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Many, large and early: Hunting pressure on wild boar relates to simple metrics of hunting effort

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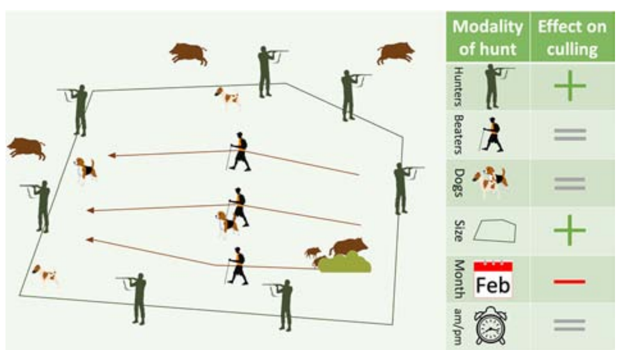
HIGHLIGHTS

- Increase of wild boar population causes many conflicts that must be managed.
- Understanding harvest through hunting effort is a timely issue for wild boar management.
- A drive hunt with more hunters leads to a higher number of culled animals.
- Hunting is less efficient on small areas and during the end of the hunting season.
- Our drive hunt model can be used as a predictive tool in wildlife management.

GRAPHICAL ABSTRACT



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ABSTRACT

Wild boar populations have increased dramatically over the last decades throughout Europe and in France in particular. While hunting is considered the most efficient way to control game populations, many local conflicts persist after the hunting period due to remaining high densities of wild boar despite the large number of animals culled every year. Therefore, increasing the efficiency of hunting is a timely issue. Herein, we assessed how hunting effort can be measured, and we determined whether the hunting effort carried out by hunters explains the observed hunting pressure. We measured the characteristics and results of all hunts that occurred in the experimental forest of Châteauvillain-Arc-en-Barrois (Northeastern France), and we modelled the number of animals culled as a function of the hunting effort, measured by the number of beaters, hunters, and dogs, as well as the size of the hunting area. We also accounted for variables suspected to affect the hunting efficiency achieved with a given effort, such as time of day (AM/PM), the month during which hunting occurred. We found that more posted hunters, larger hunted areas, and hunts carried out early in the season, i.e. before February,

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France
Sus scrofa

increased the number of culled animals. Our model can be used by wildlife managers to adjust hunting effort in order to reach the hunting pressure expected to meet management objectives.

1. Introduction

Wild boar (*Sus scrofa*) populations have been expanding (Morelle et al., 2016) and increasing (Massei et al., 2015) dramatically over the last four decades in Europe due to several possible drivers such as favorable management measures (Maillard et al., 2010), landscapes structural changes (Morelle et al., 2016) or climate change (Markov et al., 2019; Vetter et al., 2015). Wild boar can reach very high densities in agroecosystems (Hebeisen et al., 2008) and urban area (González-Crespo et al., 2018), potentially leading to conflicts such as: (i) crop damage and associated socio-economic impacts (Amici et al., 2012; Calenge et al., 2004; Schley et al., 2008); (ii) undesired ecological impacts, e.g. by uprooting rare plants (Giménez-Anaya et al., 2008), potentially impacting ground-nesting birds or snakes (Giménez-Anaya et al., 2008; Graitson et al., 2018); and (iii) serious public health and food-security concerns via the transmission of epizootic and zoonotic diseases such as bovine tuberculosis or African swine fever (Boadella et al., 2012; Guinat et al., 2017; Mentaberre et al., 2014). Therefore, limiting or controlling wild boar population size has become a common management goal throughout Europe (Apollonio et al., 2010; Massei et al., 2015).

While some demographic studies have defined the proportion of individuals or classes of individuals to be culled to bring population growth to an equilibrium (Gamelon et al., 2012; Keuling et al., 2013; Servanty et al., 2011), we still lack information on how to cull wild boar efficiently. Hunting, when considered as a predation system, seems to affect wild boar mortality more significantly than wolf predation in Spain (Nores et al., 2008), and is considered as the main cause of death (Keuling et al., 2013). Hunting involves a predator (the hunter) who tries to capture and kill its prey (here the wild boar) which has to find a compromise between avoiding the risk of predation and fulfilling other life activities, such as feeding or reproduction (Creel and Christianson, 2008; Lima and Dill, 1990). Thus, hunters have to find the best strategy to cull wild boar, while wild boar try to find the best strategy to reduce their risk of being killed (Keuling et al., 2008; Thurfjell et al., 2013).

However, the means to measure these hunter strategies remain unclear in terrestrial ecology (Rist, 2007). Terms like “hunting pressure”, “hunting effort”, “hunting efficiency”, “catch per unit of effort”, or “hunting intensity” are often used without any clear definition in the literature, sometimes interchangeably. A same word is generally used for different concepts which brings confusion in science. For example, hunting pressure expresses either a large hunting bag (i.e., all the animals culled at the end of a hunting game, Bonenfant et al., 2002), or a high death rate (Scillitani et al., 2010; Sodeikat and Pohlmeyer, 2007), or is used as a synonym of hunting effort (Broseth and Pedersen, 2000). Although each author may have a clear understanding of the meaning of these terms in their study, the use of vague terminology distorts our communication and may impair the scientific progress (Hall et al., 1997). Moreover, these terms may be given without means to quantify them (Fa et al., 2000), or associated with different measurement units (Rist, 2007). To our knowledge, no attempt has been made to unify all these concepts in a unified framework. Contrastingly, this terminology has been clarified in fisheries, as “fishing effort” and “fishing pressure” are often used in fisheries management (Gascuel, 1995; Marchal et al., 2006). Fishing effort is a measure of the volume of resources devoted to fishing (Marchal et al., 2006; Squires, 1987), and fishing pressure reflects the pressure exerted by fishing activity on the fish population (i.e., the biomass of fish extracted, Gulland, 1969; Laurec, 1977; Laurec and Le Guen, 1981). This clarified terminology makes it possible to link fishing effort and fishing pressure through catchability (i.e., the probability of being culled, Laurec and Le Guen, 1981). Thus, by analogy we can define hunting effort as the set of labors implemented to hunt and hunting pressure as the resulting mortality rate (Cunningham and Whitmarsh, 1980). Marchal et al. (2006) identified the fishing variables characterizing fishing effort that reflect catch patterns (like the fishing net size, the engine power, etc.). Using this clarified framework, we hope to calculate the catchability of wild boar using hunting effort variables that must be identified to improve the cull.

Herein, we assessed the relationship between hunting effort (labor provided by hunters) and the consequence in terms of culling wild boar (hunting pressure) in an experimental forest of Châteauvillain-Arc-en-Barrois, France, hunted by drive-hunting. In France, drive hunts (‘battues’) are the method of choice for most ungulate hunting (Maillard et al., 2010): beaters with dogs drive game outside a given area, so that posted hunters, in ambush on the area's limits, have increased opportunities to shoot them. Specifically, we designed a statistical model relating variables thought a priori descriptors of the hunting effort to the number of culled animals.

The number of posted hunters appears to be a major element of the hunting effort explaining the number of culled wild boar (i.e., more effort leading to more culling, see review in Rist, 2007). We first expected that the higher the number of posted hunters, the higher the number of wild boar shot would be. Second, dogs should be an important factor in the hunting process by flushing wild boars out of bushes, and outside the hunted area. However, previous studies could not highlight a specific effect of dogs (Caley and Ottley, 1995; McIlroy and Saillard, 1989). Thus, we did not expect any effect of dog number on hunting success. Third, in the same way, the role of beaters was expected to be identical to that of dogs, i.e., no increase in the number of culled wild boar with the increase of the beaters' number (Scillitani et al., 2010). Fourth, habitat and environmental conditions such as weather or climate could affect the way a given effort results into a given hunting pressure, through components of prey catchability. According to Jensen et al. (2017) we expected that large plots of forest would encompass more suitable hiding zones, or may provide reduced disturbance regarding the hunt. We expected a higher number of culled wild boar when hunted plots are wide. As the posted hunters are placed around the hunting plot, the size of the perimeter seems more relevant. Moreover, we hypothesized that wild boar could be more vigilant at the end of the hunting season (i.e., non-lethal effect of mortality risk, Keuling et al., 2008; Lima and Bednekoff, 1999; Thurfjell et al., 2013), but less at the beginning of the season. Furthermore, hunting may cause a decrease in the number of individuals in the population resulting in greater difficulty in culling at the end of the hunting season (Creel and Christianson, 2008; Grau and Grau, 1980). For this reason, our fifth prediction was that, at constant effort, less wild boar would be culled at the end of the hunting season than at the beginning. Finally, wild boar exhibit a night activity pattern and are not active much during the day, when they stay in their resting place (Boitani et al., 1995; Keuling et al., 2008). Thus, we assumed that there would be no difference in detectability of wild boar between morning and afternoon, leading to no effect of the time of-day on the number of animals culled. Furthermore, the relationships between effort and culling may not be linear, i.e. there can be a saturation effect. In other word, it is possible that the number of culled wild boar can reaches an asymptote when a variable describing the hunting effort increases (i.e., the number of posted hunters, beaters and dogs, see Caley and Ottley, 1995).

We used a Bayesian variable selection approach to identify the relevant effort and obtain catchability values, which allowed us to predict the number of wild boars that can be expected to be culled according to the hunting effort and the hunting condition. Furthermore, our modelling allows us to investigate saturation effects of the hunting effort on resultant culling by checking quadratic effects on the number of culled wild boar.

2. Material & methods

2.1. Study area

We studied wild boar hunting over the 8500 ha of the forest of Châteauvillain-Arc-en-Barrois, north-eastern France (47°59′14.2″N 5°02′50.6″E). This forest is dominated by oak (*Quercus petraea*), beechnut (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*; Saïd et al., 2012). The data were collected in the part of the national forest of 8500 ha rented by the national administration in charge of forest management (*Office National des Forêts*) to a private manager who welcomes hunters paying fees to practice on this area.

2.2. Wild boar ecology

Wild boar are opportunistic mammals with a widespread world distribution (Keuling et al., 2017), with a very high growth rate (Gamelon et al., 2012), sows producing up to 6 piglets per litter (Servanty et al., 2009). Wild boar live in matriarchal social groups ("company") led by a large sow accompanied by her piglets, whiles adult males are solitary (Dardaillon, 1988; Kaminski et al., 2005, Vassant et al., 2010). Males join female social groups during rutting period in the winter, i.e. during the hunting period (Nivois et al., 2014). Piglets can be easily identified by their color patterns (the piglet has stripes before 4 months, and becomes red between 4 month and a year, Moretti, 1995). The population structure is dominated by juveniles (about 60%), followed by sub-adults (about 25%), and finally by adults (about 15%) which is also concordant with a generation time of 2.27 years (Servanty et al., 2011).

2.3. Local organization of a drive hunt

All drive hunts were organized by the same manager, throughout the whole study period (2009–2013). The period during which hunting is permitted runs from September to February. During this period, the local manager chooses the hunted forest plots (thereby defining a hunted area covering between 30 ha and 300 ha) and defines the shooting instructions to achieve the government objectives of a balance between the interests of the farming, forestry and hunting interest groups ("*équilibre agro-sylvo-cynégétique*", Maillard et al., 2010). Wild boar of all age and/or sex categories can be culled according to the shooting instructions (young individuals are preferred to old sows). All wild boar culled and drive hunt metrics (as well as sex and weight) were recorded in a notebook by ONCFS (Office National de la Chasse et de la Faune Sauvage) technicians, who could assign a location for each cull and therefore attribute a hunting area size for each drive hunt.

During a drive hunt, the beaters and dogs form a tracking line that advances through the hunting area to flush out wild boar from the inside of the hunting area to the border near the posted hunter (Fig. 1). When wild boar are flushed and when they are near the posted hunters' lines, the beaters shout information about the direction of wild boar, the likely point of crossing, and their group size. Hunters are allowed to shoot only escaping wild boar, after they have left the limits of the hunting area, by crossing the hunters' line. Such safety rule recommendations prevent any shots in the beaters' direction.

Wild boar hunting occurs two days a week (Saturday and Sunday). During a hunting day, there can be several drive hunt events (between 1 and 5 drive hunts events per day). 64% of them occurred in the morning and 36% after lunch break (afternoon). Thus, adjustment to hunting teams, if any, occurred only at that break time. The size of the hunter groups participating in the different drives were almost identical, with the following average differences between the morning and the afternoon (−0.03 posted hunters ± 0.57, −1.38 beaters ± 1.56 and −1.12 dogs ± 0.57 in the afternoon). However, the number of hunters could

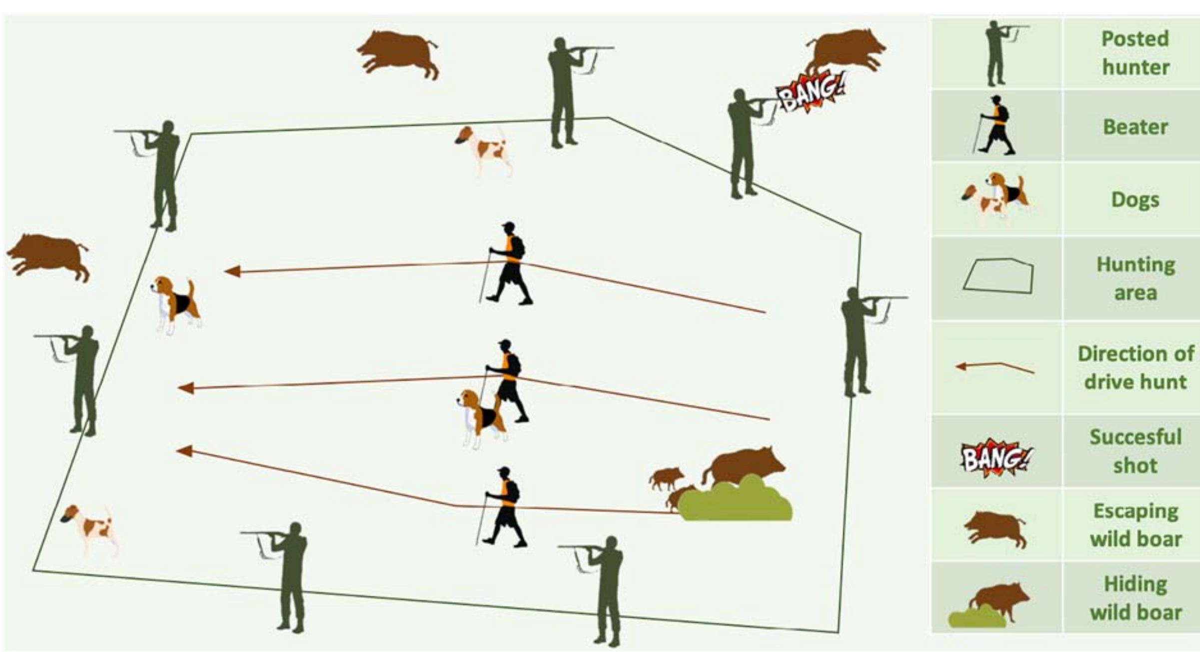


Fig. 1. In our study area, drive hunts take place in a hunting area with two types of people, the posted armed hunters (green with rifle) and the beaters (black and orange), who may be accompanied by dogs. The beaters and dogs' role is to push the wild boar outside the hunting area, allowing posted hunters to shoot them after they have crossed the line. Before starting the hunt, hunters armed with rifles are posted backwards around the hunting area. Then, when the hunts start, the beaters walk in the enclosure of the hunted area in a straight line and as much as possible parallel to each other, while the dogs that may accompany them can flush out wild boars. Posted hunters can only fire when the wild boar crosses the line of fire and when they are in his firing angle. Thus, wild boar can be flushed out or not, and they can be successfully shot or not. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

vary across two consecutive days and/or between different weeks (ranges of posted hunters from 26 to 59, for beaters from 10 to 30 and for dogs from 3 to 30 (see Table 1).

2.4. Data collection

We collected the hunting notebooks containing the description of the drive hunts carried out during four hunting seasons (see Table 1; 2009/2010, 2010/2011, 2011/2012, 2012/2013). Each hunt was described by the perimeter of the hunted area, the number of hunters who participated in the drive (mean per drive hunt event = 46.67 hunters, sd = 7.56), the number of beaters (mean per drive hunt event = 19.14 beaters, sd = 4.28) and the number of dogs (mean per drive hunt events = 13.52 dogs, sd = 4.62). As noted above, we chose to use the perimeter as a measure of the size of the hunted area, rather than the surface area. The perimeter and the surface of the hunted area were strongly correlated (R = 0.91), so that both variables are redundant in measuring the size of hunted area. We chose to work with the perimeter, because (i) an increase in surface area increases the probability of presence of a wild boar in the area and decreases at the same time the probability of flushing the animal by the beaters if it is present (so that the two opposite effects of the area cancel each other out; Calenge, unpublished data), and (ii) as the posted hunters are placed around the plot, the number of posted hunter per linear meter of the perimeter is positively correlated with the probability that the animal is shot if it crosses the perimeter line. Thus, the size of the perimeter of the plot seemed more relevant to measure its size, but again, given the strong correlation with the surface area, we do not expect this choice to have a strong effect of our results. Thus, 361 drive hunt events were described, leading to a total of 2407 wild boar culled (mean of wild boar culled per drive hunt = 6.67, sd = 5.84). For our modelling approach, we transformed some of these variables to facilitate the model fit (see below). Thus, we classified the perimeter of the hunted area into three classes, based on the tertiles of its statistical distribution, small [2219–4723] meters, medium [4723–5728] meters, and large [5728–8560] meters. A preliminary exploratory analysis revealed that the last month of the hunting period (February) seemed to be characterized by a much smaller efficiency of hunting drives (see Supplementary material Fig. S1), and we modelled the difference between the two subperiods (October, November, December and January, n = 276 drive hunt events versus February, n = 85 drive hunt events). Finally, we considered two types of drive hunt events depending on the time of the day when the drive was carried out (morning, n = 232 drive hunt events, versus afternoon = 129 drive hunt events).

Table 1
Grouping descriptors and classification of drive hunt variables in our study area at Châteauvillain/Arc-en-Barrois forest, France during four hunting seasons (2009–2013). Part A) describe quantitative variable by mean, standard deviation and the range. Part B) describe qualitative variable with the levels of modalities and the number of observation (on 361 drive hunt fallow).

A) Quantitative data

Variables	Mean & sd - per drive hunt	Range
Number of wild boar culled	6.67 ± 5.84	[0−32]
Number of posted hunters	46,67 ± 7,56	[26–59]
Numbers of beaters	19,14 ± 4,28	[10−30]
Number of dogs	13,52 ± 4,62	[3−30]
The size of the perimeter of hunting area	5269.84 ± 1264.99	[2219–8560]

B) Qualitative data

Variables	Levels	Total number (on 361 drive hunt)
The moment of hunting season	October, November, December, January,	276
	February	85
The time of the day	Morning	232
	Afternoon	129

2.5. Modelling of the wild boar drive hunt process

Let P_i be the hunting pressure (mortality rate in the population) caused by the drive hunt *i*, and let N_i be the population size at the beginning of this hunt. Let S_i be the number of wild boar culled during the drive hunt *i*. We suppose that the number of culled animals is a draw from a binomial distribution $B(N_i, P_i)$. Thus, ignoring natural mortality, it follows that the population size at the beginning of the following drive hunt $i + 1$ is $N_{i+1} = N_i - S_i$ individuals in the population. Thus, as the hunting season progresses, we can expect that a given hunting pressure level will result in an increasingly smaller number of culled animals. However, the preliminary exploratory data analysis did not reveal any regular decrease of the number of animals culled as the hunting season progressed. Actually, the hunting pressure implemented in a typical drive hunt did not seem to be enough to reduce the size of the wild boar population. Therefore, as a rough approximation, we can suppose that (i) the population size does not change strongly as the hunting season progresses, and for every drive hunt $N_i \approx N$ with N a constant population size, and (ii) the hunting pressure P_i is close to zero for any drive hunt *i*. It is well known that, under these conditions (small P_i and constant and large N), the binomial distribution converges towards a Poisson distribution with mean $\lambda_i = N.\ P_i$ (e.g, Leemis, 1986). In other words, as a rough approximation, we can suppose that the number of culled animals S_i during a given drive hunt *i* is drawn from a Poisson distribution with parameter λ_i.

However, we can also suppose that some of the variables describing the hunting effort (reported in the hunting notebooks) affects the hunting pressure, and thereby the number of culled animals. Thus, we suppose a log-linear model relating the logarithm of the hunting pressure P_i and the variables describing the hunting effort and the catchability x_i^j:

$$\log(P_i) = \theta_0 + \sum_{j=1}^{K} \theta_j x_i^j + \varepsilon_i$$

where K is the number of explanatory variables x_i^j considered in the model, θ_0 is the intercept of the model, θ_j is the coefficient of the variable x^j, and ε_i is a residual describing the random environmental fluctuations affecting this mortality rate.

Given the Poisson approximation, it follows that the number of culled animals during drive hunt *i* can be modelled as a Poisson variable with parameter λ_i, with:

$$\log(\lambda_i) = \theta\prime_0 + \sum_{j=1}^{K} \theta_j x_i^j + \varepsilon_i$$

with $\theta'_0 = log\,(N) + \theta_0$. Note that because N is unknown, we are unable to separate N and θ_0. With this Poisson regression, we are therefore modelling the relative hunting pressure, i.e. the mortality rate multiplied by an unknown constant. However, this is sufficient to identify the variables describing the hunting effort that affect hunting pressure the most. Moreover, we supposed that the random errors ε_i were normally distributed with standard deviation σ_ϵ. Finally, we used a variable selection procedure to select the K variables x_i^j to include in the model (see section "variable selection procedure" below). We fitted this model in a Bayesian context, and in the absence of prior information on the system, we used non-informative priors for all parameters. We examined the goodness of fit of our model by calculating Pearson's correlation coefficient between the (log-transformed with $\log(X + 1)$) observed number of culled wild boar during each drive hunt and the number predicted by our model.

2.6. Variable selection

We used a Bayesian procedure of variable selection to identify the effort variables affecting the most the hunting pressure. Even if the approach developed by Kuo and Mallick (1998) to select the relevant variables (O'Hara et al., 2009) is well known in statistics, it is still rarely used in ecological research. We describe this approach in detail in this section. This method makes it possible (i) to estimate the probability that each effort variable is part of the true model explaining the resulting number of animals culled, and (ii) to estimate the probability of each possible combination of variables to be in the final model.

The Kuo and Mallick's approach consists in the fit of the following Bayesian model:

$$log\lambda_i = \theta'_0 + \sum_{j=1}^{K} \gamma_j \theta_j x_i^j + \varepsilon_i$$

This model is similar to the classical Poisson regression model described in the previous section, but each explanatory variable x^j is now multiplied by two coefficients: (i) the classical regression coefficient θ_j describing the effect of the variable x^j on the number of animals culled when it is in the model, and the binary coefficient γ_j taking either the value 1 if the variable x^j is in the model, or the value 0 otherwise. In a Bayesian context, the value of this latter parameter is supposed to be the realization of a Bernoulli variable with posterior probability p_j that the variable x^j is in the model. The Bayesian fit of this model allows us to estimate this probability, which can be used to assess whether this variable is an important one in the model. Thus, Kuo and Mallick's approach consists in separating in the model the presence of a variable in a model from its importance, and then to estimate the probability of presence of each variable in the model from the data. We used a Bernoulli (0.5) prior distribution for all these binary coefficients.

Posterior distributions of all the parameters were obtained by Monte Carlo Markov Chain (MCMC) simulations. We ran four chains for an initial period of 1000 cycles (burn-in period) and then collected information for the next 100,000 iterations with a thinning of 10. We implemented the MCMC simulations with the JAGS software (Plummer et al., 2006) operating in the R software (R Development Core Team, 2017).

From our analyses, we could (i) identify those variables with the largest influence on the resulting number of animals culled and calculate the posterior probability p_j that each variable x_i^j belongs to the best model ($\gamma_j = 1$); (ii) identify the best models predicting the number of animals culled and calculate the posterior probability $P(\gamma_1, \gamma_2, \gamma_K)$, for each possible combination of the coefficients ($\gamma_1, \gamma_2, \gamma_K$) that the corresponding model is the best model. We checked the mixing properties of the MCMC by verifying that the posterior probabilities estimated for the coefficients γ_j were identical across the three chains.

Because we expected saturation effects in the relationship between the effort variables and the resulting hunting pressure, we tested the possibility of nonlinear effects of effort variables on the hunting pressure by including both a linear effect and a quadratic effect of the selected numeric (i.e. not categorical) variables in our model. We examined the 90% credible interval (CI) on the coefficients associated with the quadratic effect to determine if we should include a saturation effects in the relationship between the identified effort variables and the resulting hunting pressure (i.e. when these CI did not include 0). Once the final model was selected, we computed an estimation of the parameters of these variables according to our Bayesian model of multiple regression in log Poisson.

3. Results

The model including the variables "Number of posted hunters", "Perimeter", and "Month" was considered as the most probable combination (Table 2), with one chance out of two to be the true model explaining the hunting pressure. This combination was twice as probable as the second most probable combination of variables ("Number of posted hunters" and "Perimeter").

Table 2
Posterior probabilities of the six most likely models relating the hunting effort variables to the hunting pressure on wild boar during the drive hunts carried out in the Chateauvillain/Arc-en-Barrois forest (France), identified by our variable selection procedure (Kuo and Mallick, 1998).

Model structure	Posterior model probability
Month + Number of posted hunters + Perimeter	0.42
Number of posted hunters + Perimeter	0.25
Month + Number of posted hunters	0.15
Number of posted hunters	0.06
Month + Perimeter	0.02
Month + Moment of the day (morning or afternoon) + Number of posted hunters + Perimeter	0.01

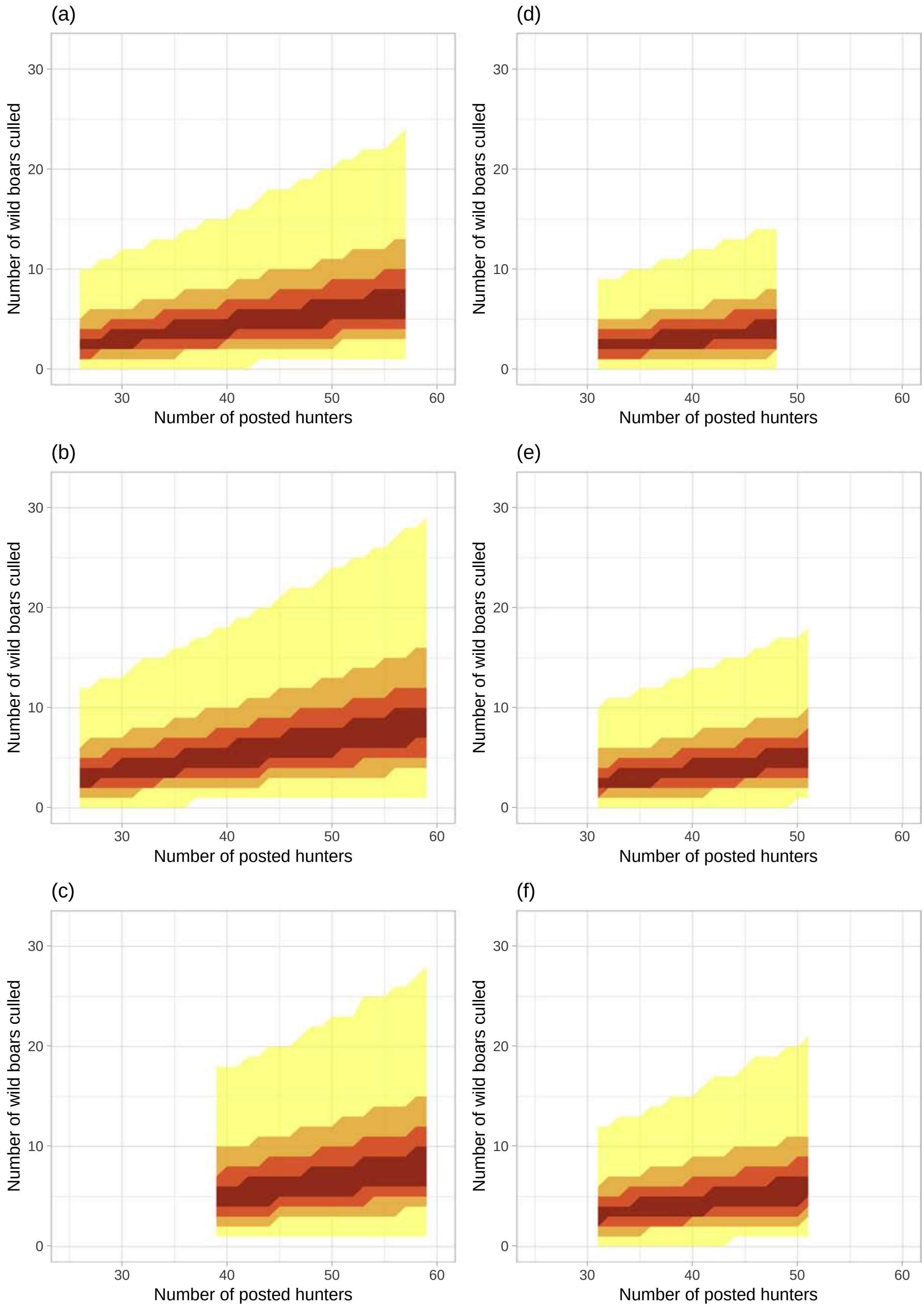
The goodness of fit of our model was good (R = 0.43). All parameters had a 90% credible interval differing from 0 (Table 3). Two variables "Number of hunters" and "Perimeter" have positive coefficients, indicating an increase in hunting pressure when these variables increased (Table 3; Fig. 2). In contrast, the variable "Month" showed an opposite trend, with a negative coefficient, indicating that for a given number of hunters and a given hunted perimeter, the hunting pressure decreased in February in comparison with the previous months (Table 3; Fig. 2).

The number of posted hunters was the most influential variable on the number of culled wild boar. For example, before February, on a small area (Fig. 2a), 26 posted hunters could expect to cull between 2 and 4 wild boar, whereas 57 hunters could expect to cull 6 to 9 animals, corresponding to an increase from +125% to +200%. A similar conclusion could be drawn for the two other variables: "Month" and "Perimeter". Indeed, before February, 57 posted hunters could expect to cull between 6 and 9 wild boar on a small perimeter, vs. 8 to 11 on large perimeters, corresponding to an increase from +22% to +33% (Fig. 2a and c). Finally, the culling was weaker during February than the three months before: 48 posted hunters could expect the cull of 5 to 7 wild boar, before February, on a small perimeter vs. 3 to 5 during February on the same size perimeter, corresponding to an decrease from −28% to −40% (Fig. 2a and d).

We fitted again the model identified by our variable selection procedure, but this time, including quadratic effects to account for a possible saturation of the effects of the identified variables. The 90% credible intervals on the coefficients associated with quadratic effects included value 0 for all numeric variables (Number of posted hunters: [−1.78; 2.61]; Perimeter: [−1.51; 0.14]). Thus, no saturation effect was observed either in the relationship between the number of posted hunters and the hunting pressure, or between the size of the perimeter and the hunting pressure. Within the range of values observed for all variables, the effect of the effort variables on the hunting pressure can be considered to be linear.

Table 3
Parameter estimates of the most probable model of hunting pressure on wild boar in the Chateauvillain/Arc-en-Barrois forest, as a function of hunting effort variables identified by Kuo and Mallick's (1998) variable selection approach. Posterior medians are provided along with 90% posterior credible intervals (i.e. intervals containing 90% of the simulated values).

Parameter	Median	90% Credible interval
Intercept	1.66	[1.57; 1.75]
Number of posted hunters	1.19	[0.62; 1.76]
Month	−0.36	[−0.58; −0.14]
Perimeter	0.76	[0.42; 1.11]
Error	0.73	[0.66; 0.80]


(a)
(b)
(c)
(d)
(e)
(f)
Number of wild boars culled
Number of posted hunters
0
10
20
30
40
50
60

4. Discussion

The number of posted hunters, the size of the hunting area and the hunting season period were central to explain hunting pressure. Thus, for a given month, the best metrics of the hunting effort carried out during a given drive hunt are a combination of the number of posted hunters and the surface unit of hunted area (Table 4). Our predictive model proposes a clear and simple result that relates a measurable hunting effort to a quantity of individuals that one can cull. To cull more wild boar, one must increase the hunting effort by increasing the number of posted hunters during a hunt, and by selecting larger or more hunting areas (i.e., increasing the hunting size area). Our results have a direct application for local managers to modify hunting effort on the wild boar population to expect reaching the low limit of imposed quotas (i.e. number of wild boar to be culled).

Hunters can opt for a group strategy by increasing their hunting effort by the strength of numbers, similarly to predators which improve their hunting success by forming pack (Mech, 1970; Schaller, 1972). In our study, the number of posted hunters was the best explanatory variable of the number of wild boar culled. This result can be explained by the simple fact that with the increase in the number of posted hunters, there will be an increase in the number of rifles and therefore an increase in the chances of culling wild boar, whether alone or in a herd. This is congruent with previous studies that showed a similar effect of hunting effort, including the number of hunters in a hunting game (Diekert et al., 2016), on hunted populations (Goudreault and Milette, 1999; Grau and Grau, 1980; Rivrud et al., 2014). Moreover, our results show an absence of saturation effect of the number of posted hunters, which means that if we want to kill more wild boar on a management area, we can simply invest more hunting effort.

Hunters can also exploit wild boar flight behaviors to improve their chances of culling them by flushing them out of hunting areas (example of human disturbance effect: Frid and Dill (2002)), and thus increase the probability of detecting them (Lima and Dill, 1990). This is, in theory, the central role of dogs and beaters. Interestingly however, the number of beaters and the number of dogs did not appear to explain hunting pressure in our study, whether for dogs (Caley and Ottley, 1995; McIlroy and Saillard, 1989) or beaters (Scillitani et al., 2010). Firstly, our data were fairly homogeneous. In 50% of the cases, the beaters came with exactly 15 dogs. Secondly, we did not have a dogless or beaterless hunting scenario that would have allowed us to model the dog or beater effect in a presence/absence framework, possibly more contrasting. In addition, the number of beaters and dogs could quickly see their effectiveness saturated (Caley and Ottley, 1995; Scillitani et al., 2010). For example, if dogs can saturate after only three encounters with wild boar during a hunt, they would be more effective in capturing wild boar on small populations and on solitary individuals (Caley and Ottley, 1995; Cruz et al., 2005; McIlroy and Saillard, 1989). In addition, the structure of the habitat, and particularly the dense bramble cover, can hamper the progress of both dogs and beaters (Acevedo et al., 2009), making it difficult to flush out the wild boar (Mysterud and Østbye, 1999). It has been shown that landscape structure can modulate non-lethal disturbance effects on wild boar space-use (Fattebert et al., 2017). Indeed, our study area is composed of mixed habitat types, like bush or coppice, that provide protection to wild boar (Mysterud and Østbye, 1999). Finally, dogs were not used to pursue wild boar for hours on our study area. Dogs were merely auxiliaries for flushing wild boar out of bushes. Thus, hunters used short-legged hounds (terrier breeds and russel breeds). Furthermore, the races and the lack of specialized education could decrease their effectiveness in detecting wild boar (Dahlgren et al., 2012).

Table 4
Grouping the different predictions on the hunting effort variables explaining the hunting effort associated with their results according to our model.

Predictions	Results
The number of posted hunters is the main determinant of the hunting pressure	Positive effect of the number of posted hunters
No effect of the number of dogs on the number of animals culled	No effect found
No effect of the number of beaters on the number of animals culled	No effect found
The number of animals culled is higher in larger hunting area (i.e. perimeter of hunting area)	Positive effect of the size of the hunting area
No difference between hunting in the morning or afternoon on the number of animals culled	No difference found on the number of animals culled of wild boar
The number of animals culled is harder at the end of the hunting season	Negative effect of the month of February on the number of animals culled

The number of culled wild boar depends on the ability of hunters to shoot several individuals as they try to escape from the hunted area (depending on their experience, Doerr et al., 2001; Rivrud et al., 2014). Although we do not have access to data of ability (such as the ratio number of shots/number of animals culled), this could explain the effect of the size of the hunting area in addition to the number of posted hunters, even though these two variables are not totally independent. Indeed, hunting on a larger territory offers more chances to include more solitary individuals and groups of wild boar, and therefore offers a higher probability to shoot a wild boar. This is in accordance with Jensen et al. (2017) who showed a greater probability of occurrence of geese in large fields because they have a greater chance of attracting more geese. Before the hunt, the manager has the choice of the forest that he wants to hunt. Thus, by allocating larger or smaller plots, the manager can modulate the cull.

Hunting managers set the amount of drive hunts organized in the morning or afternoon, for different hunting parcels. Grau and Grau (1980) documented differences in deer cull between morning and afternoon and showed a greater difficulty in culling in the morning. In the morning, deer being more active than in the afternoon, they would be more vigilant and more able to respond quickly to a hunting event. In our study, we did not find any differences, given equal hunting efforts, between morning and afternoon hunting pressure. Unlike deer, wild boar are nocturnal (Boitani et al., 1995) and are inactive during the day (i.e. during hunting hours, between 8:00 and 17:00) (Keuling et al., 2008). We can therefore assume that there are no differences in behavioral vigilance depending on the time of the day in wild boar, which could have resulted in a different vulnerability according to the time of day. In other words, this means that within the same hunting day, one drive hunt equals another in our study.

However, the catchability of animals is not constant throughout the hunting season. For a given hunting effort, February was characterized by a lower hunting pressure than the months before February. This is congruent with studies on deer hunting where there were less opportunities for shooting a deer as the hunting season progressed (Grau and Grau, 1980), and a decrease in the number of catches with the accumulation of hunting days (i.e with the progress

Fig. 2. Prediction of the number of wild boar culled as a function of the number of surrounding hunters in 6 different cases: before (a, b, c) or during the month of February (d, e, f) – two columns; we defined three classes of perimeter size, small (a, d), medium (b, e) and large (c, f) hunted area (see Material and Methods for more details on these sizes) – three rows. For each case, the prediction of the hunting pressure (number of wild boar culled) was carried out for the range of observed number of posted hunters in our dataset (e.g. this range is [39; 59] in case (c)). The dark red areas in the figure represent the areas delimited by the 20% credible interval on the predicted number of animals culled. The other colors of the gradient represent respectively the 40% (light red areas), 60% (orange areas) and 90% (yellow areas) credible intervals on the predicted number of animals culled. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of hunting season, Rivrud et al., 2014). This was possibly driven by a decrease of animals' availability in the environment over time (Creel and Christianson, 2008), or learning by the animals (Lima and Bednekoff, 1999; Thurfjell et al., 2017). However, in our case, hunting pressure did not seem to be gradually decreasing over time, but specifically and suddenly decreased in February. This could result from management decisions once the minimum quota is reached, when shooting instructions are imposed at the end of the season in order to preserve the wild boar population (shared point of view with Rivrud et al., 2014).

In our study, we did not consider the effect of habitat or weather on catchability, which could affect how a given hunting effort translates into hunting pressure (Acevedo et al., 2006; Rivrud et al., 2014) through dogs' effectiveness (Conover, 2007; Gutzwiller, 1990; Shivik, 2002), either by affecting the hunters themselves (Curtis, 1971), or wild boar behavior (Thurfjell et al., 2014). Also, hunters' motivations to hunt (recreation, management, (Dalerum and Swanepoel, 2017)) or what drives them to maintain a high-hunting effort, whether during a hunting day or during the season, needs to be explored as it could explain parts of the variation of wild boar cull (Curtis, 1971; Rivrud et al., 2014; Stedman et al., 2004). Studying the hunting effort in different contexts could allow us to improve our understanding of hunting, and optimize the effort to reach management goals.

Our study allowed us to get practical information in order to be more efficient in wild boar culling in a context of general increase of wild boar populations in France (Massei et al., 2015). We found empirical evidence that hunting effort explains the hunting pressure, which can be easily quantified and reduced directly to a number of individuals culled in the context of hunting by quota. Moreover, our work responds to a pressing social (Keuling et al., 2016; Liordos et al., 2017) and administrative demand in the context of the African swine fever epidemic (Podgórski and Śmietanka, 2018). Indeed, one current management goal is the creation of a depopulated area close to the Belgian boundary, i.e. the complete destruction of the wild boar population to create a buffer to avoid the propagation of the African swine fever in France, for which large means are currently being deployed. To reach this goal, managers now have the quantitative tools to manipulate the hunting effort by increasing the number of hunters involved, hunting over large areas, and preferably in the early part of the hunting season, before February.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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