

# Predator–prey spatial game as a tool to understand the effects of protected areas on harvester–wildlife interactions

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**Abstract.** No-take reserves are sometimes implemented for sustainable population harvesting because they offer opportunities for animals to spatially avoid harvesters, whereas harvesters can benefit in return from the reserve spillover. Here, we used the framework of predator–prey spatial games to understand how protected areas shape spatial interactions between harvesters and target species and determine animal mortality. In these spatial games, the “predator” searches for “prey” and matches their habitat use, unless it meets spatial constraints offering the opportunity for prey to avoid the mortality source. However, such prey refuges could attract predators in the surroundings, which questions the potential benefits for prey. We located, in the Geneva Basin (France), hunting dogs and wild boar *Sus scrofa* L. during hunting seasons with global positioning systems and very-high-frequency collars. We quantified how the proximity of the reserve shaped the matching between both habitat uses using multivariate analyses and linked these patterns to animals' mortality with a Cox regression analysis. Results showed that habitat uses by both protagonists disassociated only when hunters were spatially constrained by the reserve. In response, hunters increased hunting efforts near the reserve boundary, which induced a higher risk exposure for animals settled over the reserve. The mortality of adult wild boar decreased near the reserve as the mismatch between both habitat uses increased. However the opposite pattern was determined for younger individuals that suffered from the high level of hunting close to the reserve. The predator–prey analogy was an accurate prediction of how the protected area modified spatial relationships between harvesters and target species. Prey-searching strategies adopted by hunters around reserves strongly impacted animal mortality and the efficiency of the protected area for this harvested species. Increasing reserve sizes and/or implementing buffer areas with harvesting limitations can dampen this edge effect and helps harvesters to benefit durably from source populations of reserves. Predator–prey spatial games therefore provide a powerful theoretical background for understanding wildlife–harvester spatial interactions and developing substantial application for sustainable harvesting.

**Key words:** harvesting; hunting; match mismatch; mortality; predator–prey; refuge; reserve; spatial game; survival; *Sus scrofa*; wild boar.

## INTRODUCTION

Protected areas are often a major key for the success of wildlife conservation and management politics (Diamond 1975, Simberloff and Abele 1982). In harvested systems, reserves have been advocated for several decades as a way to limit overharvest and increase yield (Gerber et al. 2003, Neubert 2003), but behavioral mechanisms underlying these “reserve ef-

fects” remain poorly studied. Understanding how protected areas influence the behavior of the target species and harvesters and modify their encounter probability is critical, because any catch involves both protagonists (Rudstam et al. 1984). Target species have been shown to escape from harvesting similarly to natural predators by joining refuges (e.g., Fox and Madsen 1997, Madsen 1998, Tolon et al. 2009) and harvesters to use habitats similarly to natural predators by maximizing yield over patches of prey (Bertrand et al. 2007, Kellner et al. 2007, Lande et al. 2009). Therefore, the analogy of natural predator–prey interactions could provide a powerful theoretical background to understand and predict how protected areas impact wildlife–harvester interactions and ultimately animal mortality.

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Within this framework, the joint investigation of prey and predator (harvester) behavior is of prime importance (Lima 2002). Indeed, habitat use by both prey and predator is highly interactive because prey typically avoid predators and predators hunt prey (Fauchald et al. 2000, Mitchell and Lima 2002, Sih 2005). The possible outcomes of this two-way spatial game are positive (match), negative (mismatch), or unstable associations (Fauchald 2009) with contrasting consequences on prey survival. These outcomes are determined by the respective spatial constraints for both protagonists (Rose and Leggett 1990, Sih 2005, Fauchald 2009). When predators move freely in the environment, they should match habitat use of prey that could not outdistance the mortality source (Rose and Leggett 1990, Fauchald 2009). In contrast, stable mismatches could occur when prey can use refuge habitats that have no or limited access by predators (e.g., thermal refuges for capelin, *Mallotus villosus* [Rose and Leggett 1990], trees of cliffs for baboons, *Papio cynocephalus ursinus* [Cowlshaw 1997], solid ground for sea otters, *Enhydra lutris* [Estes et al. 1998], steep slopes or high elevation for ungulates [Caro 2005]), resulting in a lower prey mortality. However, high densities of prey in refuges could strongly attract predators in their surroundings and lead to positive associations patterns (matching) at a larger scale (Rose and Leggett 1990, Fauchald et al. 2000). Therefore, spatial relationships between both protagonists are highly scale dependent, as mismatches created by refuges at a fine scale may turn into matches at a larger scale due to predator searching strategy (Rose and Leggett 1990, Fauchald et al. 2000).

In this paper, we propose to extend these spatial game theories that were originally conceptualized for natural predator–prey systems to harvester–wildlife interactions. In harvested systems, protected areas play the role of refuges by introducing artificial constraints on habitat use by harvesters. Therefore, the availability of protected areas should induce mismatching patterns between harvesters and their target species. As a consequence, mortality rates of animals should decrease in response to a lower encounter probability with harvesters (e.g., Revilla et al. 2001, Duriez et al. 2005). However, the presence of such refuges was demonstrated to attract harvesters in a similar mechanism as natural predator–prey systems (e.g., the “fishing-the-line” strategy around marine reserves; Gell and Roberts 2003, Roberts et al. 2005, Kellner et al. 2007). If the reserve size is small compared to home ranges of animals, individuals may face a very high harvesting risk that could counterbalance the beneficial effect of protected areas on mortality.

This predator–prey analogy was applied to a terrestrial hunted system by investigating how the proximity of a protected area determines the relationship (match or mismatch) between habitat use of hunters and wild boars (*Sus scrofa* L.; see Plate 1) and how these patterns ultimately influence animal mortality. In our system,

only part of the wild boar population used the protected area in response to hunting disturbance (Tolon et al. 2009), and hunters were expected to intensify efforts in the vicinity of this reserve. Therefore, there is a possible trade-off associated with using the reserve that may provide the best protection at a fine scale (no hunting within the reserve), but the highest risk at a large scale (high hunting activities in the vicinity of the reserve). In this context, there is uncertainty if strategies to minimize mortality risks should involve being far from the reserve and facing low, unavoidable hunting activities (i.e., scarce, but free, “predators”) or close to the reserve and coping with a higher, avoidable risk source (i.e., abundant, but constrained, “predators”). We studied space use of radio-marked wild boars and of global-positioning-system-collared hunting dogs (*Canis lupus familiaris*) as a measure of the hunting effort in space (e.g., Broseth and Pedersen 2000, Stedman et al. 2004, Lande et al. 2009). We first explored whether both wild boar and dogs differed in habitat selection tactics depending on the proximity of a protected area (the “predator” constraint). At the vicinity of the reserve, wild boar home ranges should be increasingly exposed to hunting activities due to concentration of hunters around the protected perimeter. In response, wild boar and dogs’ habitat uses should disassociate when hunters meet the spatial constraint close to the reserve. Second, we investigated how this variation in habitat selection tactics influenced wild boar mortality. Because the match/mismatch within home range should better reflect the encounter probability between dogs and boars than the overall hunting activity, we expected mortality to decrease with increasing mismatch. We further examined whether this mortality decrease was stronger for adults and males that suffer generally from highest hunting pressure (Focardi et al. 2008, Toïgo et al. 2008).

## MATERIALS AND METHODS

### *Study area*

The Geneva basin is located on the France–Switzerland border and is surrounded by mountain chains and the lake of Geneva. The study site is a  $16 \times 11$  km area around a nature reserve of 318 ha, less than half the size of local wild boar home ranges (females,  $760 \pm 290$  ha; males,  $1010 \pm 250$  ha [mean  $\pm$  SD; Tolon et al. 2009]). Natural large predators of wild boar are absent in the Geneva basin and the main source of mortality is due to human encounters (hunting, culling, or road casualties). Hunting occurs from the second Sunday of September to the last Sunday of January between 08:00 and 17:00 or 19:00. The study site supports seven hunting teams and each uses a delimited hunting territory. During the hunting season, hunters perform between one and six drive hunts per week within forests of hunting territories, except in the nature reserve. Drive hunts are performed on several dozen hectares with dogs and beaters driving wild boar toward shooting lines.

TABLE 1. Habitat variables potentially linked with risk levels for hunted wild boar.

Names	Description	Link with risk	References
d-Road	distance to paved road†	generate collisions	Groot Bruinderink and Hazebroek (1996), ungulates
d-Trail	distance to trails†	enhance hunters' accessibility	Broseth and Pedersen (2000), hunted hare
Slope and altitude	slope and altitude derived from a digital elevation model‡	reduces predators (hunters) accessibility and/or success	Caro (2005), short review in ungulates with natural predators
Landscape	hygrophilous forests, oak-beech forests, urban areas, open field	determines landscape openness and resource (mast)	Boitani et al. (1994), wild boar
d-Reserve	log(distance to the reserve boundary)	provides low-risk areas	Tolon et al. (2009), wild boar; Madsen (1998), waterfowl

† Source: BD TOPO, 2008. Institut Géographique National (IGN).

‡ Source: Shuttle Radar Topography Mission, 2004. Consortium for Spatial Information, Consultative Group on International Agricultural Research (CSI-CGIAR).

#### *Wild boar tracking*

Wild boars were trapped, weighed, and ear tagged from 2003 to 2007. A total of 47 individuals (33 females, 14 males) were fitted with very-high-frequency radio-transmitters. (VHF; TXE-3 5.500; TELEVILT, Ramsberg, Sweden). Six additional animals (four females, two males) were fitted with GPS devices (3300S and L; LOTEK, Newmarket, Ontario, Canada). Wild boars were mostly nocturnal in hunted systems and remained at resting sites during daylight (Boitani et al. 1994, Keuling et al. 2008). Animals were located all year long, once daily between 07:00 and 19:00 during the resting period, and tracked between one and six times a month at night (30–60 minutes between successive locations, 15 minutes with GPS devices) from 19:00 to 07:00. Accuracy of locations was estimated to  $115 \pm 20$  m (mean  $\pm$  SD) with VHF collars in mountainous environment (Baubet 1998) and to 15 m for GPS collars (according to the manufacturer). A total of 11 individuals were tracked for two years, with one female surveyed for three years. We thus obtained 60 “individual-years” with 19 young females (<2 years), 25 adult females (>2 years), 8 young males, and 8 adult males (survey duration during hunting: range = 9–152 days).

#### *Hunting dog tracking*

Dogs were fitted with GPS collars (GEOPOINTER; Trace Pro Plus, Les Vans, France) and located every minute during 105 hunting actions performed within the 2006 and 2007 seasons between 07:00 and 18:00. During hunting actions, dogs were first on leashes and then released such that their space use revealed a mix between hunter and dog behaviors (tracking duration =  $133 \pm 79$  minutes; distance moved =  $5.85 \pm 3.31$  km; surface covered =  $70 \pm 66$  ha [mean  $\pm$  SD], 100% minimum convex polygon [MCP];  $N = 105$  hunting sessions performed by dogs fitted with GPS devices). We first computed the proportion of GPS locations for each  $50 \times 50$  m pixel of a given hunting territory. Then we summed these maps for the entire study site, giving the number of hunted day per territory as weight to integrate absolute differences of hunting effort over teams, and obtained the density index of hunting activity. Spatial variations of this

density index were considered stable over years due to the presence of the protected perimeter (Spearman rank correlation coefficient computed between densities per pixel in 2006 and 2007 is 0.702) and we extrapolated the resulting map of density index to all years of the study.

#### *Habitat selection analysis*

Several habitat variables were extracted from the same  $50 \times 50$  m resolution grid using a geographical information system (GIS; ArcView 3.2, ESRI, Redlands, California, USA). We selected variables potentially linked to mortality risk for wild boar, ungulates, or game species (Table 1). We focused on habitat selection within home ranges of wild boar (third scale of Johnson 1980) during the hunting season and the diurnal period. A K-select analysis (Calenge et al. 2005, see Hansen et al. [2009] for a biological application) was used to analyze habitat selection by wild boars. The K-select analysis is a multivariate method based on the concept of marginality (i.e., the difference between the average available habitat conditions and the average used conditions). This is a particular case of principal component analysis that returns a linear combination of habitat variables maximizing the average marginality. Hence, variables could be identified that contribute most to overall habitat selection (e.g., Fig. 1a) and individual selection strategies could be observed via their marginality vectors (e.g., Fig. 1b). For each individual-year, the “availability” corresponded to average habitat conditions for the individual over its annual home range (100% MCP) and the “use” was the habitat associated with observed diurnal locations (i.e., habitat selection within the home range). As only wild boar data were used, the results of the K-select analysis focused only on the habitat selection by the target species. We projected a posteriori, in the ecological space defined by the wild boar K-select analysis, the marginality vectors for hunting dogs covering each wild boar home range (one dog-vector per wild boar, Fig. 1c). Therefore, we analyzed habitat selection by wild boars within their home ranges using K-select analysis and we visualized the dogs response within each wild boar home range using the projection of their marginality vectors.

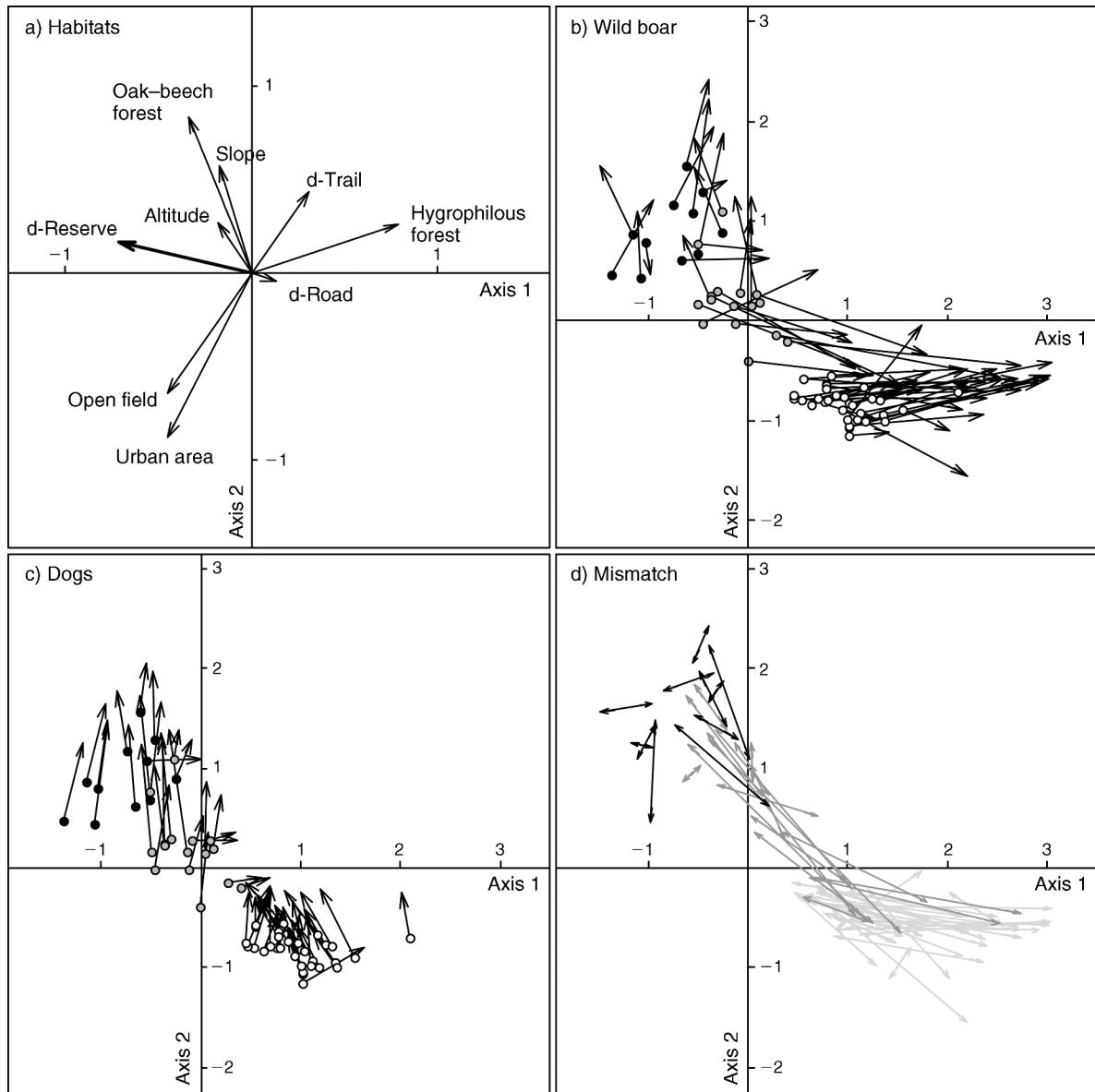


FIG. 1. K-select analysis of habitat selection within home ranges of wild boar (60 individual-years). (a) Arrow-plot showing the contribution of the six habitat variables on the first two axes of the K-select analysis (see Table 1 for details on habitat variables). The length of an arrow indicates the general strength of the selection of the corresponding habitat variable (regardless of the direction of the selection among individuals). (b) Plot of marginality vectors for wild boar on the first two axes. Each arrow corresponds to an individual-year and links the average habitat conditions on home ranges (circles, availability) to the average conditions observed on relocations within home ranges (arrow, use). The length and orientation of arrows describe the strength and direction of the selection in the ecological space, respectively. (c) Plot of marginality vectors for hunting dogs projected on the K-select analysis. Each black arrow links the average available habitat conditions (circles, wild boar home range) to the average used conditions (arrows, habitat use of hunting dogs in the wild boar home range). (d) Mismatch intensity between dogs and wild boar habitat uses for a given individual-year. Each arrow joins the end points of the two marginality vectors of a boar and hunting dogs linked to it. Circles in panels (b) and (c) and arrows in panel (d) are shaded according to overlaps of annual home ranges with the reserve [MCP100%]: black, 0–5%; gray, 5–20%; white [or light gray in panel (d)], 20–100%.

*Quantifying interactions*

For each wild boar and year, we calculated the mismatch between that animal’s habitat use and that of dogs as the Euclidean distance between their marginality

vectors within the ecological space defined by the first two axes of the K-select analysis (the variable *mismatch*). For each year, we calculated the mean density of hunting activity in wild boar home ranges as an estimate



PLATE 1. Wild boar fleeing a drive hunt. Photo credit: Sébastien de Danieli.

of the hunting risk level faced by individuals at a large scale (the variable *density*).

The influence of proximity to the reserve on wild-boar–dog interaction was evaluated by testing the Spearman rank correlations of the average distance to the reserve boundary (measured over all pixels of home ranges) with *mismatch* and *density*. We also tested the correlation between *mismatch* and *density* to verify that mismatch intensity within a home range increased with the degree of hunting activity over home ranges. To avoid pseudoreplication, we averaged values of *mismatch* and *density* per individual for animals observed several years.

#### *Mortality analysis*

A mixed effect Cox proportional hazard regression was used to model the mortality risk for animal during the hunting season depending on the individuals (random effect on the intercept) and measures of the wild-boar–dog interactions, i.e., *mismatch* and *density*. To avoid collinearity problems, we used first and second principal components computed on *mismatch* and *density* (PC1 and PC2) as fixed effects in the Cox regression (Graham 2003). Sex and age (adult or young) were also included as fixed effects. All additive and interaction terms were included in the full model, because adults and/or males could be more exposed to hunting (age  $\times$  sex) and therefore more sensitive to spatial interactions (age  $\times$  PC1, sex  $\times$  PC1, and age  $\times$  sex  $\times$  PC1). Several reduced models were built based on all additives terms combinations, with or without respective interactions. The best model was selected from among

the 19 resulting models (1 full, 1 null, and 17 reduced models) based on the Akaike information criterion corrected for small sample size (AIC<sub>c</sub>; Burnham and Anderson 2002), the difference of AIC<sub>c</sub> with the best model ( $\Delta_i$ ), and the Akaike weight ( $w_i$ ). Following Burnham and Anderson (2002), models with a difference of AIC<sub>c</sub> ( $\Delta_i$ ) lower than 2 were considered plausible and could be interpreted biologically. All analyses were performed using R software (R Development Core Team 2008) with the *adehabitat* package (Calenge 2006) for analyses of habitat selections and with *survival* and *coxme* for the survival analysis.

## RESULTS

### *Spatial interactions*

The K-select analysis demonstrated a strong pattern of habitat selection by wild boars within home ranges. The first and second axes explained 65.63% and 12.96%, respectively, of the total marginality (Fig. 1a). The first axis opposed, from right to left, hygrophilous forests in the reserve core to the peripheral unprotected environment, respectively (Fig. 1a). The second axis opposed, from top to bottom, mountainous oak and beech woods, poorly accessible to humans, against flat open fields, and heavily accessible to humans (Fig. 1a).

The plot of marginality vectors (Fig. 1b) showed that wild boar expressed differential habitat selections according to habitat available within home ranges. Animals with home ranges near the reserve tended to strongly select hygrophilous forests within the protected perimeter (arrows on the right pointing to the right, Fig. 1b). Other animals that settled far from the reserve in

mountainous environment tended to select for oak and beech woods in steep slopes that were far from trails and roads (arrows on the left pointing upward, Fig. 1b). The first habitat selection strategy (protected area) seemed to be predominant among studied animals compared to the second strategy, but such discrepancy could simply result from the highest trapping effort made near the reserve.

The behavior of hunting dogs in regard to wild boar habitat use was also strongly dependent of the location of the wild boar home range. Near the reserve, dogs avoided the protected area and therefore deviated from the behavior of wild boar (black arrow on the right, pointing upward in Fig. 1c). In contrast dogs selected, in mountainous environment, oak and beech woods in steep slopes far from trails and road, in accordance with the wild boar habitat selection (black arrow on the left, pointing upward, Fig. 1c).

The density index of hunting activity over the study site was maximal in the vicinity of the protected area (Fig. 2a and 3). As expected, the average distance from the reserve was significantly and negatively correlated with the mean hunting dog density over home ranges (*density*,  $\rho = -0.41$ ,  $N = 47$  wild boar fitted with collars,  $P = 0.0045$ ) and with the mismatch intensity within home ranges (*mismatch*,  $\rho = -0.40$ ,  $N = 47$ ,  $P = 0.0054$ ). Therefore, the variables *mismatch* and *density* were strongly and positively correlated ( $\rho = 0.64$ ,  $N = 47$ ,  $P < 10^{-5}$ , Fig. 2b).

#### Mortality analysis

During hunting, the survival probability for all animals was equal to 0.67 [0.53–0.78] ( $N = 60$  individual-year; mean [95% CI]). Seasonal survival,  $S$ , varied slightly among age classes (juveniles,  $S = 0.62$  [0.32–0.85],  $N = 13$  individual-years; yearlings,  $S = 0.79$  [0.49–0.94],  $N = 14$ ; adults,  $S = 0.64$  [0.45–0.79],  $N = 33$ ) and between sexes (females,  $S = 0.68$  [0.52–0.81],  $N = 44$ ; males,  $S = 0.63$  [0.36–0.84],  $N = 16$ ). All deaths among studied individuals were due to hunting.

The first principal component of *density* and *mismatch* (PC1) explained 80.63% of the total variance. As expected, this component opposed lightly hunted home ranges with matching patterns at fine scale (negative values of PC1, Fig. 3 [Animal 1]) to heavily hunted home range with pronounced mismatching patterns at fine scale (positive values of PC1, Fig. 3 [Animal 2]). The best Cox proportional-hazard regression selected by AIC<sub>c</sub> included PC1, age, and their interaction age  $\times$  PC1 (Table 2; PC2 was not relevant in models and was excluded from the selection procedure). The following model ( $\Delta_i < 2$ ) contained the term sex in addition. The null model was ranked third with a  $\Delta_i$  of 2.82, which demonstrated that all other models were clearly not relevant to describe the data. The best model showed that the effect of the wild boar and hunting dog spatial interaction on mortality was dependent on the age class of individuals (Fig. 4). Adult mortality ( $N = 33$

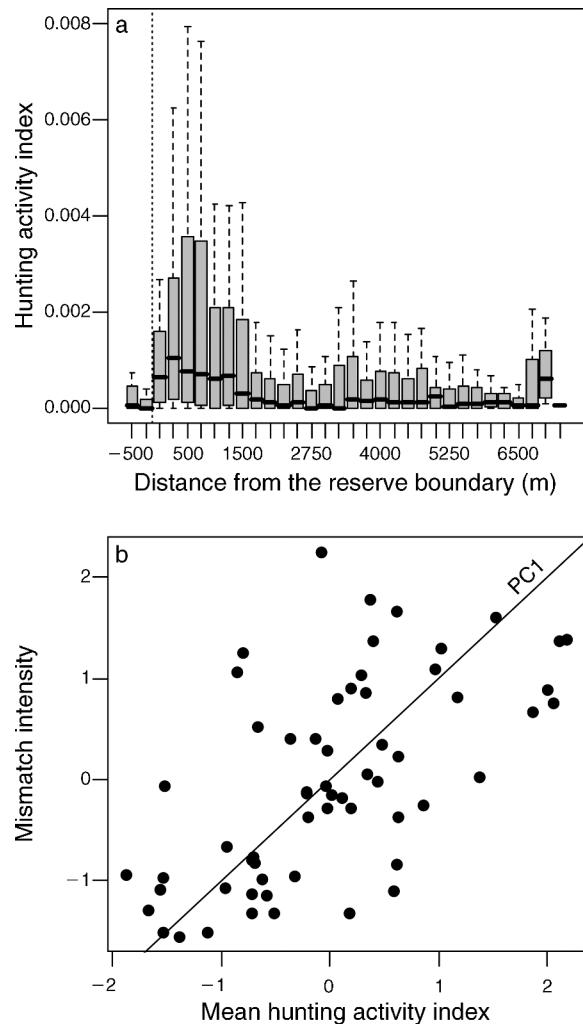


FIG. 2. (a) Boxplot of the density index of hunting activity within pixels of  $250 \times 250$  m, according to the distance from the reserve boundary (dotted line, distance classes = 250 m). The density was based on GPS tracking of hunting dogs performed during drive hunts. Black lines indicate medians, gray rectangles delimit second and third quartiles, and dashed segments join last points within the  $\pm 1.5 \times$  inter-quartile interval. (b) Relationship between the scaled average density index of hunting activity over wild boar home ranges and the scaled mismatch intensity of both habitat uses within home ranges (black line, first principal component of both variables PC1)

individuals) decreased with increasing mismatch, even at the cost of more hunting activity inside their home range (positive values of PC1, Fig. 3 [Animal 2]). Indeed, approximately 60% of adults were killed when dogs tended to match their habitat use, in contrast to around 10% for adults showing strong mismatches (Fig. 4a). Despite the strong mismatch with hunting dogs at a finer scale, mortality of younger animals (yearlings and juveniles,  $N = 27$ ) was higher in the most hunted home ranges (nearly 50% of individuals killed during the hunting season) than for the opposite situation (poorly

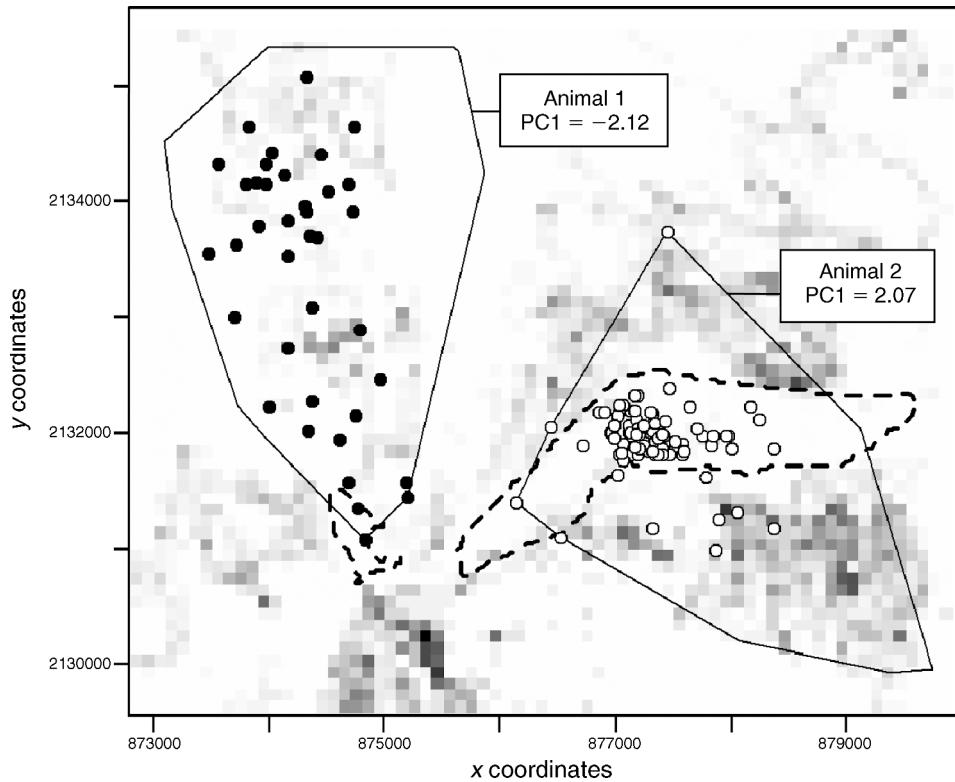


FIG. 3. Home ranges and space use of two wild boars during the hunting season in 2006 related to the density index of hunting activity. For Animal 1, individual far from the reserve with a low overall hunting activity on the home range but a matching pattern with dogs space use (negative value of PC1, see *Methods*). For Animal 2, individual close to the reserve with a high overall hunting activity on the home range but a mismatching pattern with dogs space use (positive value of PC1). Different gray levels indicate the density index of hunting activity (white, minimum; black, maximum; pixel size,  $100 \times 100$  m). Polygons outline annual home ranges [MCP 100%]. Solid and open circles indicate resting site locations during hunting. Dashed lines outline reserve perimeters.

TABLE 2. Model selection on Cox proportional-hazard regressions for survival of wild boar during hunting season (60 individual-years) according to age, sex, and spatial interactions with dogs.

Formula (fixed effects)	$d$	$AIC_c$	$\Delta AIC_c$	$w_i$
<b>PC1 + age + PC1 <math>\times</math> age</b>	<b>4</b>	<b>155.80</b>	<b>0.00</b>	<b>0.367</b>
PC1 + age + sex + PC1 $\times$ age	5	157.04	1.24	0.197
null	1	158.62	2.82	0.090
PC1 + age + sex + PC1 $\times$ sex + PC1 $\times$ age	6	158.74	2.94	0.084
PC1 + age + sex + PC1 $\times$ age + age $\times$ sex	6	159.40	3.60	0.061
age	2	160.26	4.46	0.040
sex	2	160.63	4.83	0.033
PC1	2	160.72	4.91	0.031
PC1 + age + sex + PC1 $\times$ sex + PC1 $\times$ age + age $\times$ sex	7	161.25	5.45	0.024
age + sex	3	162.29	6.49	0.014
PC1 + age	3	162.42	6.62	0.013
PC1 + sex	3	162.83	7.03	0.011
PC1 + age + sex + PC1 $\times$ sex + PC1 $\times$ age + age $\times$ sex + PC1 $\times$ age $\times$ sex	8	163.04	7.24	0.010
age + sex + age $\times$ sex	4	163.38	7.58	0.008
PC1 + sex + PC1 $\times$ sex	4	164.02	8.22	0.006
PC1 + age + sex	4	164.57	8.77	0.005
PC1 + age + sex + age $\times$ sex	5	165.64	9.84	0.003
PC1 + age + sex + PC1 $\times$ sex	5	166.20	10.40	0.002
PC1 + age + sex + PC1 $\times$ sex + age $\times$ sex	6	167.93	12.13	0.001

Notes: The model selection was performed according to the corrected Akaike information criteria ( $AIC_c$ ). Columns show:  $d$ , the number of parameters (random effect included);  $\Delta AIC_c$ , the difference between  $AIC_c$  and that of the best model;  $w_i$ , AIC weights relative to all models (best model in bold). Effects are: age, adult or young; sex, female or male; PC1, measure of the spatial interaction among habitats with dogs (the first principal component of the average hunting activity level on home range, *density*, and the mismatch intensity within home range, *mismatch*). PC1 opposed poorly hunted home ranges with matching patterns at fine scale to highly hunted home range with pronounced mismatching patterns at fine scale.

hunted home ranges with matching patterns, about 20% killed, Figs. 3 [Animal 1] and 4b). Therefore, the mortality risk switched from adults to younger age classes as the wild-boar–hunting-dogs interaction shifted from matching pattern in poorly hunted home ranges to mismatching patterns in highly hunted home ranges (Fig. 4).

#### DISCUSSION

Our results highlight a strong spatial interaction between hunting dogs (i.e., predator) and wild boars (i.e., prey), with complex consequences for individual mortality. Two main strategies of habitat selection were identified for the target species (see also Tolon et al. 2009): selection of the protected area or forested steep slopes far from human access. When dog movements were not spatially constrained by the reserve, their habitat use matched the habitat use of wild boar, which led both protagonists to select forested steep slopes. The use of steep slopes as refuges is often reported in ungulates (short review in Caro 2005), but such a response was not sufficient in our study area for animals to avoid hunting risk. In contrast, the spatial constraint for the “predator” due to the reserve allowed wild boars to avoid the risk source by shifting their activity centers into the refuge (Fig. 1; see also Tolon et al. 2009). Therefore, seasonal habitat use patterns of both wild boars and hunting dogs within home ranges showed a clear transition from matching to mismatching patterns as the proximity of the reserve increased (Fig. 1a and d).

In response to this dissociation, hunters and hunting dogs intensified their effort near the reserve boundary to benefit from the high wild boar density in the protected perimeter (analogous to the “fishing-the-line” strategy around marine reserves; Gell and Roberts 2003, Roberts et al. 2005, Kellner et al. 2007). This behavior of hunters combined with the small size of the protected area in regard to wild boar average home-range size could explain why animals near the reserve faced higher hunting disturbance in the home range. Consequently, the reserve led to a trade-off for animals between average home range safety (best far from the protected areas) and mismatch opportunities within home range (highest near the protected area; Fig. 3).

The mismatch inside home ranges resulted in a decrease in adult mortality despite an increased exposure of home ranges to hunting activities. Conversely, younger animals survived better in lightly hunted home ranges far from the reserve, even if no mismatch opportunity existed within the home ranges. Thus, younger boars appeared to be more sensitive to the average home range safety than adults, and were negatively affected by the “hunting-the-line” strategy around the reserve. Inexperienced individuals may be more likely to move into the risk belt around the reserve and die when the reserve is used as a refuge. This effect could be accentuated by progressive dissociation from the mother during exploratory behaviors (Cousse et al.

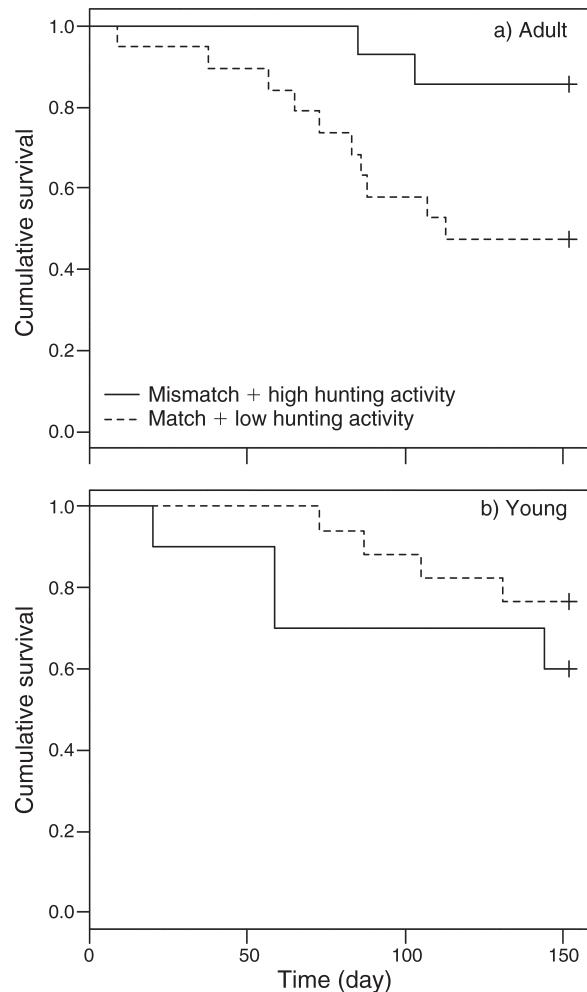


FIG. 4. Cumulative survival of wild boar (60 individual-years) during a hunting season according to age class and the spatial interaction with hunting dogs (PC1, see *Methods* and *Results*) for (a) adults (>2 years) and (b) young (<2 years). Match or mismatch refer to the association or dissociation of wild boar and hunting dogs within home ranges, and high or low refer to the global hunting dog density over individual home ranges (see *Methods* for details). Individuals of each age classes were split according to a 0.3 threshold on PC1 corresponding to the switch of mortality risk in the first Cox model (Table 2).

1994) and/or dispersal phase (Truvé and Lemel 2003). Moreover, vulnerability of each age class to hunting pressure could also depend on the availability and the behavior of others classes that could induces potential changes in hunter selectivity, similarly to natural predator–prey systems (e.g., Owen-Smith 2008). However, such effects were not obvious among sexes whereas males were reported to suffer from higher hunting pressures (Focardi et al. 2008, Toïgo et al. 2008) and to respond differently to hunting risk than females (Saïd et al. 2011). The small number of males surveyed in our study ( $N = 16$  individual-years), however, makes any interpretation of these results hazardous.

As expected by predator–prey spatial games, our results supported the general hypothesis that spatial constraints of the predator relative to prey determine the long-term outcome of spatial interactions (Fauchald 2009). The participant with lowest spatial constraints (e.g., dogs far from the reserve or wild boar near the reserve) can take advantage of the other (matching for predators or mismatching for prey) and finally succeed in this spatial game (Sih 2005, Fauchald 2009). This predator–prey analogy highlighted particularly harvester responses and counter-responses (matching patterns without a reserve [Lande et al. 2009], “hunting-the-line” strategy [Gell and Roberts 2003, Roberts et al. 2005]) similar to natural predator–prey systems (Rose and Leggett 1990, Fauchald et al. 2000). This resulted in our case to a mortality switch among age classes near the reserve. Therefore, which of the two strategies adopted by animals (safe home ranges vs. mismatching patterns) was the best for long-term individual performance is unclear, and the expected positive reserve effect is uncertain. As expected by modeling approaches (Kellner et al. 2007) and few empirical studies (Murawski et al. 2004, Goñi et al. 2006), our results confirmed that fishing or hunting-the-line behavior can strongly increase the “edge effect” by impacting the population inside the protected perimeter. Increasing reserve sizes (i.e., the area : perimeter ratio), or implementing buffer areas with harvesting limitations, can dampen this edge effect and help harvesters to benefit durably from source populations of reserves. After many modeling studies (e.g., Sanchirico and Wilen 1999, Smith and Wilen 2003, Kellner et al. 2007), there is a clear need to gather more empirical evidence of the impact of such predator-like human behaviors on harvested systems. In this study, the reason that younger animals died closer to the reserve would have been especially difficult to understand without investigating simultaneously behaviors of both participants. Predator–prey spatial games therefore provide a powerful theoretical background for understanding wildlife-harvesters spatial interactions and would allow for the improvement of strategies for optimal harvesting, conservation, and management of populations in the presence of protected areas.

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