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Recreation reduces tick density through fine-scale risk effects on deer space-use

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HIGHLIGHTS

- Tick-borne pathogens pose increasing threats to human health.
- We tested how recreational use of trails affects deer, and thereby tick density.
- We sampled plots close to and further from trails open or closed for recreation.
- Tick and deer density were lower near trails, more so near trails open for recreation.
- Recreation may be a tool to steer the distribution of ticks and tick-borne pathogens.

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ABSTRACT

Altered interactions between pathogens, their hosts and vectors have potential consequences for human disease risk. Notably, tick-borne pathogens, many of which are associated with growing deer abundance, show global increasing prevalence and pose increasing challenges for disease prevention. Human activities can largely affect the patterns of deer space-use and can therefore be potential management tools to alleviate human-wildlife conflicts. Here, we tested how deer space-use patterns are influenced by human recreational activities, and how this in turn affects the spatial distribution of the sheep tick (*Ixodes ricinus*), a relevant disease vector of zoonoses such as Lyme borrelioses. We compared deer dropping and questing tick density on transects near (20 m) and further away from (100 m) forest trails that were either frequently used (open for recreation) or infrequently used (closed for recreation, but used by park managers). In contrast to infrequently used trails, deer dropping density was 31% lower near (20 m) than further away from (100 m) frequently used trails. Similarly, ticks were 62% less abundant near (20 m) frequently used trails compared to further away from (100 m) these trails, while this decline in tick numbers was only 14% near infrequently used trails. The avoidance by deer of areas close to human-used trails was thus associated with a similar reduction in questing tick density near these trails. As tick abundance generally correlates to pathogen prevalence, the use of trails for recreation may reduce tick-borne disease risk for humans on and near these trails. Our study reveals an unexplored effect of human activities on ecosystems and how this knowledge could be potentially used to mitigate zoonotic disease risk.

1. Introduction

Ixodid ticks pose increasing threats to human health through transmission of tick-borne diseases. These tick-borne pathogens, transmitted by *Ixodes ricinus* in Europe and *Ixodes scapularis* in the US, are globally increasing in prevalence. Notably, there is a strong increase in the occurrence of Lyme disease in Europe (Sykes and Makiello, 2017) and the US (Kugeler et al., 2021). Furthermore, ixodid ticks are also the main vector of other zoonotic pathogens that can pose a serious health risk, such as tick-borne encephalitis virus, babesiosis, ehrlichiosis, and rickettsiosis (Koffi and Gasmi, 2019; Schwartz et al., 2017). Annually, these diseases affect more than 400.000 and 230.000 people in the US and Europe respectively, leading to substantial human and economic consequences (Kugeler et al., 2021; Sykes and Makiello, 2017). Since vaccination or treatment against these diseases are difficult or not possible and detection complicated, disease prevention by reducing tick prevalence or the risk of tick bites by prevention and protection measures is of pivotal importance (Bron et al., 2020). This

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risk is determined by both the exposure to ticks and questing tick density (Hofmeester et al., 2017). Efforts to decrease tick densities in natural areas through habitat modification or chemical control are ineffective or undesirable (Eisen and Stafford III, 2021). An alternative way to reduce the risk of tick bites may be through controlling the distribution of tick hosts.

Increasing ixodid tick densities and occurrences of the pathogens they transmit are associated with the strongly increasing and expanding populations of deer in Europe and North America, since deer are important hosts for adult ixodid ticks (Hofmeester et al., 2016, 2017; Takumi et al., 2019). Deer are important propagation hosts for ixodid ticks who require large bodied hosts in their third and final life stage for reproduction (Gray, 1998; Mysterud et al., 2014). Due to the strong association between deer and ixodid ticks, efforts to control tick densities have historically focued on reducing deer abundance through culling (Kugeler et al., 2016). Densities of other, smaller, tick hosts such as rodents, birds and reptiles are more difficult to manage. Yet, previous research suggests that the complete elimination of deer, or drastic reductions in their density, effectively reduces tick densities and disease prevalence (Kugeler et al., 2016). Such measures however are not in line with current focus on biodiversity restoration (Ruckelshaus et al., 2020) and with the increasing recognition that deer perform valuable ecological functions through their effects of grazing and trampling on the vegetation (Côté et al., 2004; Ramirez et al., 2018, 2019, 2021). Moreover, they represent a considerable economical value through their importance for ecotourism and through hunting as a land use (Côté et al., 2004). Considering these ecological and economical values, the traditional focus on strongly reducing or eliminating deer to manage vector-borne disease risk may be undesirable today. The strong correlation between deer abundance and tick prevalence (Gray, 1998; Kiffner et al., 2010; Kilpatrick et al., 2014) suggests that similar effects of reducing ticks could be attained by affecting deer abundance on a spatial scale, hence by redistributing deer over the landscape. Despite calls for wildlife management to aim more at affecting spatial behavior rather than focusing only on reducing densities by means of culling (Cromsigt et al., 2013), to our knowledge these ideas have not been applied or tested in disease management.

Deer are a prime example of species that are sensitive to human activities and human disturbance strongly affects deer behavior (Frid and Dill, 2002), vigilance (Ciuti et al., 2012), movement (Proffitt et al., 2009), activity (Ensing et al., 2014) and stress levels (Zbyryt et al., 2018). Deer generally avoid humans and their infrastructure (Ciuti et al., 2012; Muhly et al., 2011; Rogala et al., 2011), such as built-up areas, windfarms and recreational cabins (Nellemann et al., 2010; Rogala et al., 2011; Skarin and Alam, 2017). Similarly, deer may also avoid human activities at much finer spatial scales of several meters, such as the direct vicinity of roads (Mols et al., 2022; Rogala et al., 2011; Scholten et al., 2018). Hence, deer adapt their large- and fine-scale space-use patterns in response to human activities. These insights have led to the suggestion that, by actively planning human activities such as hunting and recreation, we may be able to steer deer space-use patterns and their impacts (Cromsigt et al., 2013). Here, we suggest that this concept may also be relevant for the management of tick-borne diseases by affecting the risk of tick bites, since deer abundance directly influence tick distribution. Deer, as tick hosts, play an important role in moving ticks across larger distances since the active movement of ticks is limited to several centimetres (Crooks and Randolph, 2006; Estrada-Peña, 2003; Qviller et al., 2016; Takumi et al., 2019) and Raši et al. (2018) indeed showed how wildlife trails can lead to increases in local tick density. As a consequence, human activities that shape fine-scale deer space-use should thus steer tick densities, but this remains to be tested (Albery et al., 2020; Eisen and Stafford III, 2021).

Here, we semi-experimentally tested this hypothesis that human-induced effects on deer space-use affect fine-scale tick density. We compared indices for deer space-use (dropping density) and questing tick nymph density (tick flagging) between transects near (20 m) and away from (100 m) forest trails that were either frequently used (open for recreation) or infrequently used (closed for recreation). We expected deer to avoid the areas near the intensely used trails to reduce perceived risks of recreating humans, in turn leading to lower tick densities near such trails. In contrast, we did not expect (strong) avoidance by deer of infrequently used trails and associated tick density. Our study hereby sheds light on how anthropogenic behaviorally-mediated effects on herbivores affect wildlife communities, in this case a zoonotic disease vector, on fine spatial scales. Moreover, we emphasize how targeted human-induced fear may help to alleviate disease risk.

2. Methods

2.1. Study area

We conducted this study in two adjacent areas situated in the Veluwe region in The Netherlands: the 'Deelerwoud' (DW) and 'National Park Veluwezoom' (NPVZ), both managed by the nature organization 'Natuurmonumenten' (Fig. 1). The areas together cover 6230 ha situated between the village Deelen (52.0811° N, 5.8977° E) and the city of Arnhem (52.0469° N, 6.0122° E). The areas are separated by the highway A50, which is fenced to prevent wildlife collisions, but a wildlife overpass connects the two areas and is intensively used by deer (Renard et al., 2008; van Wieren and Worm, 2001). Mean annual (1990–2019) temperatures were 10.51 °C (± 0.12 SE) and yearly precipitation was 849.96 mm (± 255.64 SE) (De Bilt, Royal Netherlands Meteorological Institute). The vegetation in these areas mainly consists of *Calluna* heathlands and mixed deciduous and coniferous forests. The most common forest type in the area is Scots pine-dominated (*Pinus sylvestris*) with European blueberry undergrowth (*Vaccinium myrtillus*; hereafter: 'blueberry') (Ekeris, 2015). As tick densities are vastly higher in forest than in heathland areas (Ruiz and Gilbert, 2010), we focused on this habitat type for our study. Large herbivores are abundant throughout both areas. In DW densities are high, with densities of 28, 7 and 2 ind. km^{-2} for fallow deer (*Dama dama*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) respectively (data from 12 to 04-2018, pers. comm. A. ten Hoedt, area manager; Huysentruyt and Casaer, 2015). Roe deer (*Capreolus capreolus*) is very rare in DW (Huysentruyt and Casaer, 2015; pers. comm. A. ten Hoedt). NPVZ has a similar large herbivore composition, but densities are lower, with 2, 4 and 3 ind. km^{-2} for red deer, fallow deer and wild boar respectively (data from 12 to 04-2018, pers. comm. A. ten Hoedt, area manager). Roe deer is still present in NPVZ at low densities (<2 ind. km^{-2}, pers. comm. A. ten Hoedt based on a count on 12-04-2018). Free-ranging Scottish Highland cattle graze both areas year-round with very limited human management interference (170 ind. moving between both areas, pers. comm. A. ten Hoedt, area manager). All large herbivores, except the Scottish Highland cattle, are culled yearly by trained nature managers between 1 August till 15 February. This culling takes places in designated zones (see Appendix A). For this study, all sampling was conducted within zones with or without recreation and no hunting. Yet these zones are much smaller than deer home ranges and all deer in the area come into contact with both hunting and recreation. Moreover, in a previous study (Mols et al., 2022) we compared deer's avoidance of trails between these zones and established that deer avoided trails on fine spatial scales in all zones with recreation, regardless of hunting. Large predators were not present in the area during our study but wolves (*Canis lupus*) colonized nearby areas in 2020 (i.e. two years after our study, www.wolveninnederland.nl).

2.2. Study design

Both areas are part of an intensely-used tourist region, receiving approximately 2 million visitors per year (pers. comm. A. ten Hoedt, area manager, April 2018), and have a well-visited network of trails open for hikers and cyclists during daylight hours. At daytime, the trails are used nearly daily year-round by tens to hundreds of recreationalists. Motorized traffic is not allowed, except for managers using the trails with 4WD vehicles. In addition to the intensely used trails, both areas also have trails that are closed

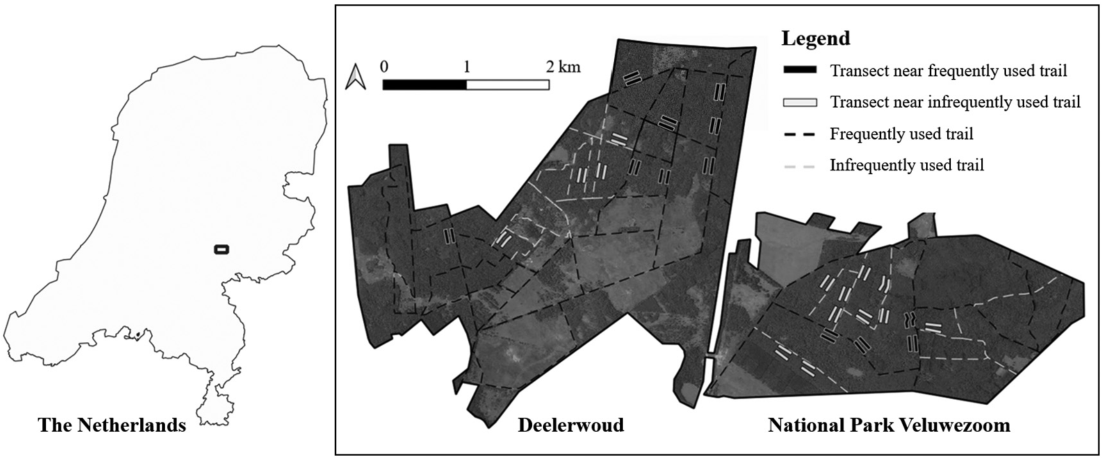

Fig. 1. The study areas situated in The Netherlands and the experimental setup of transects for sampling deer dropping and questing tick density at 20 m and 100 m parallel to trails either frequently (black) or infrequently (gray) used by people. Dark areas on the aerial photograph represent forests, lighter areas represent heathland or grassland. National Park Veluwezoom is not completely shown.

for recreation for conservation purposes, and only occasionally used by managers and researchers (each trail is used 2–3 times per week for short periods of time by 1–2 people). We used this natural experiment and, distributed over the entire study area, selected 26 sampling locations situated along trails that were either frequently used (open for recreation; $n = 12$) or infrequently used (closed for recreation, but occasionally used by nature managers and researchers; $n = 14$; Fig. 1). All trails were sandy, unpaved and 4–6 m wide and were flanked by pine-blueberry (*Pinus sylvestris* with *Vaccinium myrtillus* undergrowth) forest on both sides. Trails open for recreation were used by hikers and cyclists. We ensured trails in areas with recreation had comparable utilization by recreationalists and were used year-round by using Strava Inc. Heat Map (based on heatmap color), which uses compiled spatial data of users of Strava, a hiking, running and cycling GPS tracking application (http://labs.strava.com/heatmap). This also confirmed that the infrequently used trails in the reserve were rarely used.

Each sampling location contained two paired 150 m long transects ($n = 52$) parallel to a hiking trail: one transect at 20 m distance from the trail, and one at 100 m from the trail. These distances from the trail were chosen as previous work demonstrated that deer respond to recreation on trails at this scale (Mols et al., 2022; Mathisen et al., 2018; Scholten et al., 2018). Additionally, we located transects at 20 m from the trails to maximally exclude edge effects and ensure comparable abiotic and biotic conditions between our plots at 20 m and 100 m from the trail. This while simultaneously allowing us to measure effects that effectively reflect the probability of human-tick encounter rates and thus disease risk. This because tick densities at 20 m from the trail most likely correlate to tick densities in the fringes of the trails, and because humans stray from trails and use the proximity (20 m) from trails, resulting in exposure to ticks. The centers of transects belonging to different sampling locations were minimally 300 m apart, and at least 150 m from the next nearest hiking trail and from the closest forest edge. All transects were entirely located in pine-blueberry forest with undergrowth dominated by European blueberry (*Vaccinium myrtillus*; mean ± SD % blueberry cover = 77.7 ± 24.7) and some open patches with scattered grasses (mainly *Deschampsia flexuosa*). Blueberry cover (visually estimated as percentage cover for every 5 m along the 150 m transects) did not differ between the two distances to the trails (linear mixed model: $n = 52$, Wald's $\chi^2 = 0.92$, $P = 0.33$) or between the intensely used and infrequently used trails (linear mixed model: $n = 52$, Wald's $\chi^2 = 0.01$, $P = 0.90$). Similarly, vegetation height (mean 19.5 cm ± 0.8 cm SD), measured by means of disc and stick method (Stewart, 2001), did not differ between distances to trails (linear mixed model: $n = 52$, Wald's $\chi^2 = 0.35$, $P = 0.55$) or between the intensely used and infrequently used trails (linear mixed model: $n = 52$, Wald's $\chi^2 = 0.34$, $P = 0.56$). Additionally, canopy openness did not differ with the distance to trails (linear model: $n = 60$; $F = 0.410$, $P = 0.525$; Appendix A).

2.3. Deer dropping density and tick sampling

On each transect, we conducted deer dropping counts, as a well-used proxy for deer space-use (Acevedo et al., 2010; Alves et al., 2013), and immediately thereafter sampled questing tick density during April and May 2019, when ticks show a peak in their activity (Hartemink et al., 2021). Along our 150 m transects, two researchers walked the transect side by side in one direction, each recording all deer dropping groups in a 1 m wide strip on their respective side of the transect. Dropping groups (≥ 1 dropping) were identified as a group by assessing dropping color, shape and location (Mols et al., 2022). We did not distinguish between deer species because all deer species serve as tick hosts and species identification based on droppings is prone to misidentifications (Spitzer et al., 2019). Yet we acknowledge that the structure of the host community, which we did not incorporate in this study, could also be a parameter shaping tick abundance at local scales (Fabri et al., 2021). On each transect, we conducted tick counts using tick flagging (Tack et al., 2011; Vassallo et al., 2000). Ticks were sampled by dragging a $1 m^2$ cotton cloth attached to a bamboo pole with string at consistent speed along the 150 m long transects (Tack et al., 2011; Vassallo et al., 2000). Ticks on the cloth were counted and removed after every 5 m of dragging (Tack et al., 2011). We assumed all counted ticks were of the species *Ixodes ricinus* as it is the most abundant species by far in the Netherlands, when using this method (Hofmeester et al., 2017; Takken et al., 2017). Ticks were classified as adult or nymph. Larvae were ignored as they merely indicate an egg deposition location, do not transmit Lyme disease (Voordouw, 2021), and are difficult to count. Larval abundance reflects differences in the distribution of engorged adult females dropping of their host in the most recent temporal window. Deer are likely important hosts for tick adults and nymphs in our study area (see Discussion), and comparing questing nymph density between transects is a well-established method (Dickinson et al., 2020). We argue that our measurements of questing tick nymphs and adults, at least partly, reflect how deer space-use affects questing tick distribution. Sampling was conducted between 10.00 h and 16.00 h when tick questing conditions were ideal: on dry days on dry vegetation, when the air temperature was ≥ 10 °C, as wet weather and lower temperatures reduce tick questing behavior (Alonso-Carné et al., 2016; Hofmeester et al., 2017; Mejlon and Jaenson, 1997; Tagliapietra et al., 2011; Vail and Smith, 1998). The sequence of sampling paired plots during our study period was randomly assigned.

2.4. Statistical analyses

To test the effect of the distance to trails on deer dropping and questing tick density, we built glmer models (Bates et al., 2015) with negative binomial distribution as they best fit our overdispersed count data. Models predicting deer dropping and questing tick density included the fixed factors ‘distance to trails’ (20 m/100 m) and ‘trail intensity of human use’ (frequently/infrequently used), and their interaction. To test the effect of deer dropping density on questing tick density, the models predicting questing tick density included the additional fixed factor ‘deer dropping density’, which was not included in interactions. Each model included ‘paired plot id’ as random effect to account for our paired design. Model diagnostics were performed using the DHARMa R package (Hartig and Lohse, 2020).

3. Results

3.1. Deer

In total we counted 766 deer dropping groups on 15,600 m^2 of transect ($n = 52$; 150 m × 2 m), translating to average deer dropping densities of 4.9 ± 0.6 per 100m^2. Deer dropping group counts were lower close to trails (20 m; average 13.0 ± SE 1.7) compared to further away (100 m; 16.4 ± 2.0) (Fig. 2; Table 1). Post-hoc tests revealed that deer dropping density differed significantly between the distance to trails only near frequently used trails, where dropping density was reduced with 31% near trails compared to only 14% near infrequently used trails (Tuckey HSD; Fig. 2).

3.2. Ticks

In total we counted 6114 ticks of which the vast majority (5825; 95.3%) were nymphs and 289 (4.7%) were adults. Analyses of total tick numbers and tick nymphs separately yielded similar results (see Appendix B). Here, we present results for the analysis of tick nymphs only as nymphs are most abundant and the main transmitters of Lyme disease (Hofhuis, 2017; Sprong et al., 2013). In total, we counted 5825 tick nymphs on 7800 m^2 of transect (n = 52; 150 m × 1 m) respectively, translating to average questing nymph densities of 74.7 ± 7.7 per 100m^2. Questing nymph density was significantly (Wald's $\chi^2 = 22.44$, $P = 0.001$) lower closer (20 m vs 100 m) to trails. Moreover, the interaction between distance to trails and trail use was significant (Wald's $\chi^2 = 8.29$, $P = 0.004$), with the reduction in questing tick density being much stronger near frequently used trails (62%) compared to near infrequently used trails (14%) (Fig. 3; Table 1).

4. Discussion

We demonstrated that near (20 m) frequently used trails, deer dropping density was 31%, and questing tick density was 62%, lower than further away from (100 m) the trails. When trails were infrequently used, deer dropping density was 14% lower (and not statistically significantly) and tick numbers only 14% lower near trails than further away. These results indicate that recreation on trails changes fine-scale patterns of deer space-use and reduces deer presence close to trails, thereby strongly limiting tick density near trails. We advocate incorporating such human-induced fine-scale differences in deer space-use, and resulting changes in tick distribution, in future studies on the ecology and management of zoonotic, vector-borne, diseases.

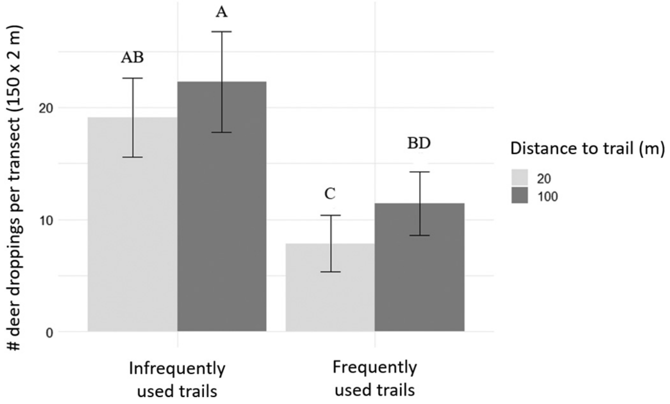

Fig. 2. Deer dropping counts on transects (150 m × 2 m) were lower close to trails (20 m; light gray) compared to further away (100 m; dark gray), but only significantly so near frequently used trails. Bars and whiskers represent means ± SEM.

4.1. Recreation drives fine-scale patterns of deer space-use

Our results are in line with the expected effects of recreational activities on deer behavior. Deer are well-known to avoid human infrastructure at a variety of scales (Borowski et al., 2021; Bubnicki et al., 2019; Meisingset et al., 2013; Nellemann et al., 2010; Skarin and Alam, 2017), and these effects could be applied in management of human-deer interactions (Cromsigt et al., 2013). Recent studies corroborate our results, showing in a variety of study systems how forest trails create fine-scale ‘corridors of fear’ where deer space-use is reduced only in the direct vicinity (< 40 m) of trails (Borowski et al., 2021; Mathisen et al., 2018; Mols et al., 2022; Scholten et al., 2018). In human-dominated systems, where visitor numbers and trail densities are relatively high, larger scale avoidance of humans by deer may be less feasible. Recent studies have reported how these human-induced changes in deer fine-scale space-use can have cascading effects such as on the vegetation (Mathisen et al., 2018; Scholten et al., 2018).

While our sample locations were all located in zones without hunting and sampling was conducted outside of the hunting season, all deer in our study area are subject to hunting in the designated zones (see Appendix A). Therefore, we could not distinguish to what extent culling contributes to deer's avoidance of trails. Yet, our results are relevant for most deer populations in areas where tick-borne pathogens pose threats, as these populations are generally subject to culling.

4.2. Human-induced patterns in deer space-use change tick abundance

Similar to the patterns in deer space-use, questing tick density was much lower near frequently used trails than further away from these trails or near infrequently used trails. In fact, on the highly used trails, the reduction in nymph density near the trails, relative to further away, was as high as 63%. This suggests that the recreational use of trails affects tick distributions through affecting deer space-use patterns. Deer density can affect ticks via two mechanisms. Firstly, after adult ticks mate on their preferred propagation host, deer, female ticks detach after which eggs are locally deposited and larvae hatch the next year (Qviller et al., 2016). Through this mechanism, deer abundance affects tick abundance at longer temporal scales across tick generations (Ostfeld et al., 2006; Wilson et al., 1985). This is possible because the position of the intensively used trails and levels of recreation in our study area have been stable for years (as indicated by Strava Inc. Heat Map and our earlier work (Mols et al., 2022)). Furthermore, deer's year-round response to recreation on trails in our study area (and others) has been well established (Brouwer, 2020; Mols et al., 2022). This suggests that deer consistently avoid trails and thereby allow long-term cross-generational effects on tick density. However, since our results are based on data reflecting processes spanning 1–2 years, longitudinal studies or a repetition of our study would be useful to confirm the robustness of results. Secondly, deer distribute ticks over the landscape because both tick larvae and nymphs may attach and detach from deer when feeding (Qviller et al., 2016; Takumi et al., 2019). It is generally assumed that tick larvae and nymphs primarily feed on small and medium-sized mammals while adults feed on large mammals, often deer (Gray, 1998; Hofmeester et al., 2016). However, the relative role of small mammals and deer as hosts for tick larvae and nymphs may depend on host density and habitat (Gray et al., 2021). This likely because tick host preference is mostly expressed through ticks questing at greater heights in later life stages, by which larger ticks reduce the change of attaching to small hosts

Table 1
Generalized Linear Mixed Model results for factors ‘distance to trail’ (20 m/100 m), ‘path use’ (frequently/infrequently used), and their interaction, included in the model predicting deer dropping counts. The model predicting questing tick density included the additional factor ‘deer dropping density’. Significant factors and interactions are depicted in bold. The random factor ‘paired plot id’ was included in all models to account for the paired design.

Response	Predictor	Estimate ± SE	Wald's χ^2	df	P
Deer dropping density	**Distance to trail**	**0.375 ± 0.121**	**10.21**	**1**	**0.001**
	Trail use	**1.002 ± 0.287**	**10.39**	**1**	**0.001**
	Distance to trail * Trail use	−0.221 ± 0.149	2.18	1	0.139
Questing tick density	**Distance to trail**	**0.973 ± 0.179**	**22.44**	**1**	**<0.001**
	Trail use	**1.105 ± 0.274**	**8.97**	**1**	**0.003**
	Deer dropping density	−0.009 ± 0.009	0.90	1	0.343
	Distance to trail * Trail use	**−0.747 ± 0.259**	**8.29**	**1**	**0.004**

(Mejlon and Jaenson, 1997). Conversely, tick larvae and nymphs still attach to deer as shown by tick counts on hunted and road killed deer, and argued by previous authors (Gray et al., 2021; Handeland et al., 2013; Huang et al., 2019; Mysterud et al., 2014; Mysterud et al., 2021). As deer density in our study system is high, the patterns in questing tick nymph density we observed can be directly shaped by space-use of the abundant deer (Qviller et al., 2016; Estrada-Peña, 2003; Takumi et al., 2019). This means that the reduction in tick density we observed near trails may thus result from both direct movement of ticks by deer as well as cross-generational effects. At the same time we acknowledge that particularly in areas with lower densities of deer, smaller host species such as rodents and birds, may be relatively more abundant and play a larger role in the fine-scale distribution patterns of ticks (notably nymphs and larvae; Van Gestel et al., 2021). The relative importance of the role of large vs. small host species in the small scale distribution of tick adults, nymphs and larvae deserves more attention in future studies, particularly in relation with TBPs in human-dominated landscapes.

4.3. Human recreation affects tick abundance

Vegetation characteristics, such as cover and height of the field layer, may also affect tick survival, density and questing behavior by influencing relative humidity and ground temperature (Hofmeester et al., 2017; Mejlon and Jaenson, 1997; Tagliapietra et al., 2011). Moreover, these same vegetation characteristics could also drive the distribution of deer as the field layer provides an important food source. It is, therefore, important to emphasize that these characteristics (blueberry cover, vegetation height, and tree canopy openness) did not differ between transects near frequently and infrequently used trails or between plots near and further away from trails. As these environmental factors did not differ between our treatments, we argue that the observed patterns in tick density are a result of human recreational activities that induce changes in deer space-use patterns. We recognize that other, smaller, species such as rodents, birds and lizards are important hosts for ticks in earlier life stages, notably for nymphs (Hofmeester et al., 2016). However, the fact that vegetation characteristics were comparable between plots near and further away from trails, makes it unlikely that the observed patterns in tick density are caused by space-use of non-cervid tick hosts such as birds, hares, and lizards. Additionally, flight initiation distances and escape distances for these smaller species are often shorter than 20 m, the distance at which our transects near trails were located, or shorter than 80 m, the difference between our paired plots (Diego-Rasilla, 2003; Samia et al., 2015; Tätte et al., 2018; Zaman et al., 2020). This makes it unlikely that the differences in tick density we observed at different distances to trails are caused by escape behavior of other tick host as a response to people on trails. Furthermore, deer in our study system are highly abundant as a result of a low culling regime (> 30 ind. km^{-1}, pers. comm. A. ten Hoedt, area manager; 4.9 ± 0.6 dropping groups per 100m^2, this study). Deer thus likely make up the majority of suitable tick host biomass and move large distances through the area (high ‘passage rate’; Takumi et al., 2019), increasing tick attachment opportunities (Estrada-Peña, 2003). Therefore, it may be assumed that deer in our study system are important hosts for both tick nymphs and adults.

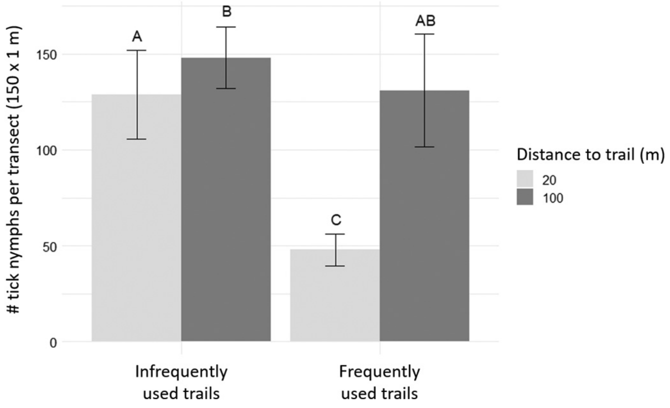

Fig. 3. Tick counts per transect (150 m × 1 m) near infrequently and frequently used trails. Letters indicate significance. Tick counts were lower close to trails (20 m; light gray) compared to further away (100 m; dark gray). Notably, the effect was significantly stronger near frequently used trails. Trends are similar to those of the number of deer droppings per transect**.** Bars and whiskers represent means ± SEM.

Previous research on the relationship between deer and tick density has shown ambiguous results. Deer generally drive tick distribution on large spatial scales as their presence enables completion of the tick life cycle (Jaenson et al. 2019). Yet evidence has shown that also on finer spatial scales, deer presence rather than abundance determines tick abundance (Hofmeester et al., 2017; Kugeler et al., 2016). We here add to this evidence by suggesting that also human-induced fine-scale patterns in deer space-use may lead to differences in questing tick nymph density on fine spatial scales. We acknowledge that deer presence rather than abundance is of pivotal importance to allow high tick densities. Yet it seems that in our study system with high deer density and presumably low alternative host density, deer may play an important role distributing ticks over the landscape at microscales. Previous studies often focused on large scale effects and averaged data on tick and deer density over larger scale areas, disregarding potential fine-scale patterns (Albery et al., 2020). Indeed, the fine-scale effects of zoonotic disease distribution are rarely studied (Albery et al., 2020). Yet, other studies corroborate our results as they documented how deer space-use can influence tick density on fine spatial scales. For example, Raši et al. (2018) showed how the presence of wildlife trails can increase local tick density. This suggests that host-tick relationships may be most strongly expressed at fine spatial scales and implies that future studies should consider within-hectare differences in deer space-use and tick distribution to assess relations between the distribution of hosts, vectors and diseases (Albery et al., 2020). It should be noted that when deer avoid trails, this could reduce relative deer densities near trails compared to densities of smaller hosts. As tick larvae and nymphs may prefer these smaller hosts, this could in turn lead to higher nymph densities near trails, as observed in our study (Hofmeester et al., 2017; Van Gestel et al., 2021). For future research it would be valuable to investigate what level of reduction in deer space-use frequency would effectively lead to decreases in questing tick abundance. This could be achieved by quantifying hosts densities and assessing tick loads on different host species.

4.4. Practical application of anthropogenic behaviorally mediated effects

We empirically demonstrated that recreation can be important factor shaping deer distribution on fine spatial scales, and that these human-induced deer space-use patterns strongly affected tick distributions. As such, recreational activities, through affecting deer antipredator behavior, may affect the distribution of a zoonotic disease vector that is leading to severe and increasing impacts on ecosystems and public health (Eisen and Stafford III, 2021).

Our results indicate that even in areas with very high deer and tick abundance, such as ours, tick numbers can be substantially reduced at fine spatial scales relevant for the risk of contracting tick-borne pathogens by humans. When tick densities are low in places where human exposure is highest, i.e. near hiking trails, tick-borne pathogen contraction risk for humans may be substantially mitigated. However, it should be noted that deer are dead-end hosts for the *Borrelia burgdorferi* bacteria which causes Lyme disease. Thus, despite a positive relation between deer abundance and tick prevalence, an inverse relationship may exist between the deer abundance and the prevalence of tick-borne pathogens in ticks (Huang et al., 2019), coined the “dilution effect” paradigm (Norman et al., 1999; Schmidt and Ostfeld, 2001). However, ticks in areas with high deer densities can still have significantly high infection rates (Takumi et al., 2019) and thus pose considerable risks, as shown by positive associations between Lyme disease incidence and deer density (Kilpatrick et al., 2014). This makes management of disease risk also in areas with high deer density relevant for human health.

Our study sheds new light on the management of tick-borne pathogens through modifying deer behavior. Culling of deer is a commonly used tool to reduce tick-borne disease risks (Gilbert et al., 2012; Kilpatrick and Randolph, 2012), but its effectiveness is increasingly debated (Gilbert et al., 2012; Hofmeester et al., 2017; Kugeler et al., 2016). Moreover, deer have substantial ecological and economical value, making their complete eradication or drastic reductions in their density undesirable in many cases (Côté et al., 2004; Ramirez et al., 2018, 2019, 2021). Our results, together with the knowledge on human-induced risk effects on deer space-use, indicate that human-induced behavioral alterations in deer may be an alternative for such culling: human recreation strongly reduces tick densities exactly in areas where these recreationists would most likely be exposed to ticks. These results indicate that spatial planning of recreation activities may be a useful tool to steer the distribution of ticks and thus tick-borne pathogens. By limiting recreation activities to hiking trails, managers may be able to maximise fear responses of deer in the vicinity of trails, and thus their effects on tick densities. Furthermore, hiking trails and their use could be promoted in places where ticks pose a potential threat, for example near playgrounds or picnic areas. Additionally, such measures would allow a reduction in the use of toxic DEET repellent and impregnated clothing which may have negative impacts on the environment and human health (Miller et al., 2011; Sudakin and Trevathan, 2003). Yet, it should be noted that we do not recommend an overall increase in recreational use of nature areas, nor an increase in hiking trail density. This because increased human disturbance could reduce the available space for deer, potentially increasing aggregation and thus pathogen transmission, which could thereby increase the risk for humans (Janousek et al., 2021). Therefore, we here advocate the spatial steering of recreation pressure in nature areas by planning the use of trails, while taking into account pathogens, as a tool to control human-tick encounter rate. Hereby, our study highlights the importance of incorporating human-induced fine-scale deer space-use patterns in zoonotic disease management.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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CRediT authorship contribution statement

The study was conceived by B. Mols, C. Smit and J.E. Churchill. B. Mols drafted the manuscript which was further developed with comments from all authors. All fieldwork was conducted by J.E. Churchill, led by B. Mols under supervision of C. Smit. BM and JEC conducted data analysis. J.P.G.M. Cromsigt, D.P.J. Kuijper and C. Smit contributed equally as senior scientists.

Appendix A. Culling regime/zones

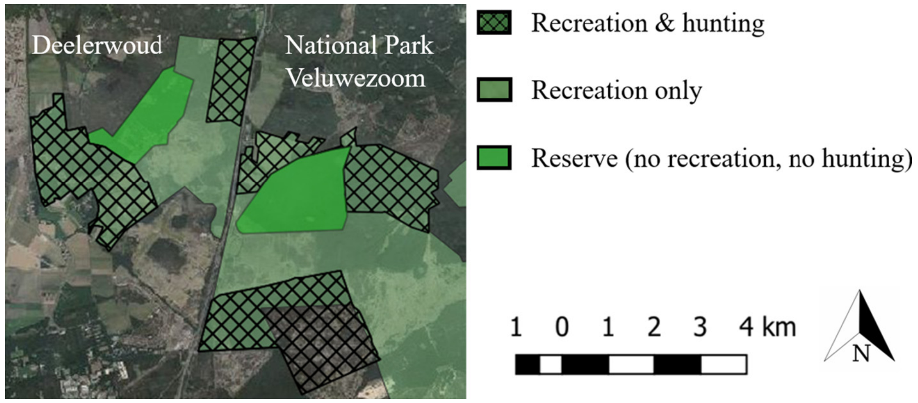

Fig. A.1. The different ‘human-use zones’ with recreation and hunting, recreation only, and no recreation and no hunting (reserve) in study areas Deelerwoud and National Park Veluwezoom. Map created on PDOK aerial photo base layer ‘Luchtfoto Actueel Ortho 25 cm RGB' in QGIS ver. 3.2.2-Bonn.

Appendix B. Measuring canopy openness

To control for variation in light availability, we measured canopy openness (a measure of canopy light) at random locations ranging from 20 m to 240 m distance to trails by taking upward photos with a regular digital camera (Nikon Coolpix B700) 1m above ground level. The photos were analyzed with ImageJ which resulted in an estimate of the percentage canopy openness (Rueden et al., 2016). We found that canopy openness did not correlate with the distance to trails (linear model: n = 60; F = 0.410, P = 0.525).

Table B.1
Results of linear model indicating the absence of a relationship between canopy openness and the distance to tails.

Response	Predictor	Estimate	t-value	*P*
Canopy openness	**Intercept**	**45.25**	**19.48**	**<0.001**
	Distance to trails	0.014	0.64	0.525

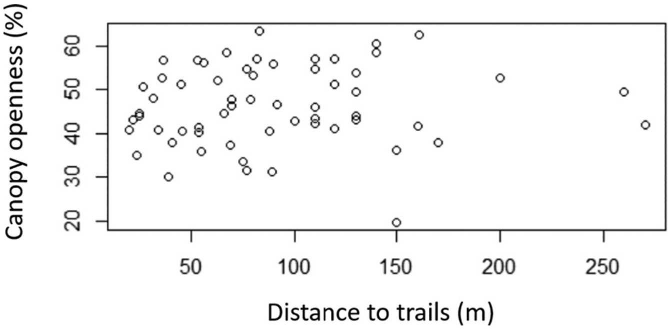

Fig. B.1. Canopy openness (%) in relation to distance to trails (m) measured at 60 random locations in our study area.

Appendix C. Total questing tick density (adults + nymphs)

Table C.1
Wald's χ^2 values and significance tests for factors 'distance to trail' (20m/100m), 'path use' (frequently/infrequently used), and their interaction, and the factor 'deer dropping density', which were included in the model predicting total questing tick (nymphs + adults) density. Significant factors and interactions are depicted in bold. The random factor 'paired plot id' was included in the model to account for the paired design.

Response	Predictor	Estimate ± SE	Wald's χ^2	df	*P*
Total questing tick density	**Distance to trail**	**0.949 ± 0.172**	**24.08**	**1**	**<0.001**
	Trail use	**1.086 ± 0.267**	**9.58**	**1**	**0.001**
	Deer dropping density	-0.009 ± 0.008	1.32	1	0.251
	Distance to trail * Trail use	**-0.701 ± 0.251**	7.81	**1**	**0.005**

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