low and high disturbance, i.e., deer that moved more or less under low disturbance were equally likely to respond more strongly to human disturbance. Consequently, during the morning activity bout, mean conditional repeatability (**Fig 3**), indicative of the amount of between individual variation in movement, increased from 0.15 under low disturbance to 0.42 under high disturbance.

As shown above, red deer move little in the middle of the day, indicating a temporal avoidance strategy towards humans but further decreased movement on days of high disturbance, however some individuals did not reduce movement in response to human disturbance (**Fig 2**): the most responsive individual decreased movement from 35 to 1 meter, while the least responsive individual maintained an average hourly step length of 53 meters. In fact, the positive correlation between random intercept and slope (**Table 1**) shows, that those individuals which already move more during the middle of the day when human disturbance is low, were more likely to maintain movement with increasing disturbance, while red deer that move over shorter distances to begin with decreased movement more strongly. Individual variation in red deer movement in the middle of the day therefore also

increased with human disturbance (from conditional repeatability = 0.03 at low disturbance to conditional repeatability = 0.35 at high disturbance, **Fig 3**), corroborating individual differences in the responsiveness towards humans.

During the evening active bout, movement was unaffected by human disturbance on the population level, but between-individual variation increased along the human disturbance gradient (from conditional repeatability = 0.1 to conditional repeatability = 0.42, **Fig 3**). In fact, deer that moved more under low disturbance responded to increasing disturbance with increases in movement, while the opposite was true for deer that moved less under low disturbance (**Fig 2,** positive random intercept - slope correlation **Table 1**).

During the night resting bout, red deer showed little between-individual variation in their propensity to move (mean conditional repeatability = 0.1), which was also largely unaffected by the number of visitors in the park during the day time.

Table 1. Estimates and 95% credible intervals (in parentheses) of fixed and random effects at four times of day in a red deer's diel activity pattern: night passive, peak morning activity, midday passive and peak evening activity. The variance explained the fixed effects (marginal R2) and by the combined fixed and random effects (conditional R2) is given under each model.

	Night passive	Morning active	Midday passive	Evening active
Fixed effects				
Intercept	3.72 [3.62, 3.82]	4.51 [4.41, 4.61]	3.18, [3.1, 3.27]	4.92 [4.82, 5.03]
Visibility	0.13 [0.08, 0.19]	0.38 [0.33, 0.44]	0.31 [0.27, 0.35]	0.05 [0, 0.1]
Human dist.	*0.02 [-0.01, 0.05]*	0.7 [0.02, 0.12]	-0.17 [-0.23, -0.11]	*0.01 [-0.03, 0.05]*
Elevation	-0.32 [-0.36, -0.29]	-0.21 [-0.25, -0.16]	-0.12 [-0.17, -0.07]	-0.1 [-0.15, -0.05]
Elevation	0.08 [0.04, 0.12]	0.14 [0.1, 0.18]	-0.06 [-0.12, 0.01]	-0.08 [-0.12, -0.03]
Canopy cover	0.09 [0.06, 0.12]	0.05 [0.02, 0.7]	0.19 [0.15, 0.22]	0.19 [0.16, 0.21]

Visibility * Human dist.	*0 [-0.01, 0.04]*	*-0.01 [-0.05, 0.04]*	-0.08 [-0.13, 0.04]	*0.01 [-0.03, 0.06]*
Random effects				
$sd_{intercept.Deeryear}$	0.32 [0.26, 0.39]	0.41 [0.33, 0.49]	0.26 [0.21, 0.33]	0.46 [0.39, 0.53]
$sd_{slope.Visibility}$	0.16 [0.1, 0.22]	0.2 [0.15, 0.26]	0.09 [0.03, 0.15]	0.19 [0.14, 0.25]
$sd_{slope.Human\ disturbance}$	0.03 [0, 0.07]	0.17 [0.13, 0.22]	0.15 [0.08, 0.22]	0.03 [0.04, 0.16]
$sd_{slope.Visibility * Human\ dist.}$	0.02 [0, 0.05]	0.09 [0.05, 0.14]	0.06 [0, 0.13]	0.09 [0.01, 0.16]
$r_{Deeryear\text{-}Visibility}$	-0.58 [-0.79, -0.3]	*-0.12 [-0.4, 0.19]*	*0 [-0.47, 0.45]*	*-0.2 [-0.45, 0.08]*
$r_{Deeryear\text{-}Human\ disturbance}$	*0.07 [-0.7, 0.79]*	*0.24 [-0.14, 0.55]*	0.46 [0.29, 0.9]	0.45 [0.02, 0.83]
$r_{Deeryear\text{-}Visibility * Human\ dist.}$	*0.01 [-0.79, 0.8]*	*-0.31 [-0.75, 0.23]*	*0.4 [-0.49, 0.91]*	*0.47 [-0.05, 0.85]*
Marginal R2	0.08 [0.07, 0.1]	0.09 [0.07, 0.11]	0.09 [0.08, 0.11]	0.05 [0.04, 0.06]
Conditional R2	0.1 [0.09, 0.11]	0.19 [0.18, 0.21]	0.11 [0.09, 0.12]	0.17 [0.16, 0.18]

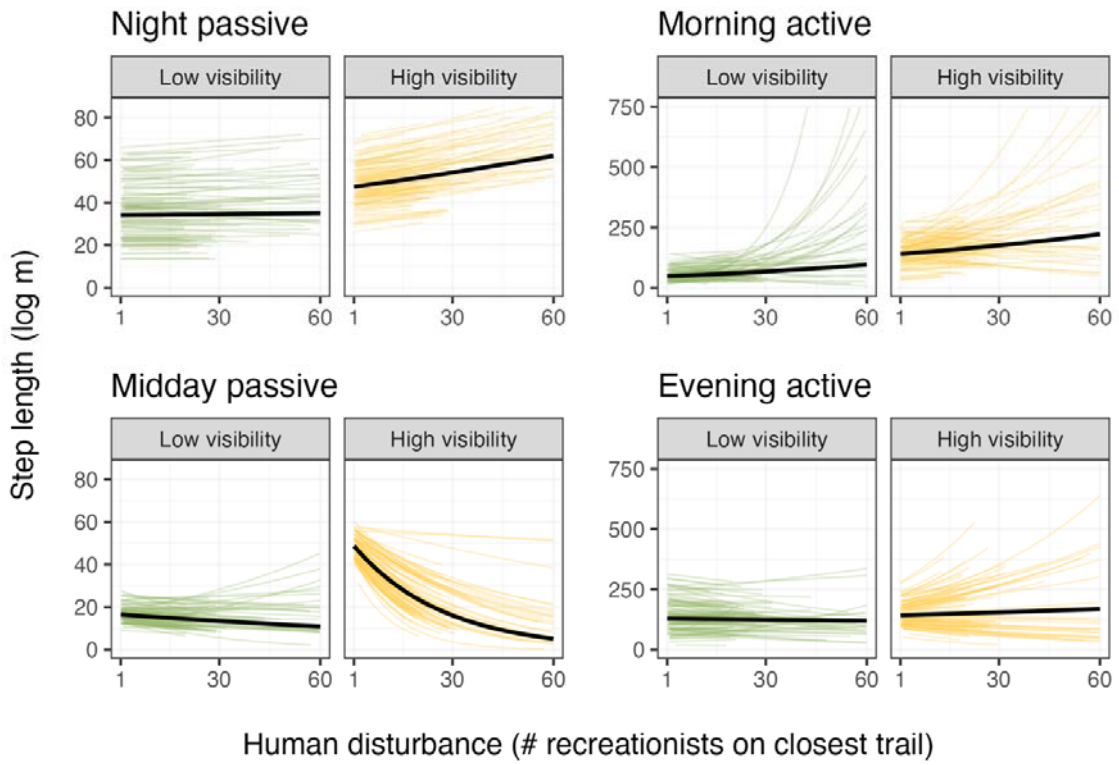

Fig 2 Effects of human disturbance and vegetation cover on movement of red deer in the Bavarian Forest National Park during peaks and troughs of daily activity. Population level effects are shown as a black line with individual-level random intercepts and slopes in green (low visibility) and yellow (high visibility). Low and high visibility were fixed at the 15th and 85th percentile of the observed distribution of cover at red deer locations. Individual predictions extend only over the disturbance gradient experienced by each individual. Human disturbance affected the movement of red deer most strongly during the morning active and

midday passive bout. Effects are back transformed to the linear scale for ease of interpretation, mind the different y-axes extents for movement during passive (left) and active (right) bouts. Y axes are truncated to a maximum of 750m for better readability, although several individuals increased movement up to 1900m at very high human disturbance.

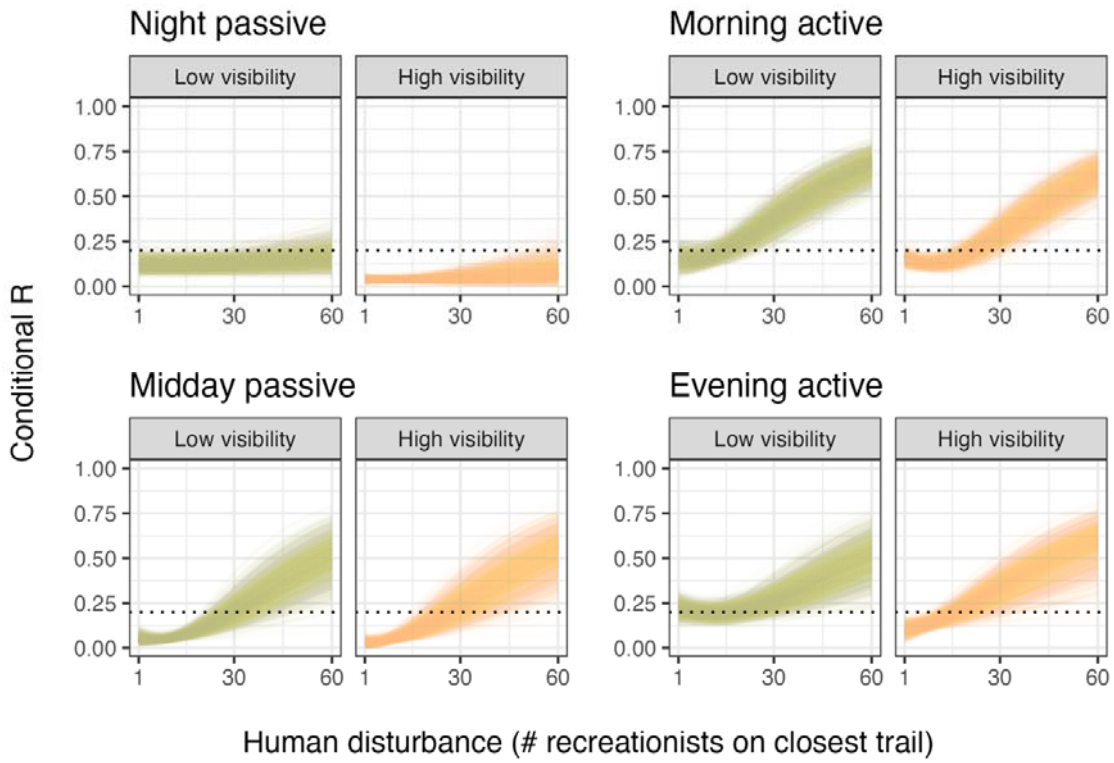

Fig 3 Conditional repeatability (i.e., variance standardized between individual variation) along a gradient of human disturbance under low and high visibility (10th and 90th percentile of visibility distribution). Lower conditional repeatability, suggests a similar average behavior of red deer or high within individual variability, while higher conditional repeatability suggests between-individual variation in behavioral expression. We added a dotted line at conditional repeatability = 0.2, which can be interpreted as a threshold beyond which repeatability can be interpreted as moderate to high.

Discussion

Red deer showed nuanced responses to human recreationists. All red deer avoided being active at the same time of day as humans, i.e., during the daylight hours in the middle of the

day, and instead primarily moved during the early morning and evening hours. There was little flexibility in diel activity patterns and all individuals followed the general population trend. Following, movement during the middle of the day was generally low (< 50 m/hr), but further decreased when deer were in proximity of a trail with many visitors. Increasing human disturbance, measured as the number of visitors on the trail closest to a deer, promoted between-individual variation in movement. Individual variation in plasticity towards human disturbance was primarily expressed during the morning or midday, on days and in areas with > 20 visitors on the closest trail and when deer moved through areas with high visibility and little concealing vegetation cover. During the morning activity bout, red deer forage preferably in such open areas and our results suggest that individual red deer solved the trade-off between foraging and perceived risk differently. For example, along a gradient of 1 to 40 visitors on the closest trail, some individuals reacted strongly by increasing their hourly movement (e.g., from 200m/hr to 790m/hr) while others did not adjust movements (e.g., from 190m/hr to 250m/hr). A contrasting behavioral response to human visitors was observed during the middle of the day. Again, between-individual variation increased with number of visitors in the park but rather than increasing, red deer decreased movements in response to humans to varying degrees. Rapid or long-distance movements likely decrease the time spent actively foraging, therefore, strong responses to human disturbance may be costly. In systems with human hunting, less responsive individuals with higher movement rates or selection for open habitats may suffer a higher mortality risk and be disproportionately removed from the population (Ciuti *et al.* 2012; Leclerc, Zedrosser & Pelletier 2017). Since red deer are protected from hunting in large parts of the BFNP, responsiveness to human disturbance does not come with a survival benefit for those deer that stay inside the park and the proportion of less reactive deer in the population can increase.

National parks are becoming increasingly more important as advocates for nature and wildlife protection. Wildlife viewing is thereby an important attractant but also an effective tool to communicate the value of nature to the general public. Compared to North America, where wildlife can be relatively easily observed, wildlife viewing options are often limited in European national parks. One likely reason for this is that in Europe, most national parks allow hunting within their park boundaries, or wildlife are heavily targeted by hunting as soon as they leave the relatively small parks (van Beeck Calkoen *et al.* 2020). Under this management regime, dispersing individuals are regularly removed from the landscape, hindering gene flow, leading to small, isolated populations with low genetic diversity (Westekemper 2021), low effective population sizes and negative effects of inbreeding (Edelhoff *et al.* 2020). Conversely, hunting is strictly prohibited in North American national parks, which are also significantly larger in size, encompassing entire home ranges of animals. Our study system in the Bavarian Forest National Park is one of the few areas in Central Europe with a hunting-free zone large enough to sustain entire home ranges (van Beeck Calkoen *et al.* 2020). In addition, the population is a transboundary population with the Sumava National Park in the Czech Republic and has therefore a relatively large effective population size (~2851) (Fickel *et al.* 2012; Tourani *et al.* 2023). Gene flow from the East, predominantly mediated by stags (Fickel *et al.* 2012), leads to a comparably low inbreeding coefficient. The combination of a relatively large hunting free zone, which has been in place since 1997, and a large effective population size suggest that sufficient genetic variability allows for behavioral variability to emerge in our population. In fact, some individuals seem to have lost their extreme fear of humans as they did not respond to higher numbers of human recreationists in their vicinity. While on the population level, red deer in our study system are still extremely difficult to observe, our study reveals the potential for an increase of less

fearful and therefore more observable red deer in the population. These are slow processes over several generations, but it seems that the current measures are effective in promoting genetic diversity that allows for behavioral diversity in human avoidance behavior.

Pseudoreplication is a common pitfall when studying between-individual variation and is of particular concern in inherently autocorrelated movement data (Niemelä & Dingemanse 2017). Pseudreplication occurs when repeated measures of an individual are falsely treated as independent, e.g., when sequential hourly intervals are included as independent measurements in a model although the behavioral state of the animal precluded a change in behavior, here hourly movement distance (e.g., during resting or foraging on an aggregated food resource over sequential time steps). Including such non-independent data points can inflate between-individual variation because the individual supposedly shows a consistent response to the same environment, while in reality its behavioral state did not change. For movement data, repeated hourly steps of inactivity or course spatial resolution of environmental covariates, not matching the resolution of movement can lead to pseudreplication (Hertel *et al.* 2020). By concentrating on specific hours of the day we could ascertain that repeated individual measures every 24hrs were truly independent. We advise that future studies of between-individual differences in animal movements pay attention to sources of pseudoreplication in their data, especially when stationary periods, such as resting, cannot be filtered out effectively, as was the case in our dataset.

Conclusion

We found great individual variation in behavioral plasticity towards human disturbance. In particular, between-individual variation in red deer movement behavior emerged at higher levels of perceived risk while individuals conformed to a common behavioral phenotype

under low perceived risk. Some individuals responded with long movement distances to many visitors in their vicinity, whereas others responded little. Whether responsive individuals pay a foraging cost or unresponsive individuals are more likely to be harvested outside the park should be subject of future research. Wildlife viewing is a main attractant of national parks today, however, observing wildlife in Europe often appears more difficult than in North America. Continuing hunting pressure in and around many European parks likely precludes wildlife from losing their fear of humans and becoming easier to observe, especially because individuals less responsive towards humans potentially suffer a higher mortality risk from hunting. Our study system suggests that large and long-lasting hunting free zones, in combination with an adequate effective population size might be the key to less fearful and more observable wildlife populations.

Author contributions

AGH and BB developed the study idea with input from MH and AP, MH and AP provided the data, VM and FS developed the model providing estimates of human disturbance, AGH and BB analyzed the data, AGH wrote the manuscript with input from all coauthors.

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Data accessibility:

Code and data to reproduce the analyses can be accessed via:

https://doi.org/10.17605/OSF.IO/62JZP

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