

Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear

V. Tolon, S. Dray, A. Loison, A. Zeileis, C. Fischer, and E. Baubet

Abstract: Predators generate a “landscape of fear” within which prey can minimize the risk of predation by selecting low-risk areas. Depending on the spatial structure of this “landscape”, i.e., whether it is coarse- or fine-grained, prey may respond to increased risk by shifting their home ranges or by fine-scale redistributions within these ranges, respectively. We studied how wild boar (*Sus scrofa* L., 1758) responded to temporal changes in risk in hunted areas (risky habitat) surrounding a nature reserve (refuge habitat). Animals with home ranges “in contact” with the reserve during the low-risk season were the only ones to shift toward the refuge when the risk increased. These shifts occurred at two temporal scales in response to the increased risk during the daytime and during the hunting season. Whereas animals not influenced by the reserve found food and shelter in forest during the hunting season, shifts to the refuge area were detrimental to the rather scarce forest areas in the reserve. This confirms that spatiotemporal changes in risk are major drivers of animal distribution when predation strongly limits their fitness. Their response is, however, scale-dependent and reflects at the individual level the perceived structure of their “landscape of fear”.

Résumé : Les prédateurs génèrent un « paysage de la peur » dans lequel les proies peuvent minimiser le risque de prédation en sélectionnant les zones de faible risque. Suivant la structure spatiale de ce « paysage », c.-à-d. à large ou fine échelle, les proies peuvent répondre à un risque accru respectivement par des déplacements de domaines vitaux ou des redistributions à fine échelle au sein des domaines vitaux. Nous avons étudié comment des sangliers (*Sus scrofa* L., 1758) répondent aux variations temporelles du risque dans des zones de chasse (habitat risqué) entourant une réserve naturelle (habitat refuge). Les animaux avec des domaines vitaux « en contact » avec la réserve pendant la saison de faible risque sont les seuls à se déplacer vers le refuge quand le risque augmente. Ces déplacements se produisent à deux échelles temporelles en réponse à l'augmentation du risque pendant le jour et en saison de chasse. Alors que les animaux hors de l'influence de la réserve trouvent nourriture et abris en forêt pendant la saison de chasse, les déplacements vers le refuge se font au détriment de l'utilisation des forêts plutôt rares dans la réserve. Ceci confirme que ce sont surtout les variations spatiotemporelles du risque qui déterminent la distribution des animaux quand la prédation limite fortement leur fitness. Leur réponse dépend néanmoins de l'échelle et reflète au niveau individuel la structure perçue de leur « paysage de la peur ».

Introduction

By definition, the act of predation leads to the death of the prey, but predator–prey interactions can also have nonlethal or indirect effects (Creel and Christianson 2008), because prey often try to avoid the risk of predation by

changing their behavior. For instance, animals can switch activity patterns (Lima and Bednekoff 1999), or modulate vigilance levels (Roberts 1996) or group size (Hamilton 1971) in response to increased predation risk, usually incurring energetic costs. The concept of the “ecology of fear” (Brown et al. 1999) concerns the behavioral responses of

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prey to stress and fear caused by predators, and their consequences for individual fitness and ecosystem functioning through trophic cascades (Ripple and Beschta 2004).

Predation risk is often structured in space and time at multiple scales. Attack success or accessibility to predators can vary in different habitats (Cowlshaw 1997), but predators' activity can also be intrinsically structured in space (e.g., Fortin et al. 2005) and in time (Sih et al. 2000). For prey that perceive these heterogeneities, these spatiotemporal variations of predation risk generate a structured and dynamic "landscape of fear" (Laundré et al. 2001), within which they can minimize risk by relocating to lower risk or safe areas. Changes in the use of space is one of the most widespread behavioral responses to spatiotemporal differences in predation risk over a given resource distribution area (Brown 1988; Abrahams and Dill 1989; van der Merwe and Brown 2008). According to Rettie and Messier (2000), the scale at which individuals respond to predation risk depends on the predominant factor limiting individual fitness (e.g., resources or predation). In a context of high predation pressure, the way animals adapt their use of space may depend on spatiotemporal variations of risk, rather than on other environmental factors, such as food abundance or thermal conditions.

However, the risk-dependent distribution of animals can also be determined by their perception or knowledge of local risk levels and (or) by their ability to move away from high-risk areas. Many adaptive distribution theories assume that individuals are omniscient and can move freely (e.g., Fretwell and Lucas 1969); however, this is rarely the case in the natural environment (Kennedy and Gray 1993; Shochat et al. 2002). For instance, the use of refuges by prey can depend on several environmental and behavioral factors, such as competition for refuges (Berryman and Hawkins 2006), their accessibility and knowing where they are located (Clarke et al. 1993), or social constraints (Banks et al. 2007). Individuals may therefore only react if differences in risk levels are perceived as spatially structured within the space available to them. Depending on the local spatial structure of risk, i.e., whether it is coarse- or fine-grained, animals may respond either by shifting their home ranges or by fine-scale redistribution within the home range, respectively.

For a broad range of animal species, a considerable proportion of their mortality is anthropogenic (e.g., road accidents; Bruinderink and Hazebroek 1996), and especially by harvesting populations (e.g., hunting; Toïgo et al. 2008). Most harvested species face marked temporal variations in risk owing to restricted seasons, specific days, or times of day when hunting is permitted (e.g., Toïgo et al. 2008). Moreover, the existence in the vicinity of protected areas where human access is restricted induces marked spatial differences in risk (Madsen 1998). This means that hunting can shape the landscape of fear for the harvested species, as the level of risk differs considerably in terms of space (the existence of protected areas) and of time (periods when hunting is permitted). If individual fitness is mainly determined by the risk of being hunted, animals will strongly seek protected areas during pulses of risk. In the absence of risk (a "flat" landscape of fear), the distribution of the animals

will be driven mainly by other factors (often the availability of resources).

The wild boar (*Sus scrofa* L., 1758) is a game species that often faces extreme hunting pressures (e.g., a 40% of chance of being harvested annually, and up to 70% for adult males; Toïgo et al. 2008). Consequently, its use of space changes markedly when the risk of being predated (through hunting) starts (Boitani et al. 1994; Sodeikat and Pohlmeier 2003; Keuling et al. 2008b). In the study reported here, we investigated how wild boar responded to temporal changes in risk in hunted areas (risky habitat) surrounding a protected nature reserve (refuge habitat). The wild boar is known to shift its home range toward forest areas providing food and shelter during the hunting season, (e.g., Boitani et al. 1994), but we expected to find that home-range shifts near the reserve would also be driven by the local protection status. Individuals for whom the presence of a reserve creates widely contrasting risk levels within their locally available environment could be expected to display the greatest shifts in their home ranges. We therefore hypothesized that there could be a threshold distance for this response, depending on how far from the reserve the wild boar range during the closed season (prediction 1). Controlling for differences in forest use, we expected diurnal pulses of risk to drive the animals back into the protected area every morning, creating a circadian pattern of space use (prediction 2). We also expected the marked increase in risk during the hunting season to draw animals deeper into the reserve than during the closed season (prediction 3). However, these seasonal movements might not appear at night (prediction 4) because the nocturnal risk does not reflect this seasonal variation.

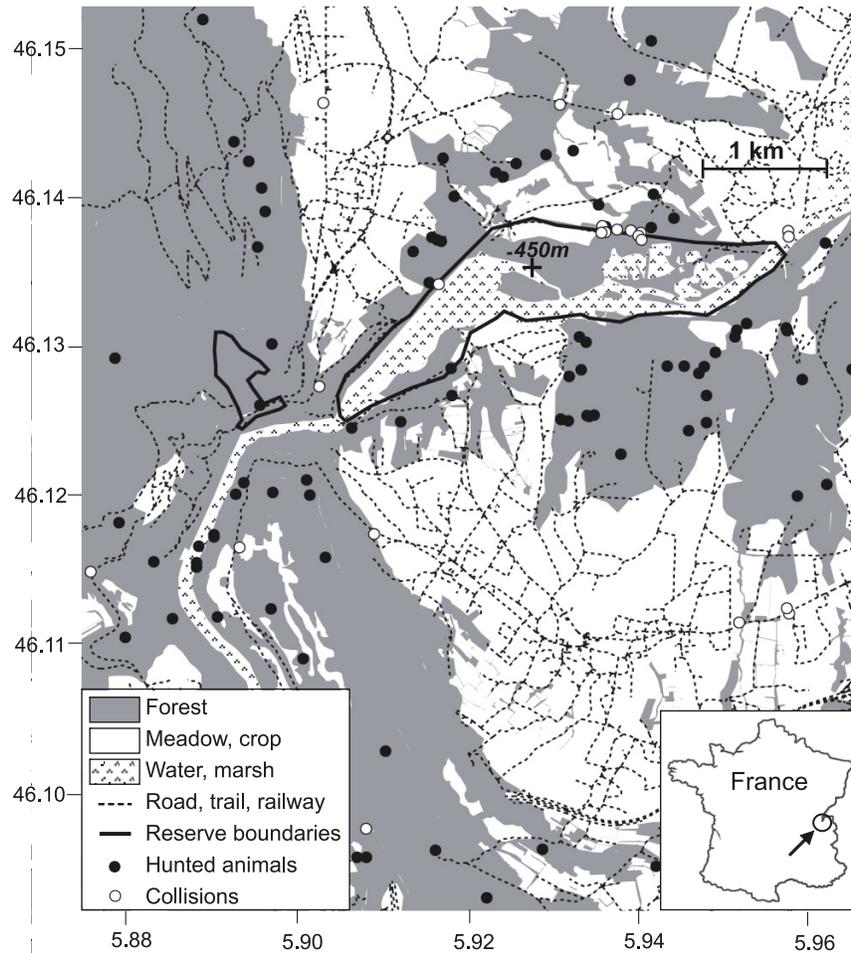
Materials and methods

Study area

The Geneva basin is located on the French–Swiss border (46.135°N, 5.930°E; WGS84), and is surrounded by ranges of mountains and Lake Geneva. The reserve was set up in 1962 and occupies 318 ha (Fig. 1). Habitat types in the reserve correspond to hygrophilous forest (alder (genus *Alnus* P. Mill.), willow (genus *Salix* L.); 44%), beds of reeds (genus *Phragmites* Adans.; 30%), surface water (16%), oak (genus *Quercus* L.) or beech (genus *Fagus* L.) woods (6%), and crops (maize, cereals; 4%). The area immediately around the reserve (the surrounding 4 km, equivalent to 9000 ha; Fig. 1) is composed of meadows (29%), oak and beech woods (27%), other types of forest (25%), and crops (12%; maize, other cereals). Supplemental feeding with maize is provided outside the reserve in the forest plots (around 200–300 kg·year⁻¹·km⁻² forest surface from March to August). Evidence of high acorn production during the autumn and winter were reported in the region (60 km from the reserve) for 2004 and 2006 (836 and 386 kg·ha⁻¹ forest surface, respectively, compared with 2–64 kg·ha⁻¹ forest area for other years; National Forestry Office 2008).

The main cause of wild boar mortality is anthropogenic (hunting or culling: 81.6%; road accidents: 15.3%; other: 3.1%; $n = 196$ dead animals recovered from 2002 to 2007). The hunting season is open in the French part of the Geneva basin between 8 and 14 September, and closed at the beginning of the following year between 25 and 31 January.

Fig. 1. The nature reserve in the Geneva basin and its surroundings. Numbers bordering the map show the latitude ($^{\circ}$ N) and longitude ($^{\circ}$ E). The value -450 m shows the point with the minimum relative position from the reserve.



Hunting takes place from 0800 to 1700 or 1900, with no hunting at night. Hunting territories range from 3 to 20 km². During the open hunting season, hunters perform up to three drives per week (with dogs, beater, and shooters) in the forest of each hunting territory, except in areas with special protection status, such as the focal nature reserve (Fig. 1). Road and rail traffic is mostly diurnal, and is especially dense around 0700–1000 and 1700–2000 owing to cross-border workers commuting to and from Geneva.

Trapping and tracking

Wild boar were trapped, weighed, and ear-tagged from 2002 to 2007 in the Geneva basin. Animals weighing >30 kg were fitted with VHF radio-transmitter collars (females: 8 juveniles, 15 yearlings, 6 adults; males: 3 juveniles, 5 yearlings, 3 adults). They were tracked by triangulation from tagging to the animal's death or collar loss (survey duration = 222 ± 169 days; mean \pm SD). While the animals were resting, their locations were determined once a day between 0800 and 1800 (Boitani et al. 1994; Keuling et al. 2008b). Animals were also tracked twice a month at night (with an interval of 30 min between successive locations) from 2200 to 0400 during their main activity period (e.g., Keuling et al. 2008b). These time slots defined the “day”

and “night” periods. On the seasonal scale, we also defined two seasons of risk: the “closed” hunting season (7 months) and the “open” hunting season (5 months), based on the official dates of the hunting season (see above).

In the analyses that follow, we use the “individual-year” (i.e., a given individual observed during a given year) as the statistical unit, because 21 of the 29 females and 10 of the 11 males were only tracked for 1 year.

Threshold effect

In the following analyses, diurnal and nocturnal locations are considered separately. We aimed to estimate the distance from the reserve below which home-range shifts of animals living in peripheral areas were influenced by the existence of the reserve. Seasonal activity centers were defined as the medians of the x and y coordinates of the individual's locations for each season (closed or open). Relative positions from the reserve (RPR) were calculated as the distances in metres between the seasonal activity centers and the nearest boundary of the reserve. If a center was located within the reserve, then the RPR was negative (Fig. 1).

The reserve's attractiveness was investigated using a linear model using the RPR during the closed hunting season (RPR_{closed}) as the explanatory variable and the RPR during

open hunting season (RPR_{open}) as the response variable. The intercept described the tendency of movement relative to the reserve among individuals, whereas the slope measured the influence of the initial position of the individual on these movements. If no movement occurred relative to the reserve, the estimated slope is equal to 1 and intercept is equal to 0 (i.e., $RPR_{open} = RPR_{closed}$). Other combinations of values (for slope and intercept) could correspond to attraction effects (i.e., $RPR_{open} < RPR_{closed}$) or repulsion effects (i.e., $RPR_{open} > RPR_{closed}$). We expected the reserve to attract animals located nearby, but not those located farther away from it (i.e., to identify a buffer zone around the reserve extending up to a specific threshold distance). The relationship between RPR_{closed} and RPR_{open} would then change beyond this threshold parameter. Technically, this implies that separate linear regression models of RPR_{open} on RPR_{closed} were fitted for animals below and above the threshold in RPR_{closed} (for an illustration see Figs. 2a–2d). We estimated five parameters simultaneously (the threshold value, as well as the two intercepts and two slopes of the linear models estimated below and above the threshold, respectively) using weighted least squares. To find out whether the regression relationships below and above the threshold were significantly different, we used a supLM test (Andrews 1993; Zeileis 2005), which takes the supremum of LM statistics over all conceivable thresholds. Threshold estimation and testing were performed using R software (R Development Core Team 2008) using the “strucchange” package (Zeileis et al. 2003). As individuals were observed at different numbers of locations during and outside the hunting seasons, statistical procedures were adapted to allow for this when performing weighted estimations and inferences (weights = geometric means of the number of locations in the two seasons).

Space use

We first determined annual home-range size (with all locations) by measuring the 95% minimum convex polygon area of each individual. Then we computed for each individual the distance of all locations with their barycenter and considered the 95% quantile of these distances as the measure of the home-range radius. Finally, we computed daily travel distances by adding distance between successive relocations during a movement phase (at night in our case).

Then for all individuals, the data set was divided into four subsets: diurnal home range – closed season, nocturnal home range – closed season, diurnal home range – open season, and nocturnal home range – open season. Only individuals that had been located at least 20 times during periods of ≥ 20 days and tracked on at least 3 different nights were included (28 female-years and 5 male-years were surveyed from 2004 to 2006).

For each subset, the kernel utilization distribution (UD; Worton 1989) of each animal was estimated using the R package “adehabitat” (Calenge 2006). We chose a single smoothing parameter value (h) for all UD estimates following the recommendations of Pellerin et al. (2008) so that any change in space-use parameters (see below) could be clearly interpreted as a change in animal behavior and not as a potential change in the smoothing parameters. An h value of 150 was chosen after graphical explorations.

Several space-use parameters were calculated for all indi-

viduals. Home-ranges sizes (HR: area of the 95% contour) were calculated in hectares. Mean interindividual overlaps (percentage) were estimated by averaging for each individual, as well as “volumes of intersections” (the VI in Fieberg and Kochanny 2005) with all the other individuals tracked during the same year. Forest overlaps (percentage of the UD in forest areas) were measured over seasons and day periods. Finally, the reserve utilization, which was estimated only for animals that lived close to the protected area, was the percentage of the UD included in the protected perimeter (similar to the PHR in Fieberg and Kochanny 2005).

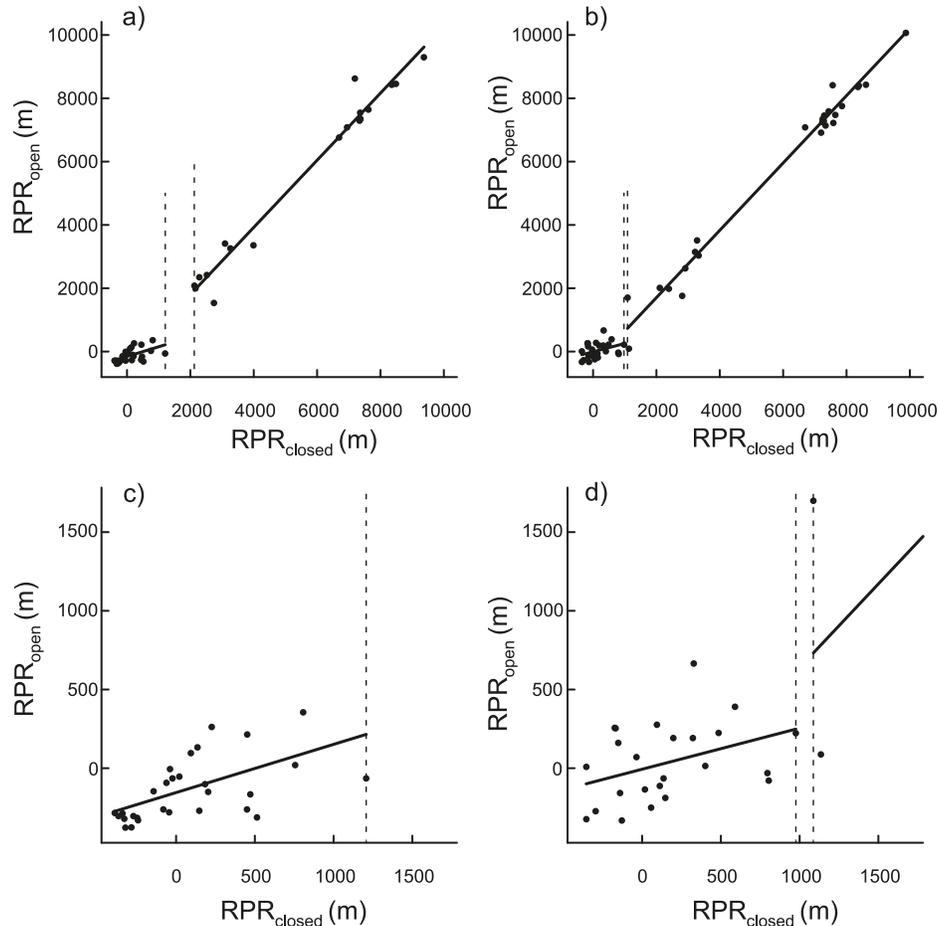
Variations of these parameters were analyzed using linear mixed-effect models with the R “nlme” package (Pinheiro and Bates 2000), setting “individuals-year” as random ($n = 132$). Three categorical variables with two states were considered as fixed effects: season (closed or open), period (day or night), and group (reserve or other). The group variable determines whether animals lived below the RPR_{closed} threshold estimated previously (reserve) or lived beyond this threshold (other). The group “other” is used as a comparative control to verify that space-use patterns are specific to the reserve surrounding or are common to the entire study site. Analysis of the reserve-utilization variation was restricted to the individuals with the status “reserve” for the group variable.

Results

Threshold effect

Significant structural changes were identified in the linear regression of RPR_{open} on RPR_{closed} (day: $n = 52$, supLM = 16.55, $P = 0.0081$; night: $n = 50$, supLM = 14.33, $P = 0.016$). Transition from first to second model occurred within an interval of $RPR_{open} = 1207$ – 2123 m for diurnal data, and an interval of $RPR_{closed} = 975$ – 1087 m for nocturnal data (these intervals correspond to the maximum and minimum observed values of RPR_{closed} for the first and second model, respectively; see vertical broken lines in Figs. 2a–2d). Models below the threshold (on the left side of the graphs; Figs. 2a, 2b) had slopes < 1 and intercepts < 0 for daytime and around 0 for nighttime (estimate (minimum and maximum 95% confidence intervals); day: intercept = -154 (-273 , -35); slope = 0.31 (0.02 , 0.59); night: intercept = -7 (-164 , 151), slope = 0.26 (-0.16 , 0.68)). These models showed that animals moved closer to the reserve during the open season, especially individuals living just outside the reserve (up to 1.2 km from the edge) during the closed season (intercept < 0 , slope < 1 ; Figs. 2c, 2d). Models beyond the threshold (on the right side of the graphs; Figs. 2a, 2b) had slopes slightly > 1 for both the daytime (slope = 1.06 (1.001 , 1.12)), and the nighttime (slope = 1.06 (1.02 , 1.11)), and a slightly negative intercept for the nighttime (intercept = -423 (-791 , -56)), whereas as expected the intercept was not different from 0 for the daytime (intercept = -318 (-702 , 65)). These models revealed a virtual absence of any attractive effect on diurnal space use (intercept = 0, slope = 1; Fig. 2a), whereas a slight attractive effect appeared for nocturnal space use for some of the animals living around 2–4 km from the edge of the reserve (intercept < 0 , slope > 1 ; Fig. 2b).

Fig. 2. The threshold effect on the attraction of activity centers of wild boar (*Sus scrofa*) by the protected areas in response to hunting, estimated by the segmented linear regressions of the relative position from the reserve during the open hunting season (RPR_{open} ; y axis) versus the closed hunting season (RPR_{closed} ; x axis): (a) full plot with the diurnal data set; (b) full plot with the nocturnal data set; (c) close up of the zone of influence using the diurnal data set; and (d) close up of the zone of influence using the nocturnal data set. Solid circles represent individual-year; solid lines represent segmented linear models; and broken vertical lines represent transition zones delimited by maximum and minimum observed values of RPR_{closed} for the first and second model, respectively.



Space use

Annual (mean \pm SD) home ranges were equal to 7.6 ± 2.9 km² for females and 10.1 ± 2.5 km² for males. Home-range radii (mean \pm SD) ranged around 1.8 ± 0.3 and 2.3 ± 0.4 km for females and males, respectively, whereas daily travel distances were equal to 4.9 ± 0.3 km·day⁻¹ for females and 6.0 ± 0.5 km·day⁻¹ for males.

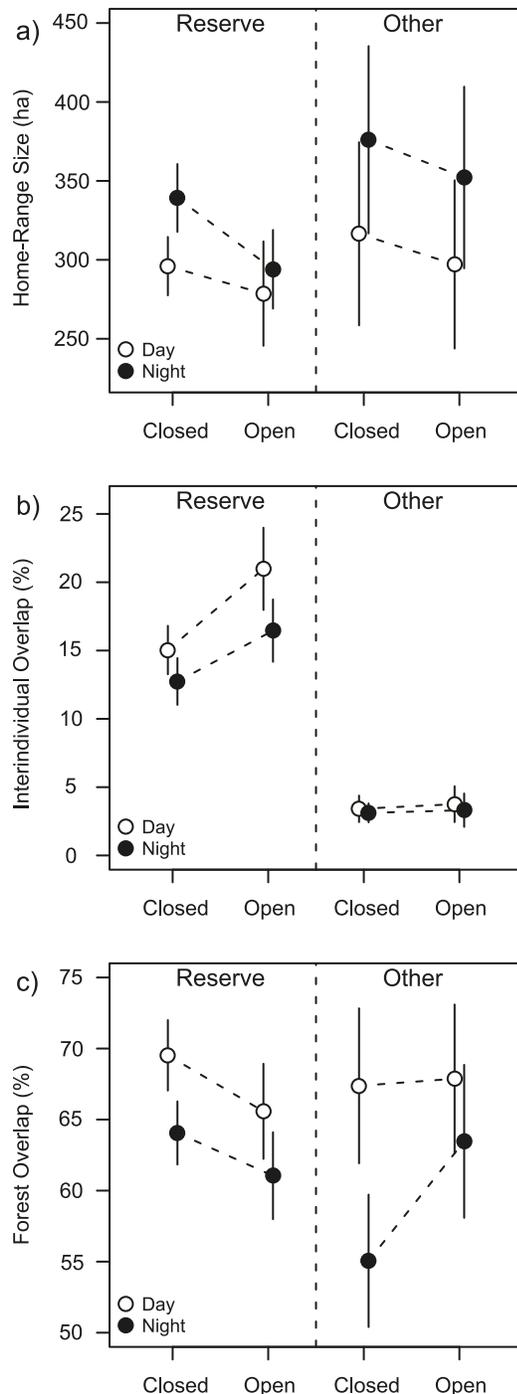
Period had a slight additive effect on changes in home-range size, whereas season displayed only a nonsignificant tendency (intercept: $F_{[1,93]} = 188.04$, $P < 0.0001$; season: $F_{[1,93]} = 2.80$, $P = 0.098$; period: $F_{[1,93]} = 6.02$, $P = 0.016$). The effect of group (group: $F_{[1,31]} = 0.51$, $P = 0.48$), as well as interactive effects between season, period, and group, were not significant (season \times period: $F_{[1,93]} = 0.32$, $P = 0.57$; season \times group: $F_{[1,93]} = 0.08$, $P = 0.78$; period \times group: $F_{[1,93]} = 0.69$, $P = 0.41$; season \times period \times group: $F_{[1,93]} = 0.12$, $P = 0.73$). Home ranges were smaller during the daytime than at night, and tended to be smaller during the open season than the closed season (Fig. 3a).

Season, period, and group had strong significant additive effects on differences in mean interindividual overlap (intercept: $F_{[1,93]} = 78.75$, $P < 0.0001$; season: $F_{[1,93]} = 14.70$, $P =$

0.0002 ; period: $F_{[1,93]} = 7.81$, $P = 0.0065$; group: $F_{[1,31]} = 24.87$, $P < 0.0001$). Interactions of season and period with group were significant or virtually significant (season \times group: $F_{[1,93]} = 7.93$, $P = 0.0059$; period \times group: $F_{[1,93]} = 3.53$, $P = 0.063$). No other interaction was significant (season \times period: $F_{[1,93]} = 0.79$, $P = 0.38$; season \times period \times group: $F_{[1,93]} = 0.41$, $P = 0.52$). Interindividual overlaps of animals living close to the protected area were higher during the day than at night, and higher during the open season than during the closed season, whereas it did not vary and remained lower for animals living far from the reserve (Fig. 3b).

Period had a strong additive effect on differences in forest overlaps, whereas the additive effects of season and group were not significant (intercept: $F_{[1,93]} = 742.15$, $P < 0.0001$; season: $F_{[1,93]} = 0.064$, $P = 0.80$; period: $F_{[1,93]} = 20.55$, $P < 0.0001$; group: $F_{[1,31]} = 0.11$, $P = 0.74$). The interaction between season and group was significant (season \times group: $F_{[1,93]} = 7.71$, $P = 0.0066$), unlike other interactions (season \times period: $F_{[1,93]} = 1.74$, $P = 0.19$; period \times group: $F_{[1,93]} = 1.39$, $P = 0.24$; season \times period:group: $F_{[1,93]} = 1.50$, $P = 0.22$). Forest overlaps were generally smaller at

Fig. 3. Variations in several space-use parameters of wild boar (*Sus scrofa*) depending on season (closed or open), period (day or night), and group (reserve or other). The group determines whether animals lived under the influence of the reserve (reserve) or out of this influence (other) according to the first analysis (see Materials and methods, as well as Figs. 2a–2d). Parameters (mean \pm SE) were estimated on 132 kernel utilization distributions (UD) estimated for 33 individual-years. (a) Home-range size (ha) is the area of 95% contours of UD; (b) interindividual overlap is the mean volume of intersection (%) with UD of other individuals alive during the corresponding year; and (c) forest overlap is the percentage of UD included in forest areas.



night than during the day, and displayed contrasting seasonal variations depending on group — they decreased during the open season for animals living near the reserve, whereas they increased for individuals living farther from the protected area (Fig. 3c).

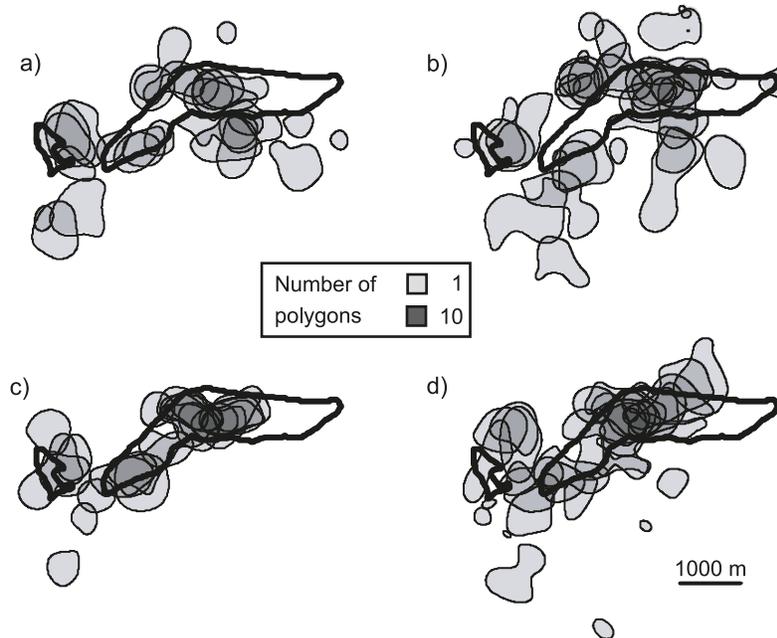
Finally, after restricting the analysis to animals influenced by the protected area, we observed strongly significant additive effects of season and day period on reserve-utilization variation ($N = 72$; intercept: $F_{[1,57]} = 57.96$, $P < 0.0001$; season: $F_{[1,57]} = 12.65$, $P = 0.0008$; period: $F_{[1,57]} = 16.31$, $P = 0.0002$). The interactive effect of season and period was not significant (season \times period: $F_{[1,57]} = 1.37$, $P = 0.24$). Reserve utilization was lower at night than in the daytime, and more pronounced during the open season than the closed season (Figs. 4a–4d).

Discussion

Our results support the hypothesis that there is a threshold distance effect beyond which animals do not respond by shifting their home ranges toward the reserve (prediction 1). Regarding diurnal space-use patterns (during the highest risk conditions), animals living more than 2.1 km beyond the edge of the reserve during the closed season were not attracted into the reserve during the open season (Fig. 2a). Interestingly, this threshold corresponds to the mean radius of the home ranges of wild boar (see Results). This suggests that animals with a home range that was “in contact” with the reserve during the closed season were the only ones to enter the refuge during the open season. Daily trajectories higher than home-range radii have been shown to be quite common for wild boar of our study site (see Results; similar values were founded in Janeau et al. 1995) and annual home-range sizes remained quite small relative to daily movement capacities (see Results; for males see also Boitani et al. 1994; Massei et al. 1997; for an exhaustive review on females see Keuling et al. 2008a). This implies that moving over distances greater than the radius of the home range to seek refuge in the protected area might not be a very limiting factor (in terms of energy and time). The lack of response may then result from limitations of the range over which the individual perceives the risk, which is probably restricted for a given individual by its home-range boundaries. Animals can benefit from having a good knowledge of refuge locations (Clarke et al. 1993), as this enables them to hide quickly, and so reduce the predation risk (Cowlshaw 1997). Individuals whose home ranges are at least partially within the reserve may therefore be the only ones to perceive its safety, and respond to increases in predation risk by shifting their home ranges toward this refuge.

Near the edge of the reserve, the wild boar responded to pulses of risk by shifting their home ranges into the protected area. This occurred as expected on a daily scale (prediction 2) in response to increased risk during the daytime (Figs. 4a and 4c vs. Figs. 4b and 4d). During the closed season, road and railway traffic may in fact have induced a greater diurnal risk outside the reserve (Fig. 1), but wild boar could also perceive any human activity in general (e.g., forestry, tourism) as a predation risk (Frid and Dill 2002). These daily shifts coincided with the greater use of forests during the daytime than at night that we observed

Fig. 4. Seasonal and daily impact of the presence of the reserve on the space use by wild boar (*Sus scrofa*): (a) day – closed hunting season, (b) night – closed hunting season, (c) day – open hunting season and, (d) night – open hunting season. Thick black contours represent the perimeter of the nature reserves, whereas gray polygons represent the core areas (50% kernel) of 20 individual-years in 2004, 2005, and 2006. Gray scale corresponds to the number of polygons overlapping a same area. Note that some overlaps are not real and come from animals observed during a different year. The same individual-years are shown on all plots.



generally throughout the study site. Wild boar commonly use shelters while resting (Boitani et al. 1994), but in our case habitat protection status appeared to be an additional factor when selecting resting sites. A similar pattern also occurred on a seasonal scale in response to the marked increase of risk during the open season, which drove animals farther into the protected areas than during the closed season (prediction 3; Figs. 4a and 4b vs. Figs. 4c and 4d). These seasonal shifts reduced forest use during the open season (Fig. 3c). Moreover, even though seasonal variations in nocturnal risk were expected to be negligible, we actually found that the nocturnal use of space around the reserve was affected by hunting as much as diurnal space use (prediction 4 not supported; Figs. 4b, 4d). The effect of diurnal risk constraints was extended to nocturnal space use, probably because of the interdependency between nocturnal and diurnal locations (owing to the need for refuge proximity while foraging; Wilson 2004). This led to an increased nocturnal use of the protected area and a decreased use of forest areas during open seasons. Forests also provide abundant food (Schley and Roper 2003; Bieber and Ruf 2005) and shelter (Boitani et al. 1994) during autumn and winter, and so were preferentially used during the open season by animals outside the sphere of influence of the reserve (Fig. 3c). These findings confirm the predominance of the landscape of fear (shaped by the existence of protected areas and hunting activities) to explain space-use patterns of wild boar. In wetlands wild boar were shown to switch to eating bulbs and rhizomes of semiaquatic plants to satisfy their food requirements during autumn and winter (Giménez-Anaya et al. 2008). Moreover, the increased interindividual overlaps during the hunting season (Figs. 3b and 4b vs. 4d) could in-

crease food competition within the refuge. This implies that the delayed concentration effect on nocturnal space use could have potential consequences for the diet and food intake of wild boar.

Daily and seasonal variations of home-range sizes (smaller during the daytime and during the hunting season) were, however, common to the entire study site (Fig. 3a). The nocturnal activity of wild boar (Keuling et al. 2008b) and heterogeneities of the sampling protocol (unequal season lengths) may explain these variations, as well as differences in spatial and temporal risk.

Our study shows that restricted harvesting periods, combined with the presence of protected areas in the vicinity, create a structured and dynamic landscape of fear for the harvested species. The close parallel between the use of the reserve and pulses of risk occurring at various different temporal scales confirms that spatiotemporal variations of risk are major drivers of animal distribution when predation is the main factor limiting their fitness (Rettie and Messier 2000). Animals outside the influence of the reserve seemed to respond to risk variations on a finer scale by increasing their use of forest areas within their home range (third level of habitat selection; Johnson 1980). This suggests that the response of prey, in terms of space use, to spatiotemporal changes in risk is scale-dependent and varies with the local structure of the landscape of fear. Protected areas, such as hunting or nature reserves, can then be used as refuge by game species and can become a key environmental feature driving their distribution (Madsen 1998). The nature reserve studied partially dissociates safety and food abundance on the large scale (Fig. 1). Individuals consequently shifted their home ranges between these two resources until the dis-

tance between the safe refuge and the rich habitat becomes limiting. These patterns could reveal a landscape complementation process (see an example on wild pig in Choquenot and Ruscoe 2003) that result in an increase in the population growth rate around the reserve. Common or invasive species (species other than those targeted for conservation) can then benefit from the protection status of a reserve. The wild boar is considered to be an engineer species that can strongly modify species richness by its feeding, rooting, stalling, or wallowing activities in protected ecosystems (see a short review by Wright and Jones 2004). Our findings highlight how harvesting activities can have a major impact on natural ecosystems, even those protected from human activities, via the mobility of refugee animals (Lenihan et al. 2001; Ripple and Beschta 2004). We encourage future research into multiscale habitat selection strategies and their consequences for the individual survival probability of game or harvested species. The high spatiotemporal variations of the human-induced predation risk can result in highly contrasting environmental conditions and can help us to understand how animals respond within their landscape of fear.

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