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Stay on trails – effects of human recreation on the spatiotemporal behavior of red deer *Cervus elaphus* in a German national park

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Human activities can affect the behavior and well-being of wildlife, and there is high potential for wildlife disturbance due to human outdoor recreation. Hiking is a popular form of outdoor recreation in many countries, including Germany. In this study, we investigate the effects of hiking and hiking trails on space-use dynamics in GPS-collared red deer *Cervus elaphus* inhabiting the Kellerwald-Edersee National Park, Germany. Specifically, we 1) experimentally assess the reactions of red deer to hiker on- and off-trail and 2) quantify the effects of hiking trails on daily space-use patterns of the deer. We found that red deer in the Kellerwald-Edersee National Park did not show a spatiotemporal reaction to recreational on-trail hiking, but were sensitive to off-trail hiking that always induced flight of the animals. With increasing trail densities, the flight initiation distance decreased, while the distance moved during a flight was similar across trail densities. Together, these results suggest that the sensitivity to off-trail hiking increases in areas with low trail density, but that the flight reaction, once induced, is uniform. We further demonstrate that red deer avoid hiking trails during the day, but not during nighttime, and that a negative relationship exists between the distance the animals keep to trails and the trail density in an individual home range. Our results indicate that off-trail hiking has the potential to disturb red deer in the Kellerwald-Edersee National Park, but that red deer are able to cope with recreational activity on trails as well as with the presence of trails in general. Our findings underline the importance of hiking rules, such as staying on trails, and visitor management focusing on minimizing conflicts between wildlife and human recreation.

Recreational outdoor activities are a common activity in many countries, including Germany, where more than half of the population hike regularly (Cordell 2008, Dicks and Neumeyer 2010). Such outdoor activities can put various pressures on the environment, and the potential negative effects on wild animals, including species of conservation and management concern, have long been recognized (Coppes et al. 2017a; reviewed by Vistnes and Nellemann 2008, Tablado and Jenni 2015). Hence, wildlife managers are often challenged by the task of finding a balance between the needs of wildlife and the demands of recreationists (Reed and Merenlender 2008, Monz et al. 2013). Effects of recreational activities on wildlife are diverse. For cervids, studies have reported behavioral effects like altered habitat use, vigilance behavior, and dietary intake (Jayakody et al. 2011; reviewed by Stankowich 2008). Furthermore, human outdoor activities can have physiological effects in cervids, such as increased energy expenditures, an increased stress response and reduced fecundity (Herbold et al. 1992, Staines and Scott 1994, Phillips and Alldredge 2000). Other studies show that increasing human activity also negatively affected the detection rate, e.g. of roe deer *Capreolus capreolus* in a nature reserve in California, sika deer *Cervus nippon* in a mountainous area in Japan and wapiti *Cervus canadensis* in Canada (Borkowski 2001, George and Crooks 2006, Rogala et al. 2011).

Importantly, several studies have shown that cervids can not only be affected by human recreational activities, but also by the infrastructures associated with these activities. Specifically, several cervid species adjust their space-use behavior to avoid close proximity to recreational trails (Rogala et al. 2011, Coppes et al. 2017b, Scholten et al. 2018), especially during times of high human use, such as during the day (Ager et al. 2003) or during weekends (Sibbald et al. 2011, Nix et al. 2018). However, most studies conducted to date have focused on the effects that varying intensities of human use have on trail avoidance in cervids. In contrast, the effects of trail density on observed

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responses remain unknown. Overall, various studies have shown that human recreation can alter wildlife behavior and that these behavioral changes can potentially have negative consequences for individuals and populations. However, we still lack a detailed, fine-scale understanding of spatiotemporal wildlife responses to specific forms of human recreation. Ideally, studies assessing these spatiotemporal responses should use experimental approaches to identify the exact drivers of observed behaviors (e.g. hiking off- versus on-trail), while also considering the effects of recreation infrastructures on general space-use patterns of the study animals. Here, we present results from such a study, where we use GPS-collared red deer in a German national park for a fine-scale analysis of their responses to hiking and hiking trails. For this, we first quantified red deer behavioral responses to human hiking using an experimental design that allowed us to measure the immediate effect on short-term habitat use by red deer. Specifically, we applied an experimental approach where we hiked both on-trail and off-trail in the field and simultaneously tracked the movements of deer and hiker during these experiments. In addition to these experiments, we also used year-round movement data from the red deer in the national park to quantify the effects of the presence of trails on red deer spatiotemporal behavior. We investigated behavioral differences between day and night and tested for an influence of trail density on observed space-use patterns.

We expected off-trail hiking to elicit stronger spatial responses of red deer than on-trail hiking as the latter follows specific routes that are more predictable for the red deer. Furthermore, we expected that responses depend on trail density, because high trail densities are likely associated with more frequent exposure to human recreation. Finally, we expected red deer in the national park to keep higher distances to trails during the day compared to nighttime, due to their avoidance of trails during diurnal recreational activities by humans.

Material and methods

Study area

The Kellerwald-Edersee National Park was established in 2004 in northwest Hesse, Germany. Until the beginning of the 20th century, it was a hunting ground of the princely houses Waldeck and Pyrmont. It encompasses 5739 ha of the Rhenish Massif with elevations between 200 and 626 m a.s.l. The climate is suboceanic to subcontinental, with an annual precipitation between 600 and 800 mm and an average annual temperature between 6 and 8°C (Panek 2004, Nationalpark Kellerwald-Edersee 2008, 2010). The national park is free of public roads and mainly covered by beech *Fagus sylvatica* forest to 71%. Parts of the national park belong to the UNESCO World Natural Heritage of Ancient Beech Forests of Germany since 2011 (EUROPARC Deutschland 2011) and only small parts of the forest within the park are managed for timber production. All five hoofed game species resident in Germany appear: red deer, roe deer, fallow deer *Cervus dama*, mouflon *Ovis ammon musimon* and wild boar *Sus scrofa*. Hoofed game outside the natural heritage areas is hunted during short intervals of hunting from stands in August and September, and by driven hunts with beaters and dogs from October until December. Currently, large carnivores (i.e. wolf *Canis lupus* and lynx *Lynx lynx*) do not occur in the park (Nationalpark Kellerwald-Edersee 2008), which is typical for the vast majority of German national parks, even though both species are increasing their range in the country (Reinhardt et al. 2015).

The Kellerwald region attracts tourists and has about 1.8 million overnight stays per year (Region Kellerwald-Edersee e. V. 2014) and about 63 000 people visit the national park every year (Schaub 2017). Hiking is the most common recreational activity in the national park and about 80% of visitors are hikers (Schaub 2014) using a trail network with a total length of about 200 km (Fig. 1). The current trail density in the national park of 29.8 m ha^{-1} will be reduced to 20 m ha^{-1} (EUROPARC Deutschland 2011). Park regulations require visitors to stay on trails at all times, but off-trail hiking occurs frequently (Schaub 2017).

Study animals

Red deer are widely distributed across Europe and both their population and harvest numbers have increased over the last decades throughout most of the continent (Milner et al. 2006, Burbaité and Csányi 2010). In Germany, red deer are of cultural, economic and ecological importance. Their large body size and impressive antlers make them one of the most valuable game species for both trophy and meat hunting. Substantial revenues can be obtained via red deer hunting, but the species can also cause massive economic damage to commercial forestry by browsing and debarking of trees (Wotschikowsky 2010). Hence, the species is heavily managed throughout the country and is not allowed to occur outside of designated red deer zones in several German states (Kleymann 1976, Kinser et al. 2010). The estimated red deer population of 240 000 in Germany mainly occur in forests and forest-edge habitats (Kinser et al. 2010) and about 79 000 individuals are killed annually by hunters or in vehicle collisions (Deutscher Jagdverband e. V. 2018). Given the high sensitivity of red deer to human disturbances (Jayakody et al. 2011, Coppes et al. 2017b), their large space requirements (Kamler 2007, Reinecke et al. 2014) and their demands to large-scale habitat connectivity (Zachos et al. 2007), the species is often used to guide habitat management and conservation, for example by state agencies and non-government organizations (Herrmann et al. 2007). Hence, actions to reduce disturbance of red deer will likely have synergistic effects for many other disturbance-sensitive species.

During our study, we investigated the reaction of eight subadult and adult red deer. All animals were equipped with GPS collars to enable precise tracking of individual spatiotemporal reactions (more details see Table 1 and Supplementary material Appendix 1). The GPS collars (VECTRONIC Aerospace, Berlin, Germany) weigh about 850 g and were unlikely to impair red deer (Kenward 2001). We conducted our experiments according to the German animal protection act with all necessary permissions for trapping and animal handling. Based on all available positions in 2011 (hereafter named fixes; usually one fix per

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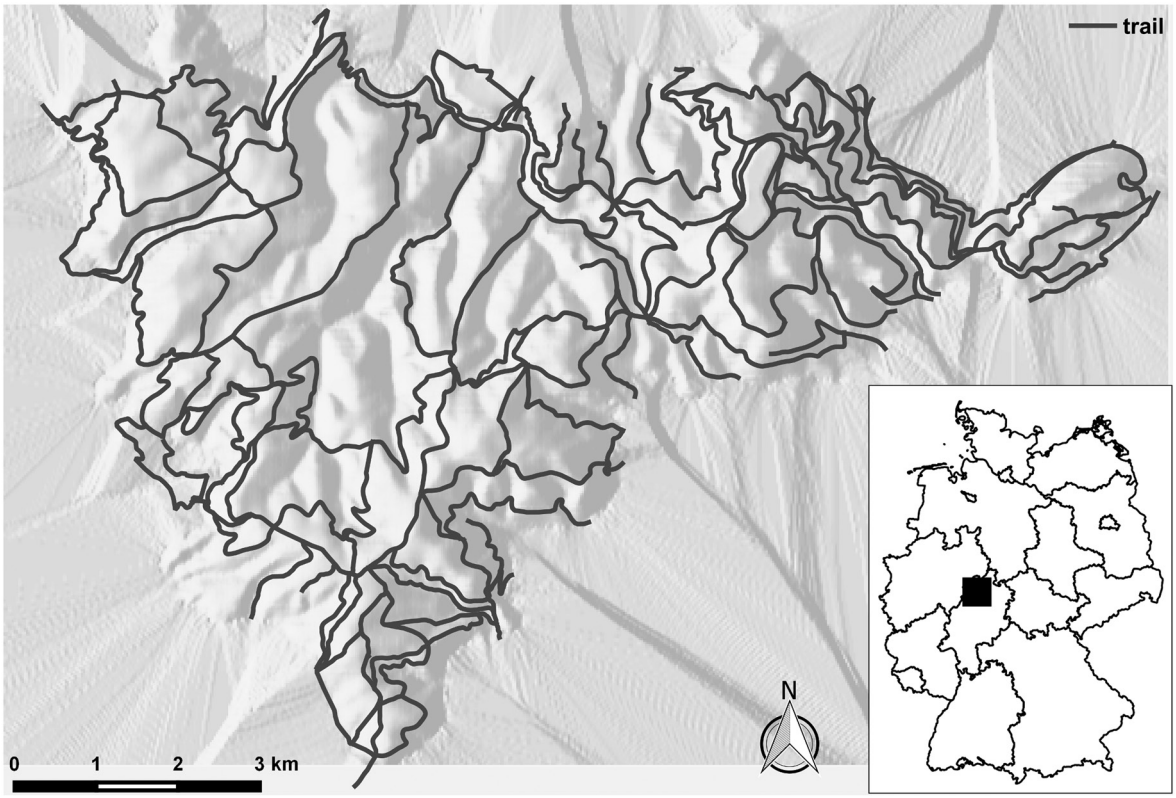


Figure 1. Trails in the Kellerwald-Edersee National Park. The inlay shows the location of the national park in Germany; gray shadings are based on a digital elevation model.

six hours), we calculated individual home ranges using the Local Convex Hull (LoCoH) method (Getz and Wilmers 2004). While other methods for home-range estimation are available, LoCoH is most suitable for our purposes and study area because it excludes areas never used by the red deer (Reinecke et al. 2014). We used adaptive LoCoH (as implemented in the R package *adehabitat*, Calenge 2006), where local hulls are created until a predefined distance (α) is used up. For α, we used the maximal distance between any two fixes of an individual available in 2011 (Reinecke et al. 2014).

We used the mean trail density of the study area (29.8 m ha^{-1}) to distinguish low and high trail density areas. With this approach, half of our study animals were exposed to high trail densities within their home ranges (> 29.8 m ha^{-1}), the other half was exposed to low trail densities (< 29.8 m ha^{-1}, Table 1), leading to a balanced sample size between low and high trail density areas.

Objective 1. Experimental on- and off-trail hiking

To investigate the immediate effect of hiking, we conducted an experiment with two different hiking treatments (on-trail and off-trail hiking) in October and November 2011. During treatments, the hiker's movements were continuously recorded with a GPS-logger (WBT-202, Wintec wireless electronics, Berlin, Germany) and red deer positions were recorded every 10 min. Experiments took place between 07:00 and 17:00 UTC when red deer movement is known to be low (Godvik et al. 2009, Pépin et al. 2009, Reinecke et al. 2014).

For on-trail treatments, the hiker walked on the trail closest to the collared red deer and tried to circle it without leaving official hiking trails. If circumnavigation was not possible, the hiker walked back and forth along the trail. In contrast, the hiker left trails and directly approached the position of the red deer during the off-trail treatments.

Table 1. Information on study animals including the number of fixes obtained in 2011, home-range size based on 95% LoCoH estimates, trail density and trail density level in each home range. A low trail density is below the average trail density in the park (29.8 m ha^{-1}), while a high density is above that density.

ID	Sex	No. of fixes	Home-range size (ha)	Trail density (m ha^{-1})	Trail density level
c5572	Female	2903	485.5	14.9	Low
c2961	Female	1812	295.9	18.4	Low
c5579	Male	2943	1287.6	24.4	Low
c7664	Female	2052	537.7	27.7	Low
c9426	Female	2942	260.8	37.7	High
c2970	Male	2214	228.3	40.0	High
c7665	Female	2167	314.0	57.2	High
c7666	Female	1908	304.9	60.0	High

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We replicated both treatments four times per study animal (four on-trail and four off-trail treatments for each of the eight animals). For all replicates, the focal animal did not move before the treatment started.

We used the following metrics to assess the reaction of red deer: 1) the minimum distance between the hiker and red deer (only for on-trail treatments), 2) the flight initiation distance, that is the distance between hiker and red deer when the red deer started its flight (only for off-trail treatments) and 3) the distance moved during flight (Euclidean distance of furthest fix during a treatment to its initial fix, only for off-trail treatments). We used two different linear mixed models: For the first model (LMM1) we used the distance to the hiker as the response and distance moved, trail density and hiking treatment (on- or off-trail) as covariates. For the second model (LMM2) we used the distance moved as the response and the minimum distance between red deer and hiker, trail density (m ha^{-1}) and hiking treatment (on- or off-trail) as covariates. We compared models using information-theoretic model selection based on Akaike's information criteria corrected for small sample sizes (AICc, Burnham and Anderson 2004). The model with lowest AICc value was considered best, but alternative models with ΔAICc values ≤ 2 were considered equally plausible. We also calculated AICc weights and estimated marginal R^2-values (R^2_{LMM}, Nakagawa and Schielzeth 2013).

To investigate the effect of trail density on red deer flight response in off-trail treatments, we fitted two additional LMMs with a two-level factor (high and low trail density) as the covariate and either flight initiation distance (LMM3) or distance moved (LMM4) as the response. Note that we only used data from off-trail treatments, as red deer remained in the area during on-trail treatments. For all models we included individual IDs as random effect to account for repeated measurements. The minimal distance between hiker and red deer was log-transformed to conform to the normality assumptions of residuals. For statistical analyses we used the program R (ver. 3.2.5, <www.r-project.org>), and packages *nlme* (Pinheiro et al. 2017) for the LMMs, *AICcmodavg* (Mazzerole 2017) to calculate AICc-values, and *piecewiseSEM* (Lefcheck 2015) to calculate marginal R^2-values for the mixed models.

Objective 2. Effects of trails on red deer space use

Our second objective was to assess whether the presence of trails in general influenced space use of red deer. Therefore, we calculated the distance of each red deer fix recorded in 2011 to the next trail, separated by individual and by time of day (i.e. civil dusk and dawn were used to divide fixes into day and night fixes). For each red deer, we generated the same number of random points in its home range (home-range level 95% LoCoH) as there were overall fixes available for this individual using random points tool in QGIS ver. 1.3.0 (<www.qgis.org>). We then calculated the distances of these random points to trails and used the distances as a reference scenario where red deer space use was not affected by the existence of trails. To statistically compare distances to trails for daytime, nighttime and random points, we used non-parametric Mann–Whitney *U*-tests.

Second, we used a linear model to investigate the effect of trail density on the distance between red deer and trails. Therefore, we determined the trail density within each animal's home range (Table 1) and then modeled the distance to trails as a function of this trail density. To test for trail-avoiding behavior at different times of the day, we included time of day (day/night) as a covariate in the model. We used the random points to assess whether the distance to trails of red deer was different from random space use during the day and night, respectively. By using the random points, we accounted for the fact that some animals will have smaller distance to trails due to higher trail density within their home range. We also included an interaction between trail density and time of day into the linear model.

Results

Objective 1. Experimental on- and off-trail hiking

Off-trail hiking induced flight of the red deer during all off-trail treatments at a median flight initiation distance of 128 m (95% quartiles 42–239 m; Supplementary material Appendix 1 Fig. A1). During a flight, the median distance moved, i.e. the distance a red deer escaped from its initial position, was 610 m (95% quartiles 66–1866 m; Fig. 2). In contrast, red deer tolerated the hiker passing by during all on-trail treatments (Supplementary material Appendix 1 Fig. A2). The median shortest distance between an individual and the hiker during on-trail treatments was 223 m (95% quartiles 100–422 m) without inducing a flight response (Fig. 2). The median distance moved by a red deer during on-trail treatments was only 39 m (95% quartiles 9–321 m; Fig. 2), and the deer never left the area around its initial position throughout the treatment, thus not showing any flight reaction.

Comparing both treatments, we found that the distance between the hiker and the observed individual was significantly shorter during off-trail treatments than during on-trail treatments (Wilcoxon signed-rank test: $p < 0.001$; Fig. 2), showing that on-trail hikers are able to circle red deer while maintaining a distance that is beyond the flight initiation distance. Using LMM1 – where we modeled distance to hiker as the response and distance moved, trail density and hiking treatment as covariates – we found that on average the minimum distance between hiker and red deer increased by 105 m for on-trail treatments compared to off-trail treatments ($p < 0.001$). Also, distances moved by red deer during off-trail treatments were significantly larger than during on-trail treatments ($p < 0.001$, LMM2).

Model selection for LMM2 – modeling the distance moved by red deer after disturbance – corroborates that distances moved by the red deer were best explained by treatment type (on- versus off-trail hiking, Table 2). The model including only treatment type as explanatory variable was by far the best model (ΔAICc > 2 compared for the second best model), had strong statistical support compared to other models (AICc-weight = 0.976), and explained about 64% of the observed variance of the distance moved by the red deer ($R^2_{LMM} = 0.643$; Table 2). Concerning an effect of

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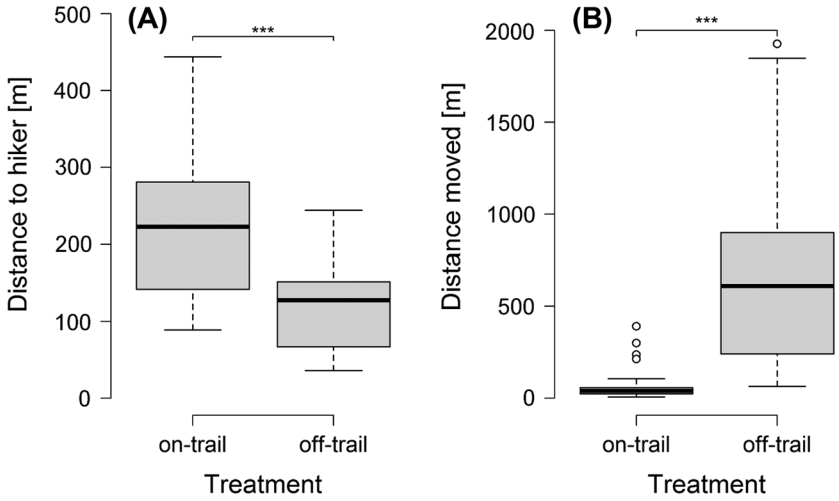


Figure 2. Boxplot of (a) Minimal distance between red deer and hiker during on-trail and off-trail hiking treatments – note that the latter depicts flight initiation distance; (b) distances moved by red deer during on- and off-trail hiking treatments. ***=$p < 0.001$. Note the different scaling of axes.

trail density on flight behavior of red deer, we found that the median flight initiation distance decreased from 148 m in areas with low trail densities to 91 m in areas with high trail densities ($p = 0.023$, LMM3; Fig. 3a). However, as expected from the LMM2 results, distance moved during flight was equal between high and low trail density level areas ($p = 0.712$, LMM4; Fig. 3b).

Objective 2. Effects of trails on red deer space use

We collected more than 18 000 fixes in 2011 (between 1908 and 2943 fixes per red deer, Table 1), and estimated LoCoH home ranges that varied in size between 228 ha and 1228 ha per study animal, reflecting the variability in home-range sizes typical for red deer (Reinecke et al. 2014). The combined individual home ranges covered most of the national park and were distributed across the gradient of trail density in the area. During the day, red deer maintained significantly higher distances to trails (median 151 m) than during night (median 100 m; Mann–Whitney *U*-test, $p < 0.001$), and also significantly higher distances than expected under a random scenario (median 95 m; Mann–Whitney *U*-test, $p < 0.001$). In contrast, nighttime distances were significantly shorter than expected under a random scenario (Mann–Whitney *U*-test, $p = 0.004$). The linear model suggests that trail densities within an animal's home range affected the distance of red deer to trails significantly: red deer inhabiting home ranges with lower trail density keep larger distances to trails than red deer in home ranges with high trail density (Table 3, Fig. 4).

Discussion

Our quantification of fine-scale responses of red deer to experimental hiking, in combination with our analysis of daily space-use patterns, revealed 1) that red deer in the Kellerwald-Edersee National Park do not react to on-trail hiking, but are disturbed by off-trail hiking, and 2) that the deer avoid close proximity to hiking trails during the day, but not during the night. Both flight initiation distances and the distances deer kept from trails were influenced by trail density, as animals in areas with higher trail density showed less sensitivity to off-trail hiking and the presence of hiking trails, respectively. Together, these results refine our understanding of hiking effects on the spatiotemporal behavior of red deer.

Response to on- and off-trail hiking

In our study, on-trail hiking did not induce a spatial reaction (i.e. red deer did not flee), whereas off-trail hiking induced a strong spatial response with flight initiated during all treatments. Since the distance between hiker and red deer during on-trail treatments was always larger than the flight initiation distance recorded during off-trail treatments, our results

Table 2. AIC-based comparison of linear mixed models explaining distances moved by red deer (LMM2 in the main text) as a function of treatment type (on- or off-trail), trail density (m ha^{-1}), and minimal distance to hiker (m).

Variable(s)	R^2_{LMM}	AICc	ΔAICc	AICc weight
Treatment type	0.643	179.115	0.000	0.976
Treatment type + Trail density	0.657	186.906	7.791	0.020
Treatment type + Minimal distance hiker – red deer	0.643	189.988	10.873	0.004
Full model	0.668	195.803	16.688	0.000
Null model	0.000	243.337	64.222	0.000
Minimal distance hiker – red deer	0.172	246.201	67.086	0.000
Trail density	0.019	251.380	72.265	0.000
Trail density + Minimal distance hiker – red deer	0.170	254.511	75.396	0.000

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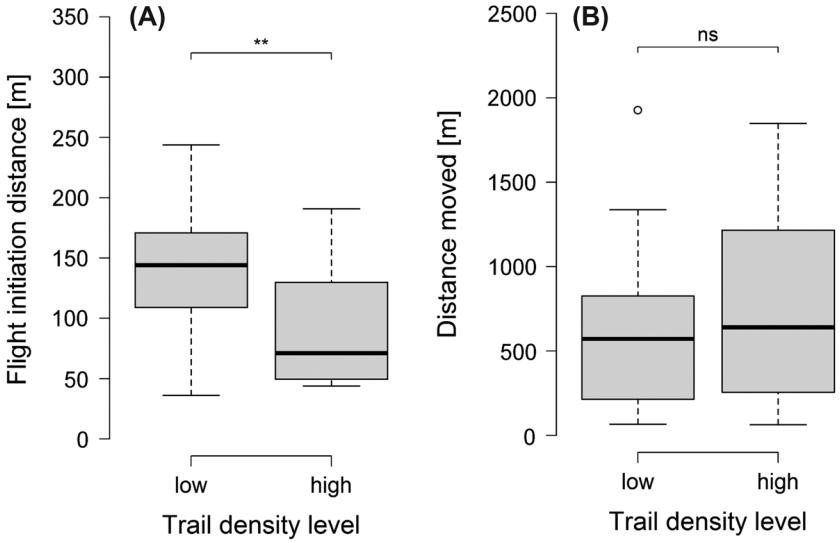


Figure 3. Boxplot of (a) flight initiation distance and (b) distance moved depending on trail density level. ** = $p < 0.01$, ns = not significant. Note the different scaling of axes.

show that red deer actively avoid close proximity to trails during the day (as suggested by our results for Objective 2) so that hikers staying on trails maintain a distance to red deer that is non-critical, i.e. the distance is large enough to not initiate flight behavior.

These results are congruent with those of Taylor and Knight (2003), who observed the reactions of mule deer *Odocoileus hemionus* in a state park in Utah, USA, and showed that both on- and off-trail hiking can induce flight, but flight was less frequently observed in response to on-trail treatments. Similarly, Miller et al. (2001) found that mule deer in a forest around a city in Colorado, USA, escaped less often in on-trail treatments compared to off-trail treatments. They also found a decreasing escape probability with increasing distance a mule deer kept to trails and an increased distance moved when a hiker walked off-trails (Miller et al. 2001).

Other studies found that even on-trail movements by humans can cause flight in a variety of species (Mainini et al. 1993, Gander and Ingold 1997). Our results indicate that red deer can cope with humans hiking on trails, likely because hikers appear regularly on the trails, and their routes are predictable for the red deer. Contrary, off-trail activities are unpredictable and occur less frequently, making it less likely that red deer can become familiar with such activities (MacArthur et al. 1982, Moen et al. 1982, Staines and Scott 1994). We found that reactions to off-trail hiking partially depend on the trail density: there is a negative relationship between trail density and flight initiation distance (Fig. 3a), but no relationship between trail density and distance moved (Fig. 3b). Together, these results indicate 1) that red deer are more sensitive to off-trail hiking in areas with low trail densities, i.e. areas where they can maintain higher daytime distances to trails and hikers using these trails, but also 2) that flight is a uniform response once it is induced. These findings are in contrast to a study on Columbian black-tailed deer *Odocoileus hemionus columbianus*, as Stankowich and Coss (2006) found an increase in distances moved with an increasing flight initiation distance. Another study on enclosed fallow deer investigated their spatial behavior in response to a transect-hiking human and revealed a positive relationship between trail density (as a measure of human activity) and the probability of flight, presumably because fallow deer is less reactive the more experienced it is with human activities (Recarte et al. 1998). This is in accordance with our findings and underlines the connection between repeated experience and reactivity to humans, which can eventually decrease reactivity to humans in areas experiencing higher human activity levels. For example, Colman et al. (2001) measured the spatial reaction of Svalbard reindeer *Rangifer tarandus platyrhynchus* to an approaching human in areas with varying human activity intensities. They found a negative relationship between the degree of human activity and both flight initiation distance and distance moved, with the least reactive individuals found in the study area with highest human activity. In light of these studies and our own results, we conclude that red deer in Kellerwald-Edersee National Park have developed a higher tolerance to on-trail hiking over time and that there is a positive relationship between trail density and degree of tolerance. Animals inhabiting home ranges with high trail densities are likely exposed to higher levels of human presence and activities, and should therefore have a higher probability of becoming familiar with human

Table 3. Results of the linear regression to model the distance to the next trail as a function of time of day and trail density within an animal's home range. We used daytime fixes as reference category. We also generated random points within each animal's home range to compare to random space use. Although the squared term for trail density was not significant at $\alpha = 0.05$ level, we included it to better reflect the functional form of the response (Fig. 2).

	Estimate	Standard error	t-value	Pr(>|t|)
Intercept	341.707	43.118	7.925	< 0.001
Trail density	–7.656	2.536	–3.018	< 0.001
Trail density^2	0.059	0.033	1.804	0.090
Night	–57.394	15.987	–3.590	< 0.001
Random	–58.631	15.987	–3.667	< 0.001

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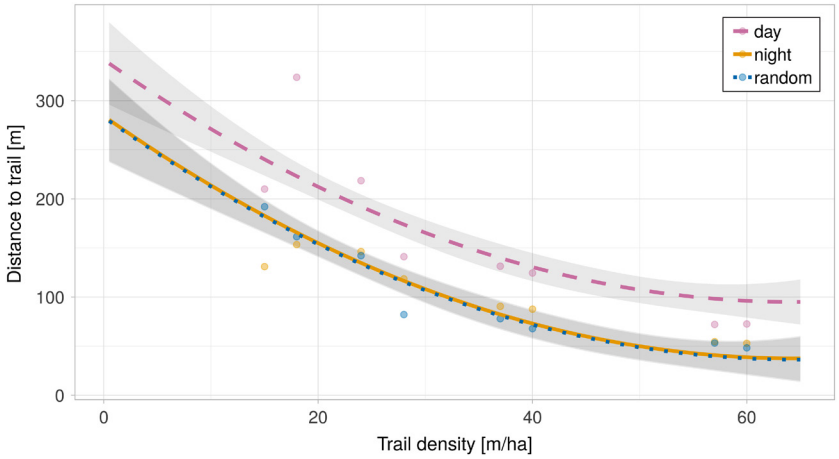


Figure 4. Relationship between distances to trails and trail density within red deer home ranges for different fix types (day, night and random). Predictions from the model (Table 2) are shown with error bands. Points show each study animal´s median distance to the next trail.

activities (Blumstein 2016). Overall, our study provides evidence that on-trail hiking in our study area is an outdoor activity that the red deer can cope with by adjusting their spatiotemporal behavior, while off-trail hiking has substantial disturbance potential and should therefore be regulated.

Effects of trails on red deer space use

Red deer in the Kellerwald-Edersee National Park adjust their daily space-use patterns in response to hiking trails, depending on time of day and trail density. We found effects of trails during daytime, but not during nighttime when red deer distances to trails were indifferent from random (i.e. trail-independent) space use (Fig. 4, Table 3). These effects were influenced by trail density, as an increase in trail density led to decreased distances to trails. Thus, red deer in areas with higher trail densities kept lower distance to trails compared to the ones living in home ranges with lower trail densities.

Since we compared distances to trails for actual red deer fixes versus random points within the deer home ranges, we accounted for varying trail densities that individuals were exposed to. Thus, the decreasing distances to trails with increasing trail densities are not simply due to a reduced availability of areas far away from trails in areas with high trail density. Instead, we can conclude that that the observed pattern is due to an adaptation of spatiotemporal behavior in response to trails, which is a common effect reported in wildlife. For instance, red deer in Europe and elk *Cervus canadensis* in Canada adjust their habitat use in response to recreational trails and avoid close proximity to them (Rogala et al. 2011, Coppes et al. 2017b, Scholten et al. 2018). Some species were also found to adapt their spatial behavior to time of day and follow the periodic peaks of recreation. For example, elk and mule deer have been shown to keep larger distances to open roads and shorter distances to cover during daytime than at night when human use of roads is reduced (Ager et al. 2003). Similar results were obtained in sika deer, where trail avoidance was related to time of the day in an area with high disturbance levels, whereas distances to trails and roads at daytime and nighttime did not differ significantly in a less disturbed area (Uzal et al. 2013). Sibbald et al. (2011) even found that red deer adapted their habitat use to the level of human activity, and stayed further away from hiking trails on weekends when human use of trails was highest. This has also been reported for mule deer, which have been shown to be less active during weekends compared to weekdays as response to human activity (Nix et al. 2018). As in our study, red deer in the Southern Black Forest, Germany, a region highly frequented by recreation all year long, showed a pattern of trail avoidance during day but attraction during night (Coppes et al. 2017b). Contrary to the national park in our study, the study area has a spatial zonation scheme (to reduce forest damage by red deer) with areas where recreation is banned and where it is allowed. This scheme is reflected in the space use of red deer with high proportions of time spent in areas where recreation is banned or of low amount, independent of season. Nevertheless, red deer adapt their diurnal behavior and avoid trails even in the areas free from recreation (Coppes et al. 2017b). This behavior seems counterintuitive but is likely an effect of forage availability as trails in the national park are associated with forest edge vegetation, which is highly attractive for large herbivores (Ruzicka et al. 2010). While such compensatory habitat use along hiking trails is not always observed (Sibbald et al. 2011), trail edge habitat appears to be behaviorally unavailable to the deer in our study during the day, when human hiking occurs. Hence, red deer in our study area likely compensate for the unavailability of food resources along trails during the day by increasingly foraging along trails during the night.

Limitations and conclusions

To our knowledge, our experimental study was the first documenting the immediate effects of human hiking to red deer with GPS on such a fine spatiotemporal scale. We acknowledge that due to this experimental approach, our sample size is relatively small. However, as our results are very consistent across individuals and treatments, we believe that an increased sample size would result in the same conclusions. Nevertheless, future research should increase sample size to

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reveal population effects of red deer to hiking and other outdoor activities, as well as their associated infrastructures.

Despite the small sample size for our experimental study component, our overall results emphasize the sensitivity of red deer to off-trail hiking while also illustrating their capability to deal with predictable human activities on trails. Thus, we call for a strict enforcement of existing hiking rules in Kellerwald-Edersee National Park as stated in the national park guidelines, including the rule that hikers should stay on trails. We suggest expanding specific visitor guidance concepts and adapting it to the needs of different types of recreational activities (e.g. hiking, biking, mushroom picking or geocaching) to further reduce human–wildlife conflicts in the Kellerwald-Edersee National Park. These suggestions likely apply not only to our study area, but also to many other national parks in Germany and across the globe, where they can help to avoid potential negative effects of human recreation on cervids and other wildlife species.

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Supplementary material (available online as Appendix wlb-00403 at <www.wildlifebiology.org/appendix/wlb-00403>). Appendix 1.

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