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Context-dependent responses of naïve ungulates to wolf-sound playback in a human-dominated landscape

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Predation risk is a major driver of the distribution of prey animals, which typically show strong responses to cues for predator presence. An unresolved question is whether naïve individuals respond to mimicked cues, and whether such cues can be used to deter prey. We investigated whether playback of wolf sounds induces fear responses in naïve ungulates in a human-dominated landscape from which wolves have been eradicated since 1879. We conducted a playback experiment in mixed-coniferous and broadleaved forest that harboured three cervid and one suid species. At 36 locations, we played wolf sounds, sounds of local sheep or no sounds, consecutively, in random order, and recorded visit rate and group size, using camera traps. Visit rates of cervids and wild boar showed a clear initial reduction to playback of both wolf and sheep sounds, but the type of response differed between sound, forest type and species. For naïve wild boar in particular, responses to predator cues depended on forest type. Effects on visit rate disappeared within 21 days. Group sizes in all the species were not affected by the sound treatment. Our findings suggest that the responses of naïve ungulates to wolf sound seem to be species specific, depend on forest type and wear off in time, indicating habituation. Before we can successfully deter ungulates using predator sound, we should further investigate how different forest types affect the perception of naïve ungulates to these sounds, as responses to predator sound may depend on habitat characteristics.

The distribution of prey animals in space and time is thought to be driven largely by food and predation risk (Laundré, 2010; Sih, 2005). Animals prefer locations and times that optimize the intake of food (Shipley, 2007; Weterings et al., 2018), while they avoid locations and times that involve danger or require additional behavioural costs to reduce predation risk (Lima & Dill, 1990; Weterings et al., 2016). Distribution of prey is thus the outcome of a cost–benefit trade-off between food and safety (Robbins, 1993). Complex interactions between habitats, predators and antipredator behaviour of prey therefore produce heterogeneous distributions of prey across landscapes. For example, habitat use of hares, *Lepus europaeus*, was affected by predation risk, competition, food quality and food quantity (Weterings et al., 2018).

Prey animals use a variety of cues to sense the presence of predators and assess predation risk while foraging (Prugh et al., 2019). These include direct cues such as visual observation of the predator, and indirect cues such as habitat characteristics, predator smell and sound. Responses to predator cues include antipredator behaviours of prey such as flight, vigilance, grouping or avoidance that can result in a reduced foraging efficiency (i.e. nutritional or energetic costs) or increased stress (Creel, 2018). For example, red deer, *Cervus elaphus*, spent more time vigilant and less time foraging in forest habitat that contained wolf, *Canis lupus lupus*, scat, compared to forest habitat without wolf scat (Kuijper et al., 2014). Père David's deer, *Elaphurus davidianus*, spent less time foraging in response to sounds of allopatric predators, and were able to discriminate between different predators (Li et al., 2011). Bushbuck, *Tragelaphus sylvaticus*, avoided floodplain and woodland habitats with predator playbacks of leopard, *Panthera pardus*, vocalizations (Atkins et al., 2019). Smaller group sizes of elk, *Cervus canadensis*, were related to lower encounter rates and attack success by wolves (Hebblewhite & Pletscher, 2002), suggesting that group size reduces individual predation risk.

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Because of the responses of prey animals, predator cues have been used successfully as a repellent. For example, application of predator odour to woody plants reduced levels of browsing by deer (Melchiors & Leslie, 1985; Swihart et al., 1991). Repeated cues at a location can result in long-term deterrence if the risk is predictable and controllable (Creel, 2018), if habituation does not take place (Blumstein, 2016) and if individuals respond to cues even when they have never encountered the predator (i.e. naïve prey; Hettena et al., 2014).

Examples of taxa for which naïve prey show a response to predator cues are invertebrates (Turner et al., 2006), fish (Hawkins et al., 2004), birds (Amo et al., 2011; Veen et al., 2000) and mammals (Du et al., 2012; Sündermann et al., 2008). For some naïve prey, the presence of a response depends on the type of cue presented (e.g. Australian brush-turkeys, *Alectura lathami*: Göth, 2001). Moreover naïve prey can express different responses depending on the amount of experience with other predators (e.g. freshwater snail, *Physa acuta*: Turner et al., 2006), while others show a response only to certain predators (e.g. black-tailed deer, *Odocoileus hemionus sitkensis*: Chamaillé-Jammes et al., 2014), or a combination of both (various cervid species: Hettena et al., 2014). Such discrepancies between studies could be related to variation in habitat characteristics (Blumstein, 2016).

Whether or not naïve prey show fear responses is relevant for species management (i.e. pest control; see Martin et al., 2020). It would allow animal distributions to be manipulated by simulating predation risk in human-dominated areas that lack predators, for example, by playback of sounds, placement of models or application of faeces or scent (Jones et al., 2016). In addition to the disturbance and risk generated by humans (Frid & Dill, 2002), managers in predator-free areas could thus create artificial landscapes of fear (sensu Bleicher, 2017) to drive wildlife away from places where they are not desired, such as plantations or croplands and roads. This situation is common for ungulates, as they can cause economic and ecological damage to forest production systems (Beguin et al., 2016; Nuñez et al., 2010; Ramirez et al., 2018, 2019), and can cause traffic collisions with high socioeconomic costs (Colino-Rabanal et al., 2018). In general, there is incomplete knowledge about the number and complexity of factors that affect animal behaviour in human-dominated landscapes (Kuijper et al., 2016; Tablado & Jenni, 2017; see also Shannon et al. (2016) for effects of noise pollution). However, there is a particular lack of studies on the effect of repellents on behavioural changes of naïve ungulates in human-dominated landscapes (Hettena et al., 2014). Nevertheless, studies with non-naïve ungulates in human-dominated areas have reported that the efficacy of repellents depended on the personality and degree of isolation of individuals (Found and St. Clair, 2018), the application rate, human density and the duration of evolutionary experience with humans (Swihart et al., 1991). Furthermore, ex situ experiments showed that the effectiveness of repellents can be reduced if no alternative food sources are available and over time (Stutz et al., 2019). Finally, studies in landscapes not dominated by humans showed a reduction in behavioural response to predator cues by naïve ungulates compared to non-naïve ungulates (Berger, 2007).

Previous studies have argued that auditory cues of predators can ‘demonstrate a high certainty of immediate threat’ to prey animals (Peers et al., 2018, p. 1718). In small mammalian prey species, distribution and local density were found to be strongly affected by predator sound (Suraci et al., 2016). Auditory cues are generally more significant for species in closed environments in which visual assessment of predation risk is limited, such as dense forests (Lynch et al., 2015; Yip et al., 2017).

In this study, we experimentally tested whether naïve ungulates show fear responses to the playback of wolf sounds. We established an experiment in a seminatural human-dominated landscape from which wolves had been eradicated more than a century ago and that harbours three cervid (roe deer, *Capreolus capreolus*, fallow deer, *Dama dama*, red deer, *C. elaphus*) and one suid species (Eurasian wild boar, *Sus scrofa*). At 36 forest locations, we played wolf sounds, sounds of local sheep or no sounds, consecutively, in random order, and recorded fear responses using camera traps. We then tested whether playback of wolf sound reduces the visit rate (see Atkins et al., 2019) thus affecting prey distribution in space and time. We also investigated the effect of playback on ungulate group size. This could be related to their body size (Putman, 2003) and corresponding antipredator strategy, such as hiding, escaping or deterring predators (Lingle, 2001). However, evidence from the literature is too scattered and contradictory to predict the effect of playback on cervid and suid group sizes (Kasozi & Montgomery, 2020). For example, variation in group size could not be explained as an antipredator response in red deer in contrast to roe deer and fallow deer (Apollonio et al., 1998; Barja & Rosellini, 2008). For roe deer, group size was smaller in forest than open habitat, probably because predation risk in forest habitat can be reduced by hiding or immobility (Barja & Rosellini, 2008), which is facilitated in smaller groups.

METHODS

Study System

The experiment was conducted in National Park the Veluwezoom (52°05′N, 6°00′E), The Netherlands, a 5000 ha seminatural area with heavy use by recreationists (± 5500 visitors/day; Fig. 1). This forested landscape on clay and sandy soils (Ritzema & Stuyt, 2015) consists of a mosaic of forests, with patches of heath, shifting sands and estates. The area is home to four ungulate species: roe deer (300 individuals in spring), fallow deer (850 in summer), red deer (840 in summer) and Eurasian wild boar (550 in summer) (numbers based on 2016 twilight and daytime total counts in spring and summer respectively from Schoon & Schrauwen, 2016). These species have a strong impact on forest structure and dynamics at all stages of growth and development in this region (Ramirez et al., 2018, 2019). The population of ungulates is controlled by hunting from raised seats near plots with forest production damage between 1 August and 15 March (numbers shot in 2015–2016: roe deer 95, fallow deer 171, red deer 165, boar 348; Schoon & Schrauwen, 2016). The main native predator of all the adult ungulates is the Eurasian wolf, which was eradicated from this region in 1822. In March 2019, wolves re-established in the Netherlands, but had not yet reached the study area. Ungulates in this area were thus entirely naïve to wolves. The heathlands in Veluwezoom are grazed with Veluwe heathland sheep, *Ovis orientalis f. aries*, a local breed.

Experimental Set-up

We randomly selected 36 locations within the 2450 ha of forest habitat in the southeast of the study area, which contains patches of broadleaved, mixed and coniferous forest (Fig. 1). Locations were on average ±SD 630 ± 215 m (range 381–1174) apart to avoid spatial autocorrelation and were situated at least 50 m from the nearest path to reduce visual disturbance by recreationists. We applied three treatments in a Latin square design: (1) playback of wolf sounds, (2) playback of sheep (neutral playback) and (3) no playback (control). The experiment ran outside the hunting season during three sequential periods of 17.9 ± 0.7 days (mean ± SD) separated by a 5-day washout period, between 26 March and 30 May 2019. We randomly assigned one of six different treatment schemes with alternating

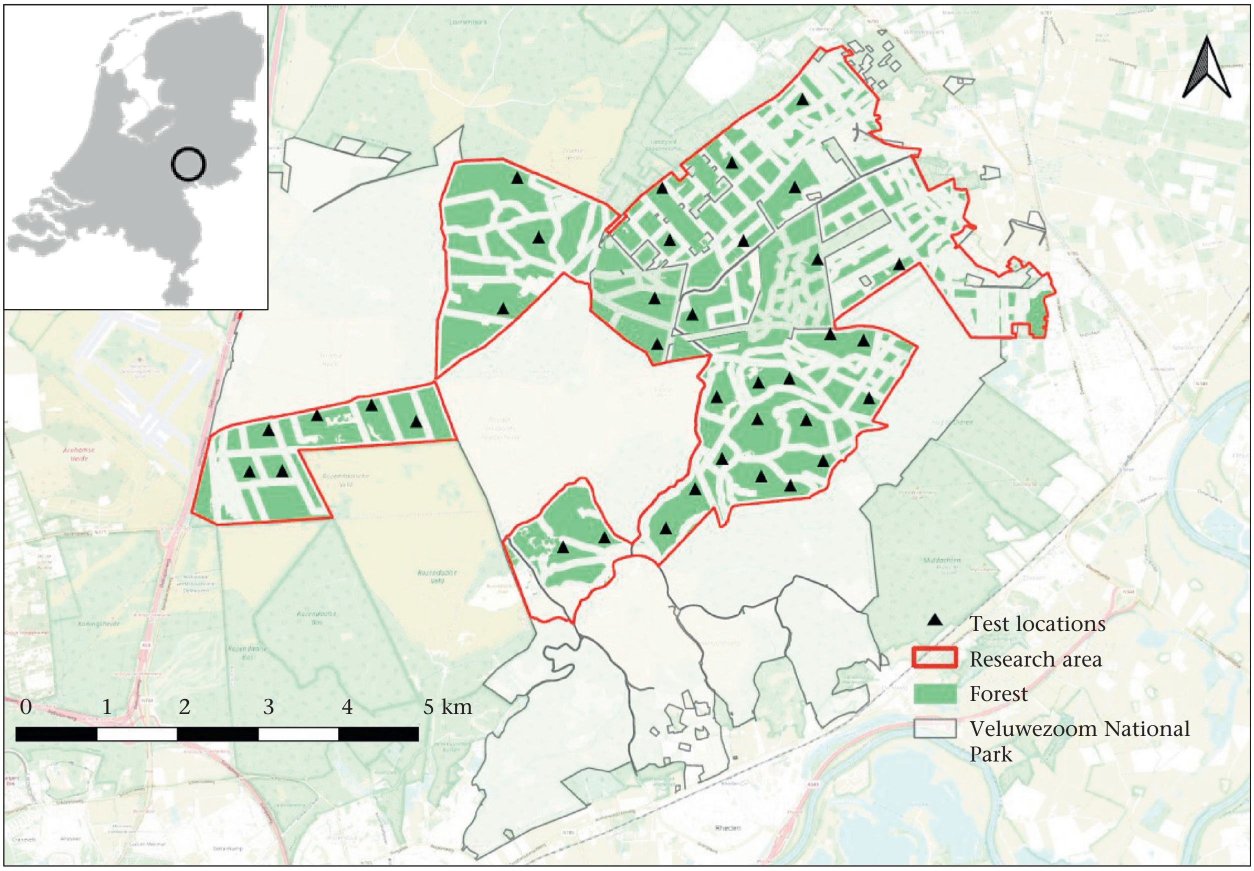

Figure 1. Overview of the 36 test locations (triangles) across the study area and within the Netherlands. Research area shows forested (green) and nonforested (white) areas.

treatments to each of the 36 locations, in such a way that each treatment scheme occurred six times.

At each location we positioned a playback station (sound box: MIFA Mini 4.2) + car battery (Landport LP12V-50Ah Lead battery) + voltage regulator (USB car charger 12–24 V) + red LED light (LAOMAO, 12 V)) opposite to a camera trap (Reconyx Hyperfire with infrared trigger: HC600 + HS2X (on HC600 setting)) (Fig. 2). Both the camera trap and the sound box were attached to a tree (diameter at breast height >20 cm) at a height of 50 cm, opposite to each other, spanning a level area between both trees. On average ±SD, camera traps and sound boxes were spaced 14.7 ± 1.1 m apart, which corresponds to the average effective detection distance of camera traps for cervids and wild boar in Dutch forests (Hofmeester et al., 2017). Cameras were aimed at the playback station in a northerly direction to avoid overexposure of photos by sunlight. The line of sight measured from the camera lens was calibrated to run parallel to the soil surface at a height of 50 cm up to at least 5 m (see Jansen et al., 2014), without clearing any vegetation. Cameras were set to record a burst of 10 photos when triggered, without any delay between bursts. The power supply of each sound box was connected with a small LED light with a narrow light beam in the red-light spectrum, which is poorly visible to ungulates, which have dichromatic vision (Cohen et al., 2014). Whether the sound box still had power was determined by checking for the LED light on midnight time lapse photos.

To reduce habituation to the playback, we broadcast sounds for only 40% of the (total treatment) time. Playlists were randomized for both playbacks and silent periods of different lengths. Each playlist included 6 whole days in which no sounds were broadcast. Six different vocalizations of the Eurasian wolf were included in the predator playlist, such as choir howling, warning sounds, barking, snarling, whimpering and pup sounds, acquired from online audio databases (see Supplementary Material 1–2). As neutral playback, we used sounds of the Veluwe heathland sheep: eight different vocalizations recorded in the area itself, including sounds from different life stages (see Supplementary Material 3). We assumed that these vocalizations are a familiar, harmless sound to wildlife in the study area.

Preparation of playbacks followed Suraci et al. (2016). To prevent differences in sound characteristics between the playbacks, we matched the temporal properties (amplitude peaks) of playbacks by visually examining the spectrogram, oscillogram and waveform of each exemplar, using Audacity (Crook, 2019). Sound exemplars were on average ±SD 48.3 ± 37.1 s long, with no difference in the overall duration between playbacks. We broadcast the playbacks at a lower volume than did Suraci et al. (2016), because sound transmission in closed landscapes is over a much shorter distance than in open landscapes (Weissburg et al., 2014; Yip et al., 2017). We chose to broadcast the playbacks at a mean volume ±SD of 63.3 ± 15.9 dB (at an average distance of 9.7 ± 1.1 m from the sound box), at a slightly higher volume than rural ambient sound in a human-dominated forested landscape (i.e. 44–50 dB; Engineering ToolBox, 2003). We thus assumed that broadcasting sounds at a lower volume at shorter distances of detection would elicit a more biologically realistic response (Prugh et al., 2019; Weissburg et al., 2014). Notwithstanding, stronger auditory cues might decrease the possibility of habituation (Blumstein, 2016). All in all, the volume of playbacks was not significantly different between wolf and sheep ($t_{52} = 0.17$, $P > 0.05$).

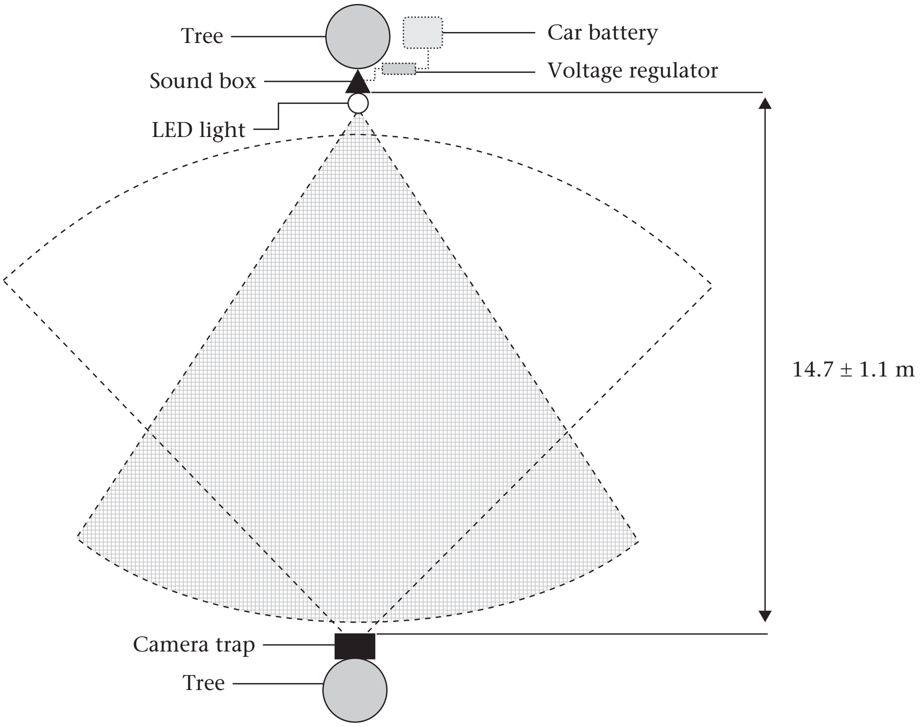

Figure 2. Layout location and set-up of playback station, including the average distance ±SD between sound box and camera trap ($N = 36$). Detection area of camera (white) and area of sound propagation (dotted) are presented in a schematic way.

Measurements

Visit rate and group size were estimated from sequences of photographs collected from camera traps placed near the playback stations. The photos were uploaded to Agouti, an application for standardized processing of camera trap photos (Casaer et al., 2019). Visits were treated as distinct if two sequences of photos were separated by more than 120 s, which is much longer than the average duration of cervid and wild boar visits (mean ±SD = 1.0 ± 11.7 s) to the location (average camera detection distance: 8.5 ± 5.7 m, $N = 142$; angle: 15.1 ± 11.7°, $N = 141$). Visit rate was determined by summing the total number of encounters per day. Group size was determined by summing all adult and subadult individuals that appeared during a single encounter. We did not consider young individuals in our study, as we assumed that changes in group sizes as a response to predator sound were determined by the behaviour of the (sub)adults in contrast to the young individuals, which would not make independent choices.

At each location, we also recorded forest type (i.e. broadleaved, coniferous or mixed), depending on the dominant tree vegetation, to account for a habitat effect. To determine tree density, we counted trees with a diameter at breast height of more than 10 cm in a circle with a 5 m radius in front of the camera trap. To assess vegetation changes during the season, we measured forest habitat characteristics (see Côté et al., 2004; Milligan & Koricheva, 2013; Table 1) at the start of the first and at the end of the third treatment period. Canopy cover at each location was estimated indirectly via light interception from hemispheric photographs taken vertically upward at a standard height of 50 cm above the ground. The percentage of canopy-covered sky (leaf area index) was calculated with IMAGEJ (Schneider et al., 2012). Ground cover vegetation height was estimated at five locations in a 15 × 15 m orthogonal layout in each of the 36 study locations at the start and end of the experiment (Massé & Côté, 2009). We also measured the distance between the centre of each playback station and the nearest infrastructure (i.e. settlement, parking space and paths). The potential temporal variation in reproductive status and body condition was controlled for by including the period of treatment (i.e. three periods: 27 March–11 April, 19 April–4 May, 12 May–27 May) in the analysis. Weather variables (e.g. temperature, wind speed and rainfall) that could affect the animals' ability to respond to the playbacks were measured daily by a weather station close to the study site. For each ungulate visit, we determined the dark (sunset–sunrise) or light period using the R package 'suncalc' (version 0.5.0), because this affects the perception of predation risk (Kohl et al., 2018).

Table 1
Forest habitat characteristics at the 36 study locations

Forest class	Forest type	N	Tree density (trees/100 m^2)	Canopy cover (% of maximum)	Average ground cover vegetation height[a] (cm)	Distance to nearest infrastructure (m)
Mixed-coniferous	Coniferous	18	6.0 ± 4.1	64.7 ± 8.8	25.3 ± 9.2	127.0 ± 50.4
	Mixed	9	5.8 ± 2.8	63.1 ± 8.2	23.1 ± 11.8	112.0 ± 47.4
Broadleaved	Broadleaved	9	6.7 ± 5.0	54.0 ± 13.7	8.3 ± 11.4	109.1 ± 64.9

Means are shown ±SD.

[a] Average based on the vegetation height at the start and end of the experiment, estimated at five locations in a 15*15 m orthogonal layout in each of the 36 study locations.

Ethical Note

This research was approved by Wageningen University & Research and assessed by the Wageningen University Animal Welfare Body.

Data Analysis

Data exploration followed Zuur et al. (2010).

Visit rate

We used a generalized linear mixed-effect model in R (glmmTMB version 0.2.3; Brooks et al., 2017) with negative binomial error and a log link function to assess the effect of fear from predator sound on the total number of cervid and wild boar visit rates per location per day (see Supplementary Material 4). We removed the first and last days from each treatment to reduce effects of disturbance on the visit rate and removed all data beyond day 17 to standardize the length of the treatment period for a balanced design. Differences between locations were accounted for by fitting random intercepts for each location. Daily measurements per location within a treatment period were accounted for by fitting random intercepts for each treatment period nested within location. We also included crossed random intercepts for the date of the observation day because several locations were observed on the same day. Temporal autocorrelation among subsequent days within a treatment period was not taken into account, based on autocorrelation and partial autocorrelation plots of the residuals. We used a negative binomial generalized additive mixed model (NB GAMM) with log link function to test whether there was a nonlinear relation between the visit rate and the number of days since the start of the treatment (see Zuur, 2016). Cross validation showed linearity.

We specified our fixed-effect structure based on a proactive ungulate behavioural response, i.e. a long-term effect that lasted throughout the treatment period, which, if habituation occurred, should show a nonlinear asymptotic decline in the frequency or magnitude (Blumstein, 2016). Our global model featured the sound treatment, the number of days since the start of the treatment, forest type, their two- and three-way interactions, period of treatment, tree density, distance to nearest sand road and weather characteristics. We used the drop1 (backward selection) procedure (Zuur et al., 2009) to find the best fitting model that included the sound treatment.

The period of treatment, tree density, distance to nearest sand road and weather characteristics were added as control variables only if the Akaike information criterion was substantially reduced (>2 units; Burnham & Anderson, 2002) using the R function drop1 (Zuur et al., 2009). Visual inspection of box plots of canopy cover and ground cover vegetation height for each forest type showed little overlap between forest types (i.e. were correlated), and were therefore not included in the final model.

A specific concern for the final models was the high number of zeros (cervid model: 1338 of 1488 days (89.9%); wild boar model: 1212 of 1488 days (81.5%)). However, 10 000 simulations from each of the final models produced data sets with a similar percentage of zeros as the observed data (Zuur & Ieno, 2016). The negative binomial distribution modelled thus explained the high number of zeros. Additionally, the observed dispersion parameters (cervid model: 0.85; wild boar model: 0.98) complied with the range of values produced by another 10 000 simulations from each of the final models (Zuur & Ieno, 2016; see Supplementary Material 5).

Group size

We used a generalized linear mixed-effect model in R (glmmTMB version 0.2.3; Brooks et al., 2017) to test the effect of fear from predator sounds on the (sub) adult group size of cervids and wild boars. We only included visits where at least one adult or subadult individual was captured by the camera trap. We employed a zero-truncated Poisson error for the cervid model, and a zero-truncated negative binomial error for the boar model, both with log link function. Dependency of encounters on the same location was accounted for by fitting random intercepts for each location.

Like the ‘visit rate’ model, we included crossed random intercepts for the date, and specified our fixed-effect structure based on a nonlinear asymptotic decline in the frequency or magnitude. Our global model featured the sound treatment, the number of days since the start of the treatment and the forest type. For this model no interactions were included, because too few individuals were captured by the camera traps in mixed and coniferous forest during predator and neutral playbacks. We included the same control variables as in the ‘visit rate’ models but included the dark–light period as a factor.

A specific concern for both models was the high number of ones (cervid model: 166 of 209 encounters days (79.4%); wild boar model: 334 of 446 encounters (74.9%)). However, like the ‘visit rate’ model, the high number of ones was explained by the distribution modelled, while the observed dispersion parameters (cervid: 1.04; wild boar: 0.9) fell within the range of values produced by additional simulations.

For all four models, we standardized continuous predictors to allow for comparison of effect sizes. Forest type was recoded into two classes: broadleaved and mixed-coniferous, because the number of camera trap visits in mixed forest was too low. Residual diagnostics were performed by using the ‘DHARMa’ R package version 0.2.6 (Hartig, 2017). Plots of the residuals versus the continuous and discrete covariates did not show a clear nonlinear pattern; consequently, it was not necessary to model nonlinear patterns. Spatial dependency between test locations was absent and assessed by a sample variogram of the Pearson residuals of the optimal model.

RESULTS

Visit Rates

The number of cervid visits was low compared to the number of visits for wild boar ($N_{\text{roe deer}} = 58$, $N_{\text{fallow deer}} = 42$, $N_{\text{red deer}} = 109$, $N_{\text{wild boar}} = 446$ days with encounters out of 1488 days; see also Appendix Table A1). Therefore, we pooled the three cervid species. Additionally, for both cervids and wild boar, visits in mixed-coniferous forest were less frequent than in broadleaved forest (Fig. 3a–f, Appendix Fig. A1).

Cervid visit rates were affected by the interaction between the sound treatment and forest class ($\chi^2_2 = 11.9$, $P < 0.01$), and the interaction between the sound treatment and the number of days since the start of the treatment ($\chi^2_2 = 10.6$, $P < 0.01$). During both playback treatments, and in both forest classes, cervid visits increased over time (Table 2, Fig. 3a–c). Cervid visit rates during the wolf playback were significantly lower only compared to the control in mixed-coniferous forests (first 17 days; compare Fig. 3a and b). However, visit rate during the sheep playback was significantly lower only compared to the control up to day 10.3 in broadleaved forest (Fig. 3c), and only up to day 14.5 in mixed-coniferous forest (Fig. 3c). We did not find any difference in visit rate between the wolf and the sheep playbacks. Finally, cervid visits became more frequent

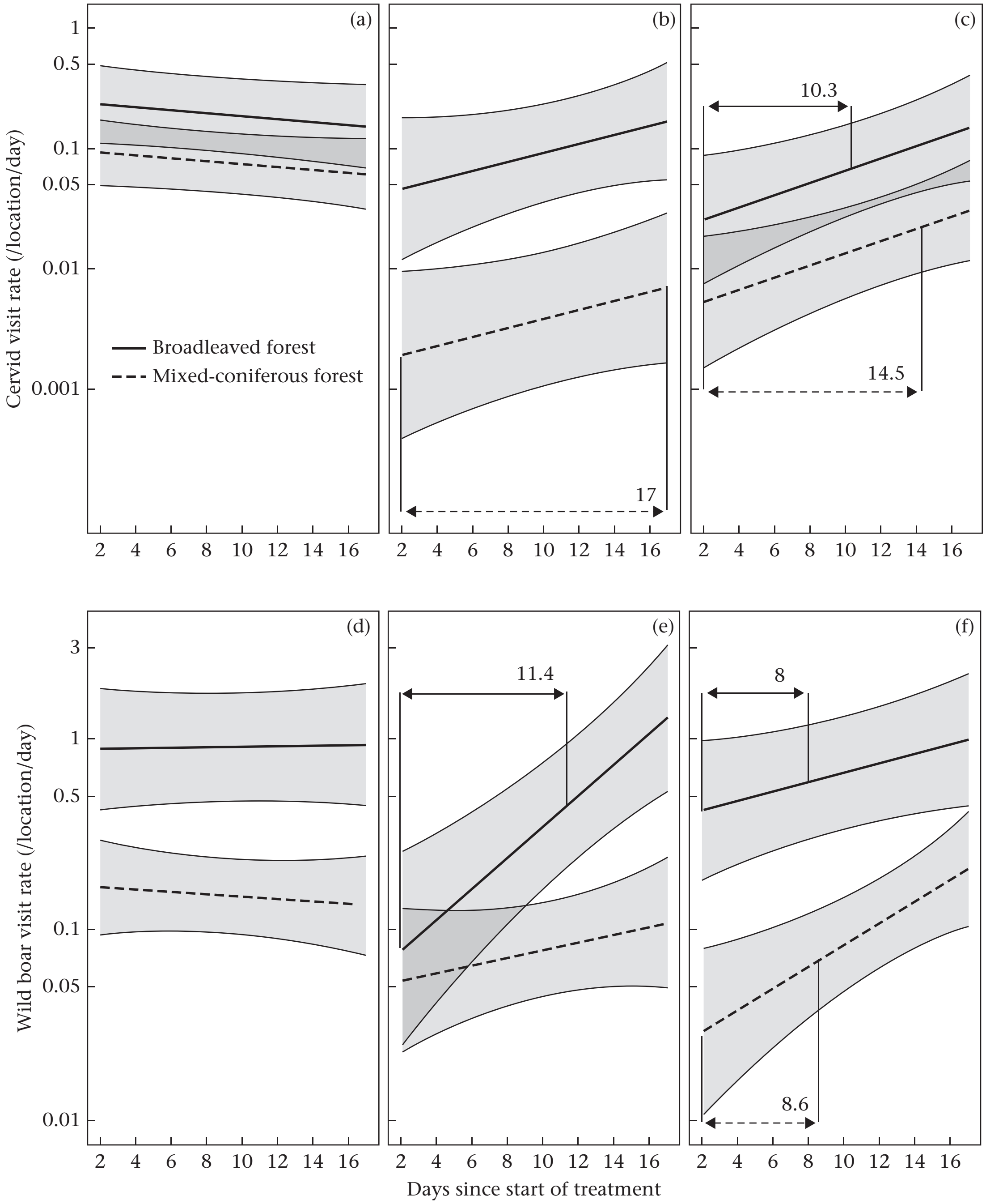

Figure 3. Visit rate (log scale) over time for (a-c) deer and (d-f) wild boar in three different playback treatments in Veluwezoom National Park, the Netherlands. Lines and grey shading show GLMM fits with 95% confidence interval (a, d) without playback, (b, e) with playback of wolf sounds and (c, f) with playback of sheep sounds in broadleaved and mixed-coniferous forest. Arrows show the average time during the treatment period when the sound treatments were significantly different from the control (black) and the wolf playback (grey; Tukey's multiple comparison test: $P < 0.05$). Data for cervids are presented for period 3 (12–27 May) and an average temperature of 11.1 °C. Data for wild boar are presented for days without rainfall.

over time (i.e. period: $\chi^2_2 = 8.4$, $P < 0.05$), and were also less frequent on warmer days (Table 2).

Wild boar visit rates were explained by the three-way interaction between the sound treatment, forest class and the number of days since the start of the treatment ($\chi^2_2 = 6.7$, $P < 0.05$). Wild boar visited the camera traps less frequently during the wolf playback than during the control only in broadleaved forest during the first 11.4 days (compare Fig. 3d and e). In mixed–coniferous forest, visits were less frequent during sheep playback compared to the control up to day 8.6 (Fig. 3f). Visit rates were significantly lower during the wolf playback compared to the sheep playback during the first 8.0 days (Fig. 3f). In addition, the slope of the predator playback for wild boar in broadleaved forest was only marginally different from the slope of the sheep playback ($P = 0.057$) in the same forest type. Wild boar visits became more frequent over time during both playback treatments, and in both forest classes (Fig. 3d–f). Wild boar had higher average camera trap visit rates in broadleaved forest than mixed-coniferous forest (Fig. 3d–f, Table 2). Finally, wild

Table 2

Responses of deer and wild boar to experimental playback of sounds

Parameters in final model	Cervids				Wild boar			
	Visit rate (/location/day) ($N = 1488$)		Group size (/visit) ($N = 209$)		Visit rate (/location/day) ($N = 1488$)		Group size (/visit) ($N = 446$)	
	β ± SE	P	β ± SE	P	β ± SE	P	β ± SE	P
Intercept	−1.68 ± 0.36	< 0.001	0.54 ± 0.34	0.11	−0.10 ± 0.33	0.76	−0.71 ± 0.55	0.20
Treatment Sheep[a]	−1.11 ± 0.35	< 0.01	−0.67 ± 0.47	0.15	−0.34 ± 0.20	0.08	−0.39 ± 0.25	0.12
Treatment Wolf	−0.75 ± 0.36	< 0.05	−0.83 ± 0.58	0.15	−1.04 ± 0.26	< 0.001	−0.53 ± 0.32	0.10
Forest class Mixed-coniferous[b]	−0.91 ± 0.39	< 0.05	-	-	−1.80 ± 0.39	< 0.001	-	-
Days[c]	−0.03 ± 0.02	0.18	-	-	0.003 ± 0.02	0.88	-	-
Treatment Sheep*Mixed-coniferous	- 0.67 ± 0.50	0.18	NT[d]	NT	−0.31 ± 0.32	0.33	NT	NT
Treatment Wolf *Mixed-coniferous	−2.27 ± 0.69	< 0.01			0.37 ± 0.36	0.30		
Treatment Sheep*Days	0.14 ± 0.05	< 0.01	NT	NT	0.05 ± 0.04	0.17	NT	NT
Treatment Wolf *Days	0.11 ± 0.06	< 0.05			0.18 ± 0.05	< 0.001		
Forest class Mixed-coniferous*Days	-	-	NT	NT	−0.02 ± 0.03	0.59	NT	NT
Treatment Sheep*Mixed-coniferous*Days	-	-	NT	NT	0.09 ± 0.06	0.15	NT	NT
Treatment Wolf *Mixed-coniferous*Days					−0.12 ± 0.07	0.09		
Period (19 April – 4 May 2019)[e]	0.60 ± 0.26	< 0.05	−1.15 ± 0.43	< 0.01	-	-	-	-
Period (12 May – 27 May 2019)	0.78 ± 0.28	< 0.01	−3.21 ± 0.78	< 0.001				
Dark[f]	NA	NA	−0.75 ± 0.26	< 0.01	NA	NA	−0.43 ± 0.22	< 0.05
Average daily temperature[g]	−0.27 ± 0.10	< 0.01	-	-	-	-	-	-
Rainfall present[h]	-	-	-	-	- 0.32 ± 0.13	< 0.05	−0.65 ± 0.28	< 0.05
GLMM Model	Negative binomial		Zero-truncated Poisson		Negative binomial		Zero-truncated negative binomial	
Cnest	$\sigma_{\mathrm{Location}} = 0.70$		$\sigma_{\mathrm{Location}} = 0.52$, $\sigma_{\mathrm{Date}} = 0.58$		$\sigma_{\mathrm{Location}} = 0.90$, $\sigma_{\mathrm{Block:Location}} = 0.08$[i]		$\sigma_{\mathrm{Date}} = 0.55$	

Estimated regression parameters, SEs and P values of the parameters of the final GLMM models for visit rate and group size are shown. NA: not applicable.

[a] Reference: no sound.

[b] Reference: broadleaved forest.

[c] Days (since start of treatment) centred around day 9.

[d] NT: interaction terms not tested, because of too few encounters.

[e] Reference: period (27 March–11 April 2019).

[f] Reference: light (between sunrise and sunset).

[g] Betas are standardized.

[h] Reference: rainfall absent.

[i] Block = 16-day treatment period for a location.

boar visits were less frequent during rainfall than on days without rainfall (Table 2).

Group Size

We found no effect of the playback of sounds on boar or cervid group size (Table 2). However, boar ($P < 0.05$) and cervid ($P < 0.01$) group size was smaller during the dark than the light period and cervid group size decreased during the season (Table 2).

Forest Characteristics

Canopy cover in mixed-coniferous forest was denser ($t_{34} = -3.3$, $P < 0.01$) and ground cover vegetation was higher ($t_{33} = -3.7$, $P = 0.01$) than in broadleaved forest.

DISCUSSION

Fear of predators has been demonstrated for naïve prey species, such as small and large mammals in natural landscapes (Atkins et al., 2019; Chamaillé-Jammes et al., 2014; Suraci et al., 2016), and for some ungulates habituated to humans (Hettena et al., 2014). Our study suggests that responses of ungulates to playback of wolf sounds depends on habitat characteristics. In particular for naïve wild boar, responses that reduced visit rate differed between forest types (i.e. context dependent). Moreover, responses to playbacks declined over the weeks of the study, indicating fast habituation. Playbacks thus seem suitable for creating a landscape of risk in specific habitats in European forests only in the short term.

Prey use multiple cues to assess risk; therefore, behavioural responses to predation risk can be 'complex, plastic and context dependent', even at an individual or population level, especially for ungulate prey species (Bonnot et al., 2018; Chivers et al., 2001; Prugh et al., 2019). The context-dependent response in our study corroborates research on nonmammalian species like zebrafish, *Danio rerio* (Filosa et al., 2016), but also research on mammal species like mice, *Mus musculus* (Procacci et al., 2020), rats, *Rattus norvegicus* (Schreiber et al., 1976) and dolphins, *Tursiops truncatus* (Lopes et al., 2016). Responses of naïve prey can be modulated by internal state and the context of the environment, such as variation in habitat characteristics or the presence of humans (Filosa et al., 2016; Greggor et al., 2020; Hettena et al., 2014). For example, variation in habitat riskiness can affect perceived risk by prey (Moll et al., 2017; Peers et al., 2018; Weterings et al., 2019). In particular, a change in visibility, protective cover or vegetation structure affects the possibility of detecting an approaching predator (Rearden et al., 2011; Tablado & Jenni, 2017), but can also hinder prey movement, group coordination or escape (Kuijper et al., 2015; Lagory, 1986; Weterings et al., 2016). In our system for example, canopy cover in mixed-coniferous forest was denser and ground cover vegetation was higher compared to broadleaved forest. This could explain the relatively low visit rate in mixed-coniferous than broadleaved forest. Differences in responses between habitats can also be the result of a mismatch between the way the auditory cues were broadcast and the distribution and intensity of sounds in the two forest classes as expected by prey species (Parsons et al., 2018; Peers et al., 2018). For example, in Poland, wild boar were thought to avoid coniferous forest because of predators (Fonseca, 2008). Wild boar could thus have experienced (and expected) a lower predation risk in broadleaved forest. This could explain the difference in behavioural response to a predator cue between forest classes as shown in our study. Additionally, we found a reduction in cervid visit rate on warmer days, and a reduction in wild boar visit rate on days with rainfall. The former could be the result of decreased movement rates on warmer days in spring, which require less energy for thermoregulation, while the latter could be related to reduced movement rates on rainy days (Rivrud et al., 2014). However, if ungulate prey responses depend on the environmental characteristics, earlier research into the response of naïve ungulates to predation risk should be carefully interpreted in the context of the study set-up and local setting.

We did not find any effects of playback of wolf sound on the group size of ungulates. Species' group sizes are the product of environmental and social conditions (Kasozi & Montgomery, 2020), whereas the interaction between prey group size and the characteristics of the habitat strongly affect the risk perceived by prey (Kuijper et al., 2015; Liley & Creel, 2008). Compared to open landscapes, ungulate species may disaggregate in forests to avoid predator detection (Creel & Winnie, 2005), as closed habitats such as forests can offer more protection against wolf predation such as increased concealment (Barja & Rosellini, 2008; Grovenburg et al., 2012). In contrast, large group sizes of prey can reduce the chance of a successful predator attack but come at a cost of increased detection by and encounter rates with predators (Kasozi & Montgomery, 2020). The role of group size in reducing predation risk may also be related to body size and morphology of the prey and avoiding predation risk may show a trade-off between various other behaviours, such as foraging, mating and space use (Dial et al., 2008; Lingle, 2001; Lingle & Pellis, 2002). For example, small ungulate species that are selective such as roe deer may have more success in escaping or hiding from predators in smaller groups, while larger bulk-feeders such as fallow deer and red deer are thought to benefit from aggregation in larger groups (Jones et al., 2009; Lingle, 2001; Putman, 2003). Furthermore, antipredator behaviour of prey is affected by predator choices (Liley & Creel, 2008). For example, wolves seem to prefer the larger red deer (240.9 kg) over the smaller roe deer (22.5 kg) and wild boar (84.5 kg) affecting each species differently (Jędrzejewski et al., 2000; Roder et al., 2020). In general, large animals have been hypothesized to be less vulnerable to predation risk than small ones (Sinclair et al., 2003; Thaker et al., 2011; but see ; Creel, 2018; Roder et al., 2020), because predation risk is higher when the relative size difference between prey and predator is larger. For example, red deer did not change group size in response to predation risk of Iberian wolves, possibly because of their relatively large size compared to wolves, in contrast to the smaller roe deer (Barja & Rosellini, 2008). Moreover, large animals have a relatively greater energy expenditure than small ones and therefore risk effects that involve movement are hypothesized to be more costly. Large animals 'should thus gain a relatively greater benefit from habituation' (Blumstein, 2016, p. 259). Hence, large ungulate species could potentially be less affected by cues that elicit fear from predator sound. Moreover, the contrasting antipredator strategies and ecology of roe deer, fallow deer and red deer possibly nullified the effect of playback on cervid group size. Nevertheless, we did find smaller group sizes of wild boar and cervids during the dark period, which might reflect a reduced risk perceived during low light intensities (Caro, 2005; Creel, 2011).

The ungulates in our experiment responded to sound cues, as their visit rate differed between the playbacks and the control treatment without sound. However, group size and most ungulate visit rates did not differ between wolf and sheep playback. This could mean that in this situation: (1) ungulates could not differentiate between the two sounds and did not perceive them as threatening, (2) ungulates could differentiate between the two sounds, but did not perceive the predator playback as threatening, or (3) ungulates perceived both sounds as threatening, regardless of whether they could differentiate between them. The first two possible explanations (i.e. dosage effect only) could suggest that our naïve cervids lost their ability to respond to sound cues of a locally extinct predator. In contrast, responses of naïve wild boar to predator playback differed from those to the sheep playback and the control treatment during the first 8 days of the experiment in broadleaved forest. The third possible explanation (i.e. dosage effect and antipredator response) could suggest that the response to sheep sound was not neutral. However, sound does not play a role in exploitative competition between herbivores. Nevertheless, in general, cervid and wild boar density in mixed-coniferous forest was very low, making our results more prone to type two errors.

Ungulates in human-dominated landscapes have shown to be better able to discriminate between threatening and nonthreatening sounds (Carrasco & Blumstein, 2012). Additionally, naïve ungulates in human-dominated landscapes have been shown to lose the ability to respond to predator cues (see e.g. Berger, 2007; Carthey & Blumstein, 2018; but see Dalerum & Belton, 2015), because of human displacement of top predators and habituation to cues that elicit predation risk (Hettena et al., 2014). The ability to respond to cues of extinct predators depends on when prey and predator became ecologically separated. The duration of this separation determines how prey antipredator behaviour adapted over time (i.e. relaxed selection, recoverable template or adaptation; Carthey & Blumstein, 2018). In the Veluwezoom, for example, naïve wild boar could still respond to wolf sound, even though the wolf became ecologically separated from wild boar in 1879. Furthermore, background noises from people or traffic in the human-dominated Veluwezoom could negatively affect the ability of prey to sense auditory cues of predators (Francis et al., 2009; Lynch et al., 2015), or stimulate over-responsiveness to cues that are perceived more intensely than expected (Peers et al., 2018). For example, cervid responses in mixed-coniferous forest differed between no sound and playback, but responses between playbacks did not markedly differ, which could indicate an over-responsiveness to sound cues.

'Habituation is a type of 'single-stimulus' learning that allows animals to avoid costly responses in situations where there is no benefit from responding to repeated stimulation' (sensu Blumstein, 2016, p. 256). Our results show that habituation occurred quickly (mean ±SD = 8.1 ± 10.1 days, range 0–21), and did not differ between ungulate species groups, forest class and sound cue administered (but note the differences in wild boar responses (i.e. slope) between cues and forest class; see Fig. 3e and f). However, as individuals, populations and species differ in their response to predation risk (Bonnot et al., 2018; Perry et al., 2020), habituation probably also varies between individuals, populations and species. In contrast to Blumstein (2016), we failed to find a nonlinear asymptotic decline in the frequency or magnitude in the ungulate response with the repeated playbacks. On the contrary, the response was nonlinear exponential in time (i.e. animals are likely to learn to rehabituate more quickly with prior experience), which could occur when the frequency of playbacks was too high, when the cue was not strong enough or when the cue was relatively benign (Blumstein, 2016), i.e. when the cue was not biologically realistic (Prugh et al., 2019; Weissburg et al., 2014).

Even though we have grouped cervid responses into one model, differences between cervid species are apparent; consequently, the model results of the cervids should be evaluated with caution. For example, grouping as an antipredator strategy is related to body size and morphology (Dial et al., 2008; Lingle & Pellis, 2002), as discussed earlier. Additionally, space use and visit rate depend on the degree to which habitats provide a combination of safety and food. Fallow deer and red deer, for example, can show extensive movements in large home ranges to forage or avoid local predation risk, while roe deer tend to defend food sources in relatively small territories (Apollonio et al., 1998; Putman, 2003). Finally, perceived predation risk is species specific, affecting space use of prey differently for different species. For example, red deer were preferred over roe deer and wild boar by wolves in the Western European Alps and in Poland, which affected their space use differently compared to other species (Jędrzejewski et al., 2000; Roder et al., 2020).

Overall, playback of wolf sound caused an initial reduction in the visit rate for wild boar, but not for cervids, whereas it did not reduce wild boar and cervid group size. In particular, responses of naïve wild boar to predation risk seem to be context dependent. All responses to sound cues wore off within a maximum of 21 days, probably because of habituation. Therefore, depending on the habitat characteristics and the species involved, stimulating responses of naïve prey using predation risk can only be a temporary management measure to repel ungulates in this forest system. It would be valuable to investigate the auditory perceptions of ungulates more thoroughly to increase the success of the use of predator sound to repel ungulates (Greggor et al., 2020). For example, which habitat characteristics trigger responses of naïve ungulates to predator sounds and what mechanisms are behind this? In addition, even though management measures are preferably single species oriented, it could be interesting to investigate multispecies measures in more depth.

Author Contributions

Conception and design: M.W., N.M., K.F., P.J. and H.K.; acquisition of data: M.W., N.M. and K.F.; analysis and interpretation of data: M.W., F.v.L. and H.K.; manuscript: M.W., N.M., K.F., F.v.L., P.J. and H.K. All authors read, reviewed and approved the final manuscript.

Conflict of Interest

The authors declare they have no conflict of interest.

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Supplementary Material

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Appendix

Table A1
Adult or subadult cervid and wild boar visit rate and group size per forest type

		Coniferous	Mixed	Broadleaved
Visit rate (camera/location/day)	Cervids (*N* = 1488)	0.11 ± 0.41 (368)	0.08 ± 0.31 (752)	0.26 ± 0.62 (368)
	Roe deer	0.03 ± 0.20	0.02 ± 0.14	0.07 ± 0.30
	Fallow deer	0.01 ± 0.07	0.02 ± 0.15	0.07 ± 0.34
	Red deer	0.08 ± 0.36	0.04 ± 0.22	0.12 ± 0.37
	Wild boar (*N* = 1488)	0.11 ± 0.37 (368)	0.17 ± 0.55 (752)	0.84 ± 1.32 (368)
Group size (/visit)	Cervids (*N* = 209)	1.10 ± 0.31 (39)	1.31 ± 0.77 (71)	1.60 ± 1.29 (99)
	Roe deer (*N* = 58)	1.00 ± 0.00 (11)	1.00 ± 0.00 (21)	1.04 ± 0.20 (26)
	Fallow deer (*N* = 42)	1.50 ± 0.71 (2)	1.18 ± 0.39 (17)	1.31 ± 1.91 (23)
	Red deer (*N* = 109)	1.12 ± 0.33 (26)	1.58 ± 1.03 (33)	1.74 ± 1.51 (50)
	Wild boar (*N* = 446)	1.17 ± 0.44 (42)	1.41 ± 0.75 (101)	1.44 ± 0.98 (303)

Means are shown ±SD with sample size in parentheses. The sample size for the visit rate is based on the number of cameras that were operational.

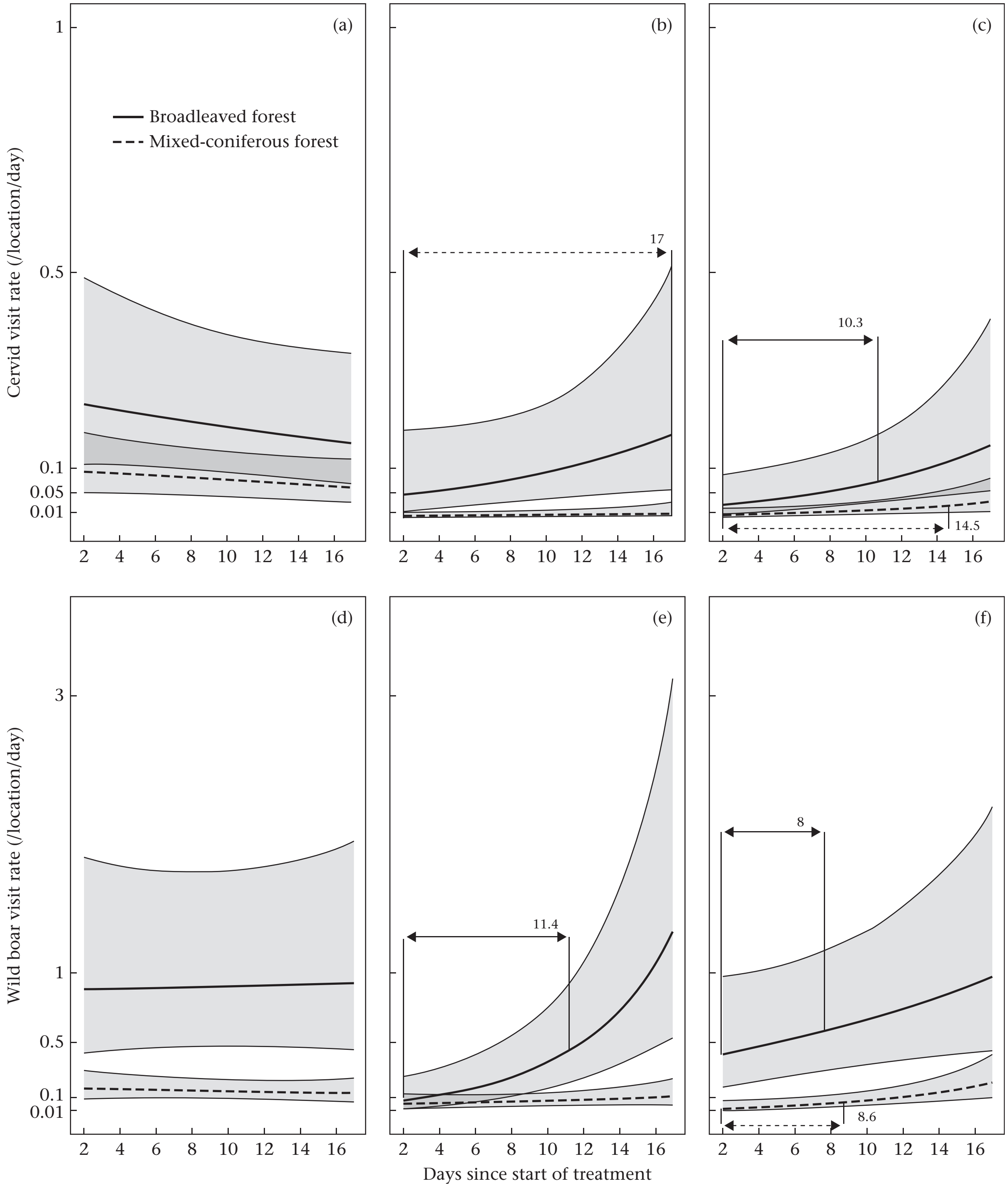

Figure A1. Visit rate (nonlog scale) over time for (a-c) deer and (d-f) wild boar in three different playback treatments in Veluwezoom National Park, the Netherlands. Lines and grey shading show GLMM fits with 95% confidence interval (a, d) without playback, (b, e) with playback of wolf sounds and (c, f) with playback of sheep sounds in broadleaved and mixed-coniferous forest. Arrows show the average time during the treatment period when the sound treatments were significantly different from the control (black) and the wolf playback (grey; Tukey's multiple comparison test: $P < 0.05$). Data for cervids are presented for period 3 (12–27 May) and an average temperature of 11.1 °C. Data for wild boar are presented for days without rainfall.