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Catch-effort model used as a management tool in exploited populations: Wild boar as a case study

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ABSTRACT

For sustainable management of exploited populations, it is required to have good knowledge on temporal trends in population density to adapt the harvest. In this regard, hunting statistics are often collected routinely by government agencies and associations. These data are used to assess demographic trends through the development of indices, which are in turn used to manage exploited populations in a sustainable way. However, these population indices depend on features of the hunting process (e.g. hunting effort, hunting conditions, probability of catch). In this study, we show how to use hunting logs to assess demographic trends in exploited populations while accounting for the components of the hunting process. In particular, we developed a catch-effort model to study how the hunting effort leads to mortality rate – hunting pressure – within a given habitat type and during a given period. We illustrated the usefulness of this approach using exploited wild boar (*Sus scrofa*) populations as a case study. We used a large hunting logs dataset to perform our study, with several hundreds of thousands hunting events for more than 10 years in two French departments in France, including information about the number of hunters, of wild boars culled and the date of the hunt. We showed that catchability is a key parameter to assess hunting pressure at a given time and place. This parameter varies both within the hunting season and between habitat types. Once this variation in catchability was accounted for, our catch-effort model allowed us to obtain estimates of relative densities of wild boar populations over the study period at the management unit scale. Thus, catch-effort models are powerful tools to assess population density and to understand the underlying hunting process. Our study offers straightforward and reproducible conceptual framework that can be applied routinely by wildlife managers on exploited populations and practitioners from hunting statistics logs.

1. Introduction

Sustainable management of exploited animal populations requires good knowledge about the temporal trends in population size (Milner-Gulland and Mace, 1998; Nichols et al., 2007). Therefore, a large amount of research on wildlife management has been devoted to the development of tools for this monitoring (Nichols and Williams, 2006). Scientists and managers have implemented a wide diversity of population monitoring tools, from complex methods to estimate population dynamic parameters from individual long-term data (e.g. mortality rate, population size, Clutton-Brock and Sheldon, 2010) to simpler population indices such as indicators of ecological change (Morellet et al.,

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2007). However, data required by these monitoring approaches are often costly in terms of money and staff (Lieury et al., 2017). Cheaper data sources can however be used, e.g. data collected within the framework of citizen science or participatory research (where data are collected by stakeholders, Isaac et al., 2014; Paul et al., 2014). In particular, harvest data collected routinely and systematically by hunter associations in many countries is an easily accessible source of data for the monitoring of game species. Such data gathers a large amount of information on the population, in particular the number of individuals culled (or hunting bag), as well as on the hunting process such as hunting date, location, number of hunters, duration of the hunting session, etc. (Brøseth and Pedersen, 2000; Rist et al., 2008; Vajas et al., 2020). Such data can be used to assess population trends (Roseberry and Woolf, 1991; Maunder et al., 2006; Imperio et al., 2010) through the analysis of the number of animals removed from the population by the harvest (Schnute, 1983; Walters, 2003).

Efficient use of harvest data to monitor population trends requires a good understanding of the hunting process leading to culling. At first, a catch and a kill of a prey result from an invested effort by a predator (Creel and Christianson, 2008; Curio, 1976). In the context of hunter-wildlife interaction, the hunting effort (i.e. the set of labors implemented by the hunters to practice their activity, Vajas et al., 2020) translates to a certain hunting pressure (i.e. mortality rate exerted by hunting, see Vajas et al., 2020). The hunting effort is commonly used to standardize the hunting bag and estimate population abundance through simple indices (e.g. Capture Per Unit Effort methods, Seber, 1986; Bishir and Lancia, 1996). However, this relationship assumes a proportionality between the number of individuals caught and the population size, and ignores that catch probabilities depend on hunting conditions (Lewis and Farrar, 1968; Maunder et al., 2006). This assumption may have dramatic effects. Indeed, in fisheries, assuming proportionality between local catch rate and abundance gives unsuitable results driving to population overexploitation (Walters, 2003) because a constant or increasing catch rate may result from an increasing harvest effort and/or from differential probability of catching individuals over time and space. Simply considering catch rate may thus hide a dramatic decrease in population size (Arreguín-Sánchez, 1996; Marchal et al., 2003; Walters, 2003). Therefore, catchability, that is the ability to catch an individual in a given area during a given period independently of population size and hunting effort (Laurec and Le Guen, 1981), appears as a key parameter, that needs to be take into account, in the harvesting system (Arreguín-Sánchez, 1996). Catchability depends on hunting conditions and can vary in time and space (Salthaug and Aanes, 2003; Wilberg et al., 2010). Variation in accessibility to the hunting area (Lebel et al., 2012; Wszola et al., 2019), weather conditions (Rivrud et al., 2014), visibility, hunterś skills during the hunting season (Hilborn, 1985; Diekert et al., 2016; Vajas et al., 2020) can lead to variation in catchability itself. Consequently, the catch of an animal results from hunting effort invested by hunters, catchability (depending on hunting conditions) and population size. Understanding all these components is essential to understand the hunting system, and thus provide relevant management tools.

Here, we developed a catch-effort model linking catchability, population density, hunting effort, hunting pressure, and hunting bag. This model relies on the decrease in the number of individuals removed over the hunting season, for a given hunting effort, resulting from an increasing complexity to cull individuals in a shrinking population. To build this model and obtain estimates of catchability depending on hunting conditions, we used hunting logs. The latter includes information about the hunting effort (number of hunters participating to the hunt), the hunting bag (number of culled individuals), the date, and the hunting place. We illustrated the usefulness of our catch-effort model using hunting logs collected on wild boar (*Sus scrofa*) in France. Wild boar is a species with strong societal concern since it has increased in Europe (Massei et al., 2015), leading to damage to crops (Calenge et al., 2004; Schley et al., 2008; Amici et al., 2012), to forest production (Gómez and Hódar, 2008; Barrios-Garcia and Ballari, 2012; Burrascano et al., 2015), and to zoonoses transmission (e.g. African swine fever, Podgórski and Śmietanka, 2018). Our main goal is to gain a good understanding of the hunting process in order to provide relevant management tools. In this collaborative framework built with hunter associations in contrasting areas in France, harvest data has been collected for many years, allowing us to compare the usefulness of our model under various hunting conditions. We developed a Bayesian catch-effort model to assess the demographic status of wild boar populations, and to estimate hunting pressure as a function of the hunting effort (measured as the number of hunters participating to the hunt during a given day) and of catchability, varying according to the habitat type in the hunting area and the time of the hunt within the hunting season.

2. Material & methods

2.1. Study areas

Data comes from two contrasting French administrative departments located in the South-East of France: Ardèche and Hérault (Fig. 1). The Ardèche department is made up by three major biogeoclimatic areas: the north, with low altitude (between 350 and 850 m), temperate climate (rare snow in winter) and mixed forests (mixture of hardwood with holm oak, beech and conifer); the western part, a plateau of medium altitude (around 1000 m) – the foothills of Cevennes mountain- with rough winter (until −20 °C) and coniferous forest (and few chestnut); and the southern part characterized by Mediterranean climate (hot and dry climate) with a scrubland vegetation composed of green oak and chestnut.

The Hérault department goes from the Mediterranean Sea with low altitude to Cevennes mountains with medium altitude (until around 1100 m). This department is characterized by Mediterranean climate with a temperate continental influence in mountainous areas. Precipitations are rare but abundant during the so-called Cévenol episode. From the north-west to the south-east, the landscape changes from the Cevennes mountains composed by coniferous and chestnut grove at medium altitude, to zones of scrubland characterized by green oak, and then to low plains, characterized by vineyards on the seafront of Mediterranean.

Regarding game wildlife management, each department is divided into Management Units (MU). MUs are defined as homogeneous areas in terms of habitat, topography, hunting activities, and crops (Maillard et al., 1999). The Ardèche department was divided into 28 MU of 172 $km^2 \pm 724$ km^2 and the Hérault department was divided into 23 MU of 206 $km^2 \pm 139$ km^2. Each MU can be managed independently of each other. Each hunting team must follow the management recommendations of the MU they belong to.

2.2. Hunting process and hunters' logbook

The hunting season generally starts from the beginning of September to the end of February, although these dates may change by prefectural decrees. Drive hunting is the most popular practice in these two departments. Drive hunting involves dogs and beaters causing the flushing of animals from the hunting ground and making them accessible to the posted hunters located around this hunting area. It differs from the drive hunt in the North-East of France (Vajas et al., 2020): movements of beaters and dogs are less linear due to a bushier vegetation, they use long-legged dogs, and beaters are armed. The hunters are located in the most strategic places considering that the hunting ground could be huge.

The hunter associations collected, through a computerized proceed, the hunting logs filled by hunting teams from 2006 to 2016 in Ardèche department (11 hunting seasons) and from 2005 to 2016 (12 hunting seasons) in Hérault department. Thus, in the two departments, hunting notebooks have been given to each hunting team at the beginning of

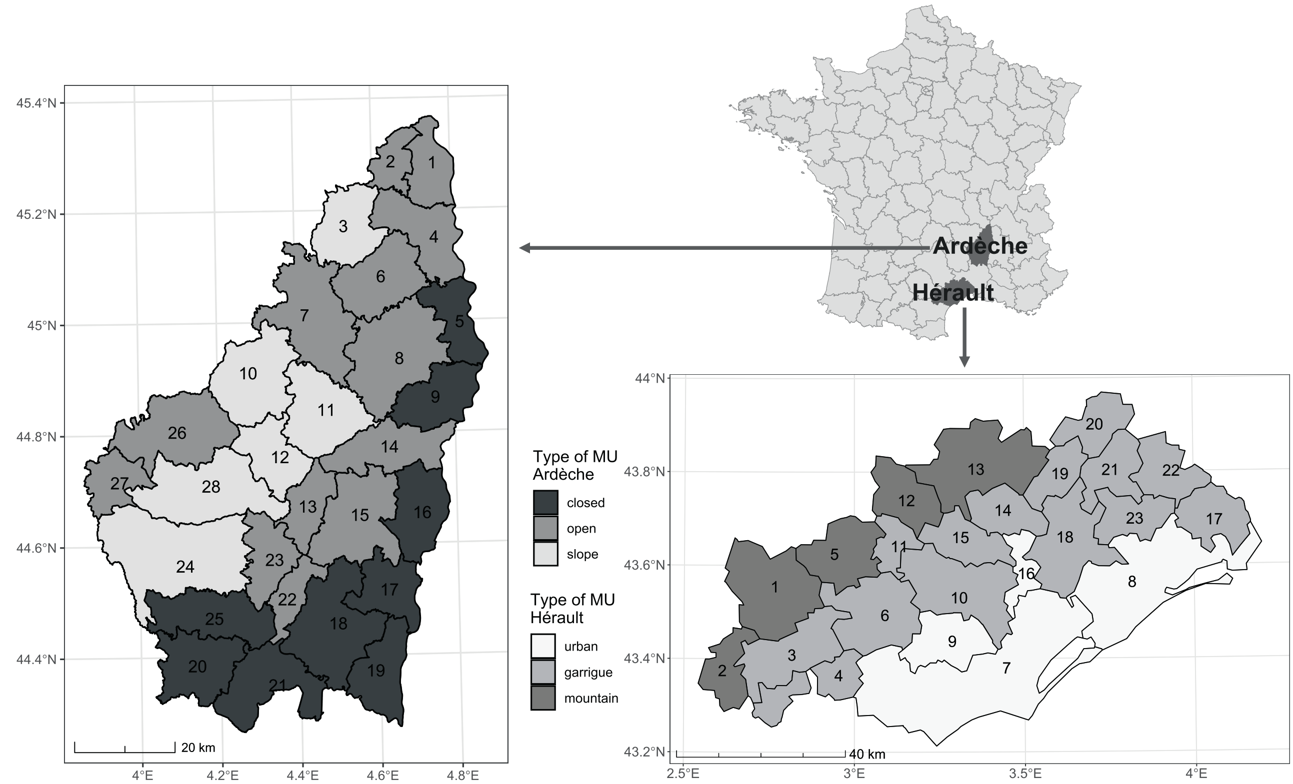

Fig. 1. Location of the two study areas in France, Ardèche and Hérault.

each hunting season. Then, data from logbooks has been stored in a database after some data cleaning and data checking by the Departmental associations of hunters. These notebooks report for each hunting drive, the number of hunters participating to the drive, its date, the name of the person in charge of the organization, the municipality, as well as the start and the end times of the hunting event and the number of culled wild boars. For each day of the hunting season and each MU, we summed the total number of hunters participating to a drive hunt, as well as the resulting number of culled wild boars. Note that we discarded two MU of the Hérault department due to missing data (table 1).

2.3. Catchability definition

Catchability is the ability to capture an individual in a given area during a given period, independently of the population density and of the hunting effort carried out by the hunters. Catchability thus varies over space and time. With the help of local managers of departmental association of hunters, we grouped the MUs in several territory types based on very specific criteria of accessibility, practicability and visibility (Fig. 1). The question asked to them was: *“In your opinion, if we imagine a homogeneous density of wild boars over the whole department (*i.e. *identical for all MUs), could you group MUs into clusters of MUs where a given hunting effort would result in a similar hunting bag? Or, in other words, could you pool together MUs in clusters characterized by a similar difficulty to cull the wild boar (accounting for terrain ruggedness, vegetation, visibility and accessibility)?”*. Thus, the local managers of the Ardèche department as well as the Hérault department have each defined three major territory types. Concerning the department of Ardèche these types are: ”closed“ territory type with a dense vegetation (holm oaks forests), low visibility, and a difficulty in progressing in the territory; “open” territory

Table 1
Data used in the catch-effort model implemented from the hunting logs in Ardèche and Hérault. Displayed are qualitative data and quantitative data.

	Ardèche		Hérault	
Qualitative data				
	Total number		Total number	
Number of Management Unity (or MU)	28		21 out of 23 (MUs #16 & #17 removed)	
Number of hunting seasons	11 from 2006 to 2016		12 from 2005 to 2016	
Number of months	6 per season from September to February		6 per season from September to February	
Number of drive hunt events	210,395 (sum)		165,572 (sum)	
Number of wild boars culled (hunting bag)	170,791 (sum)		147,112 (sum)	
Number of (unique) hunting-days per MU-season-month	28,573 (sum)		18,615 (sum)	
Quantitative data				
	Mean ± SD (per drive hunt)	Range [min–max]	Mean ± SD (per drive hunt)	Range [min–max]
Number of hunters	12.5 ± 6.2	[2–99]	18.8 ± 8.5	[3–99]
Numbers of wild boars culled	0.81 ± 1.40	[0–50]	0.90 ± 1.60	[0–25]
Forest sizes by MU	172.55 ± 72.494 (km^2)	[82.48–379.63] (km^2)	206.55 ± 139.13 (km^2)	[41.80–705.14] (km^2)

type with better visibility and better progression (mixed deciduous forests); and “slope” territory type with better visibility and difficulty of progress in the territory (corresponding to the Cevennes territories with coniferous forests). Concerning the department of Hérault these territory types are: “urban” territory type close to urban areas, easy to access but with which hunting must deal with other human activities; ”garrigue“ territory type composed of dense vegetation (Mediterranean scrubland), low visibility, difficulty in progressing in the territory; and finally ”mountain“ territory type with a difficulty of progress for hunters (this is the South of the Cevennes).

We therefore considered that catchability varied across the different MUs according to their territory types. We also supposed that catchability can vary over time, because the hunters and dogs generally gain in experience as the hunting season progresses, and because the vegetation and weather and therefore hunting conditions change with the onset of winter. We therefore considered that the catchability varied between the different months of the hunting season from September to February, but remained constant within one month, making possible to account for changes in catchability over time with a reduced number of parameters in the model.

2.4. Catch-effort model

Catch-effort models allow modelling the relationship between the different components of the hunters/population system, and in particular, between the hunting effort invested by the hunters and the resulting hunting pressure applied on the population (Fig. 2). Consider a given management unit u belonging to the catchability group g, a given hunting season s, and a given hunting day I belonging to the month m (September, October, etc.). Let H_{usi} be the known hunting effort applied by the hunters of the whole MU u during the i-th hunting day of the season s (here measured by the total number of hunters participating to a drive in this unit this day). Let $\overline{P}_{usi}$ be the unknown expected resulting hunting pressure (i.e., the proportion of animals in the units that are culled by the drive hunt). At the core of the catch-effort model, we suppose the following relationship between the expected hunting effort and the hunting pressure:

$$\overline{P}_{usi} = 1 - exp(-\gamma_{gm} H_{usi}) \tag{1}$$

with γ_{gm} the unknown (and therefore to be estimated) catchability of the wild boar in the catchability group g during the month m. Thus, the catchability is a central parameter which allows to translate the effort

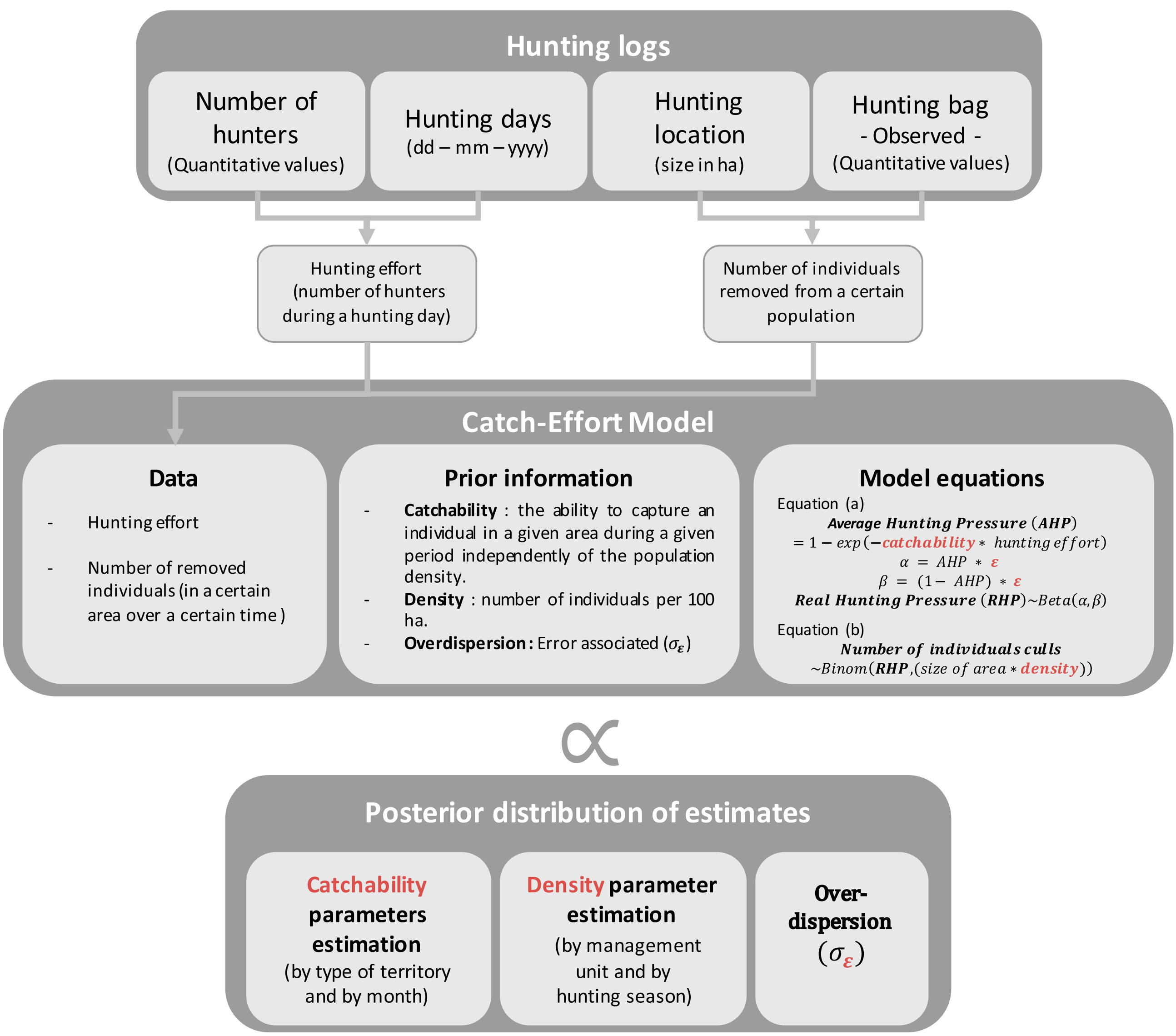

Fig. 2. Conceptual framework of the catch-effort model divided in three blocks. Upper block: data used int the catch-effort model; Middle block, catch-effort model; Lower block: posterior distribution of the parameter values.

(the cause) into a pressure (the effect of the hunt, i.e. the consequence). It measures the efficiency of the hunt in a given catchability group during a given month.

However, the actual hunting pressure during a given hunt can be more variable than the value expected under this model because the specific conditions of the hunt may vary in a way not accounted for by our model (other factors than those accounted in our model may lead to a more or less efficient hunting effort, e.g. variable composition of the hunting team, weather, etc.). We therefore supposed that the actual hunting pressure during a given day could be described by a beta distribution of the first kind with a mean corresponding to the expected hunting pressure $\overline{P}_{usi}$. This is indeed a very commonly used distribution to model probabilities and proportions in ecology, as it can have quite different shapes and accounts for the fact that probabilities must be comprised between 0 and 1 (see Ferrari and Cribari-Neto, 2004). More precisely, we supposed that the actual hunting pressure P_{usi} applied on the population of the unit u during the day I of the season s was a random variable drawn from a beta distribution:

$$P_{usi} \sim \text{beta}(\alpha_{usi}, \beta_{usi}) \tag{2}$$

Parameter α_{usi} and β_{usi} were derived from the expected hunting pressure $\overline{P}_{usi}$, with $\alpha_{usi} = \overline{P}_{usi} \times \varphi$, and $\beta_{usi} = (1\text{-}\overline{P}_{usi}) \times \varphi$, where φ is a dispersion parameter. Ferrari and Cribari-Neto (2004) demonstrated that this parameterization ensures that in these conditions, $\overline{P}_{usi}$ is a random variable with mean $\overline{P}_{usi}$ and variance $(\overline{P}_{usi} \times (1\text{-}\overline{P}_{usi})) / (\varphi + 1)$. This model describes the relationship between the hunting effort, the catchability, and the resulting actual hunting pressure during a given hunting day in a given management unit MU.

Now we describe how this general model can be fitted to our dataset. Let D_{us} be the unknown average wild boar density in the management unit u just before the beginning of the hunting season s and A_u the area of this unit. The population size N_{us} in this unit at the beginning of this hunting season can be calculated by $N_{us} = D_{us} \times A_u$. Consider the first hunting day $i = 1$ of this hunting season. C_{usi} is the number of animals that have been culled during this day. Under our model, this number is supposed to be drawn from a binomial distribution parameterized by the number of available animals N_{us} at the beginning of the day and the actual of cull – the actual hunting pressure – P_{us1}:

$$C_{us1} \sim \text{Binomial}(N_{us}, P_{us1}) \tag{3}$$

The binomial distribution is indeed the most suitable distribution to model a number of successes (the number of cull) out of a number of experiments (total number of available animals). At the end of the day, the population size in this unit is therefore reduced, and equal to $N_{us} - C_{us1}$. Similarly, on the second hunting day of this season in this unit, the cull is supposed to be equal to:

$$C_{us2} \sim \text{Binomial}(N_{us} - C_{us1}, P_{us2}) \tag{4}$$

And again, at the end of the day, the population size is reduced, and equal to $N_{us} - C_{us1} - C_{us2}$. More generally, on the day I the cull is supposed to be equal to:

$$C_{usi} \sim \text{Binomial}\left(N_{us} - \sum_{j=1}^{i-1} C_{usj}, P_{usi}\right) \tag{5}$$

Note that this model supposes that the only source of mortality during the hunting season is caused by hunting, which is not a stringent assumption for the species (Toïgo et al., 2008; Gamelon et al., 2012; Keuling et al., 2013). We know from the logbooks both the hunting effort H_{usi} that has been applied by the hunters of the unit u during the day I of the season s (which is used to calculate the hunting pressure), and the response variable C_{usi} corresponding to the number of animals that have been culled during this day in this unit. The unknown parameters in this model are the catchabilities γ_{gm} for each catchability group g and each month m, the dispersion parameter φ for the beta distribution of actual hunting pressures, and the initial population density D_{us} for the U units $\times$ S hunting seasons of interest. Note that the greater the decrease in initial abundance, the more precise the posterior estimate of the parameters (Chee and Wintle, 2010).

We used a Bayesian estimation approach to estimate these parameters. Based on a preliminary sensitivity analysis of this model to the definition of the prior distributions of these parameters, we realized that the results were highly sensitive to the definition of the prior on initial population density. We used a vague uniform prior distribution for the densities, bounded on [0, d_{max}], where d_{max} is the maximum possible attainable density in the departments (i.e. carrying capacity). It may be difficult to set a maximum possible density of wild boars, especially as large variation in their densities from 0.01 to several tens of wild boars per km^2 are reported in the literature in Europe (Melis et al., 2006; Acevedo et al., 2007; Fonseca et al., 2007; Hebeisen et al., 2008; Franzetti et al., 2012). Thus, we first defined $d_{max} = 30$ wild boar per km^2 as the maximum possible attainable wild boar density in the two departments, which seems reasonable given the densities reported elsewhere. To study the impact of this prior, we also tried to fit our model with the extreme – and unrealistic – value $d_{max} = 100$ wild boar per km^2. This allowed to give an idea of the sensitivity of the results of our model to this parameter, and thereby to give rules of interpretation of this fit.

We fitted this model for each department (Ardèche and Hérault) independently. We fitted these two models by Markov Chain Monte Carlo (MCMC) with the JAGS software (Plummer, 2010) implemented in R software (R Development Core Team, 2017), using 4 chains of 100,000 iterations thin 50, for a total of 8000 iterations saved. For each model, we checked the mixing properties of the chains both visually and using the diagnostic of Gelman and Rubin (1992).

We checked the goodness of fit of our models, using the approach recommended by Gelman and Meng (1996). For each department, each MCMC iteration generated a sampled vector of parameters (dispersion parameter, initial densities and catchabilities). For each simulated vector, we simulated a replication of the dataset for the department (i.e. we simulated a number of culled animals for each hunting day of our dataset). We then compared summary statistics calculated on the observed datasets to the distribution of these summary statistics calculated on the simulated datasets for model validation. More specifically, we used as summary statistics the total number of culled animals predicted by the model: over the whole department; per MU; per MU and per hunting season; per MU, hunting season and month; per MU and month; per month, per season. The R code for fitting the model and the data are available at https://github.com/VajasPablo/catcheffortwb. This package can readily be installed in R with the package devtools, using the function devtools::install_github("VajasPablo/catcheffortwb ").

3. Results

3.1. Goodness of fit of the model

The approach of Gelman and Meng (1996) indicated an overall acceptable fit for our model. The observed total number of culled animals predicted by the model was in the 90% credible interval for both the Ardèche department (obs. = 170,791, CI = [169,537 – 171,832]) and Hérault department (obs. = 147,112, CI = [145,919 – 148,105]). Moreover, for nearly all other criteria, the proportion of observed number of animals falling within the limits of the 90% credible interval was close to 90% (Table 2), suggesting a correct fit. Note that these checks indicated a small unaccounted overdispersion in our data when the culls were summed over all seasons per month and MU. However, even in this case, when it was not within the limits of the credible interval predicted from the simulated distribution, the observed number of culls was very close to this distribution (see Fig. 3, e.g. see october for the MU #3 in the Ardèche department).

Table 2
Goodness of fit values in percentage of the catch effort model according to the different study scales (rows) according to different ranges of credible interval (first column), for Ardèche (second column) and for Hérault (third column).

Scale	Credible Interval (%)	Ardèche (%)	Hérault (%)
MU	90	93	86
MU-season	90	98	97
MU-season-month	90	84	88
Month	90	83	83
MU-month	95	65	74
MU-month	100	82	95

3.2. Parameter estimation and informative priors

Catchability and density estimates were sensitive to the priors used for density. Indeed, the maximum values of the density distribution (or d_{max}) set either to 0.3 or to 1, led to different estimates of density and catchability. The relationship between initial densities and catchabilities in Ardèche and Hérault is shown in Fig. 4. However, the estimates obtained with different priors were highly correlated with each other. Regarding density, the Spearman correlation between estimates obtained with the two priors was equal to $Rho = 0.98$ and $Rho = 0.99$ for Ardèche and Hérault, respectively. The correlation between the two catchability estimates was also very high ($Rho = 0.67$ and $Rho = 0.94$ for Ardèche and Hérault, respectively).

3.3. Catchability estimates

Regarding Ardèche department, catchability was almost twice as large in the "open" territory type than in the "closed" and "slope" territory types, such as γ"open" > γ"closed" > γ"slope" (Fig. 5). The highest catchability occurred between December and January, and was twice as high as during the first month of hunting. Later, catchability was characterized by a sharp decline for the "open" territory type, by a lighter decrease in the "slope" territory type, and by a stabilization in the "closed" territory type. Taking the month into account, the catchability did not show any difference in February between "open" and "closed" territory types. Similarly, in January, we did not detect any difference between "closed" and "slope" territory types. In both cases, the 90% credible intervals on the difference between the catchability of the "closed" and "slope" MU, calculated from their MCMC distributions, contained 0 ("closed"-"slope" January CI on this difference: [-3.41×10^{-7} – 5.86×10^{-6}]; "open"-"closed" February CI: [-3.02×10^{-6} – 5.05×10^{-6}]).

Regarding Hérault department, catchability of "urban" territory type was twice as large as in the "closed" and "mountain" territory types, such as γ"urban" > γ"garrigue" > γ"mountain" (Fig. 5). The highest catchability occurred between December and February, and was twice as high as during the first month of hunting. In contrast to Ardèche department, there was no decline in catchability after December (i.e. we observed a stabilization of catchability). In all cases, the 90% credible intervals on the difference between the different catchability types, calculated from their MCMC distributions, do not contain the value 0 and, therefore, are different from each other.

3.4. Density estimates

We estimated relative densities of wild boars per MU and per hunting season. Thus, trends (not absolute values) in population density may be compared over time and space. Moreover, the trends can be compared among MUs, but not between the two departments since the two models have been fitted independently. As an example, density increased in some MUs like MU # 2 in Ardèche department and MU # 20 in Hérault department, respectively doubling and tripling the relative density, while this was not the case for others MUs like MU # 7 in Ardèche and MU # 6 in Hérault, remaining stable (Fig. 6). Overall, we found either an increase or a stabilization of wild boar density over time. Finally, the relative level of wild boar density may be compared between MUs of the same department. As an example, there were around 9 times more wild boars in MU # 22 than in MU # 7 in Ardèche, and about 3.5 times more wild boars in MU # 20 than in MU # 8 for Hérault (Fig. 6).

Population sizes increased in some MUs whereas they remained stable in others. In Ardèche, MUs characterized by habitats of mixed forests in the North and coniferous forests in the West (the Cévennes) had stable populations over the study period. In contrast, MUs characterized by deciduous forests with the presence of holm oaks had increasing populations. In Hérault, the MUs located in the Cévennes (North), in urban (South) and in the scrubland territories (East) had stable populations, whereas populations increased in MUs located in the scrubland characterized by holm oaks (East).

4. Discussion

Focusing on the scale of the hunting day allowed us to get additional and finest knowledge in comparison with most other studies using only hunting bags at the seasonal scale (Acevedo et al., 2014). Using hunting logs in our catch-effort modelling framework allowed us to estimate catchability parameters. They differed according to the territory types (e.g. "closed", "open", "mountain"), thus clearly demonstrating that they cannot be considered homogeneous among habitat types. Another important finding is that this framework allowed us to estimate hunting pressures at different locations (e.g. in "mountain" territory type), at any time during the hunting season (e.g. in December) according to the hunting effort. This approach also allowed us to assess the temporal trends in population size (i.e. increase, decrease, stable) during the hunting season. The trends observed indicated that not all management units (or MUs) followed the same demographic patterns, providing evidence that at a local scale, patterns might differ from the general trends documented in France and Europe concerning wild boar populations (Massei et al., 2015; Saint-Andrieux & Barboiron, 2018).

Despite the usefulness of this approach, it has some limitations. First, when hunting events are not frequent enough (e.g. 3–4 hunting events during one hunting season), the model cannot estimate correctly the parameters (e.g. MU # 16 of Hérault was removed from the dataset for this reason). Because catch-effort models are based on the decrease in the number of culls over time as a result of a decrease in the number of individuals in the population (see Chee and Wintle, 2010), the parameters of the model will be properly estimated if hunting events are frequent enough to grasp the demographic trends. Otherwise, the variance of the posterior distribution is large, and the estimated density is close to the maximum possible relative density (d_{max}) defined by the prior (see e.g. MU # 13 of Ardèche and MU # 9 of Hérault). This last point highlights the importance of *a priori* information in our study. In absence of information on the real density and of a marked reduction in the number of individuals, the priors are informative and reach the upper range of parameter values. Noticeably, modifying the values of the priors does not affect the relative relationships that exists between these estimates (Fig. 4), because the estimated values are not absolute, but relative. From a management viewpoint, this can bring important information on the trend in population size, but not on absolute density estimates. In our case study, the information from demographic trends alone is sufficient to manage wild boar populations. However, in other contexts, such as in epidemiology, absolute estimation of the population size may be necessary. In this case, our model allows a readjustment of d_{max} prior by adding specific density information. In the light of the catch-effort conceptual framework, our approach may be a useful tool both in the context of managing overabundant populations (Chee and Wintle, 2010; Barron et al., 2011; Bodenchuk, 2014), but also in the context of sustainable management (as for bushmeat context, Rist et al., 2010). Note however that it would be interesting to compare the density estimated by the catch-effort model with independent density estimates obtained using other estimation methods relying on different data (e.g.,

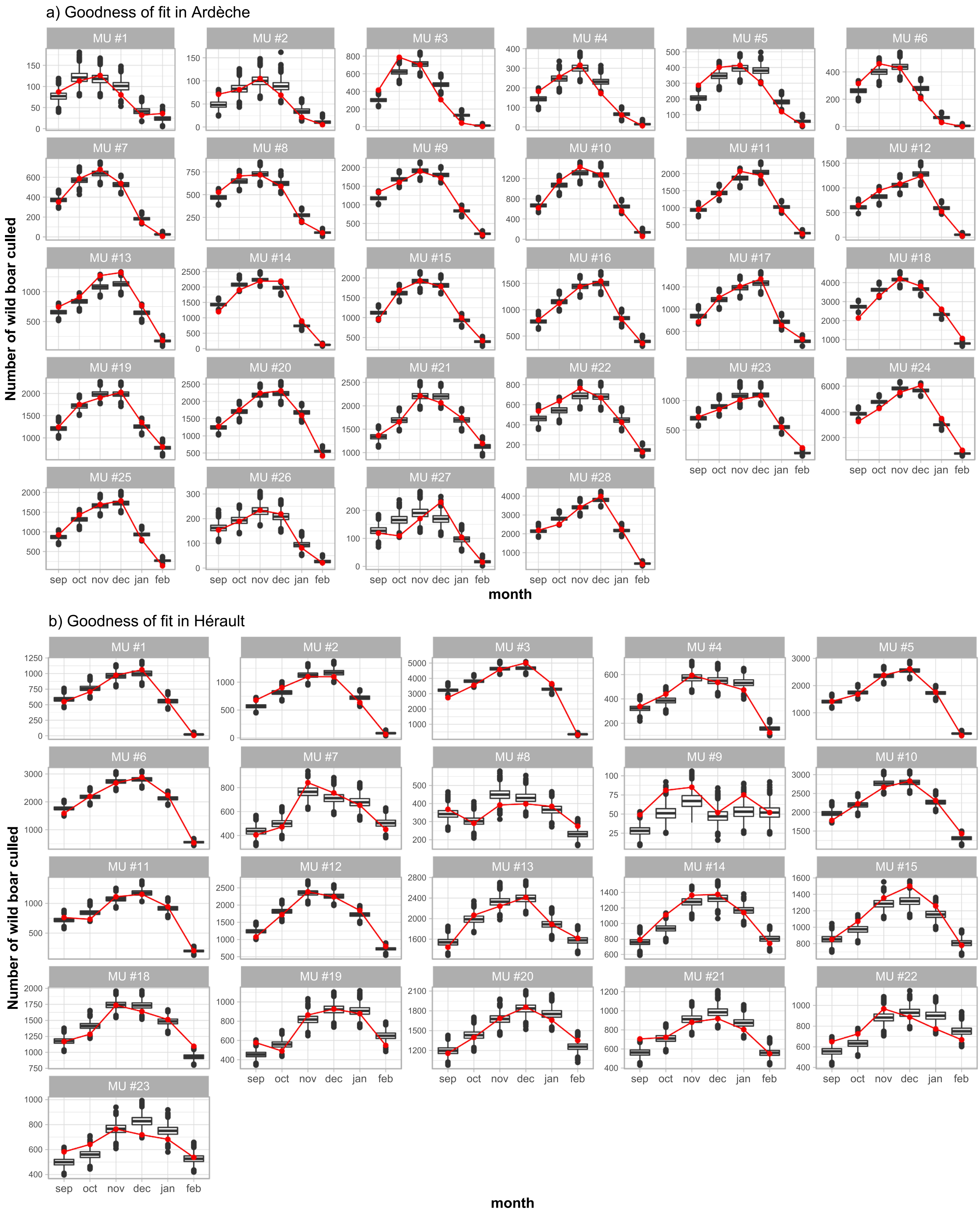

Fig. 3. Goodness of fit of the models fitted to describe the hunting process in a) the Ardèche department and b) the Hérault department. These figures show the total number of animals culled in a given management unit (MU) during a given month (in red – pooled over all hunting seasons of the study period) as well as the statistical distribution (boxplot) expected for this number by our model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

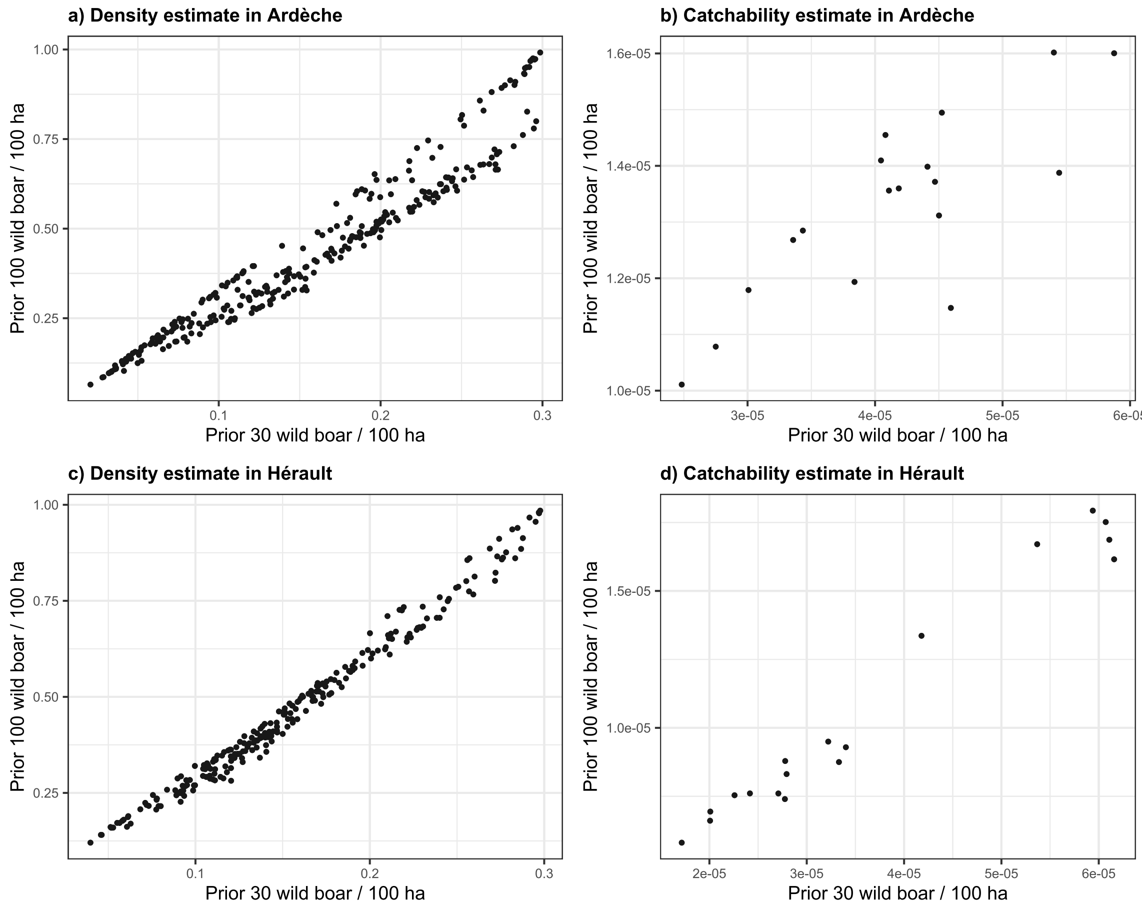

Fig. 4. Relationship between the estimates of the catch-effort models when two different uniform prior distributions were used for the initial density. Abscissa: estimates obtained when the prior distribution was bounded on [0, 30] wild boar/100 ha: ordinate: estimates obtained when the prior distribution was bounded on [0, 100] wild boar/100 ha.

capture/recapture methods). Such independent data were not available in our study, but this sort of comparison would provide an external validation of the catch-effort model as a management tool.

Our approach allows disentangling the harvest components, i.e. catchability, population size and hunting effort. A first element of catchability is the visibility (i.e. detection of game species, Brinkman et al., 2009; Lebel et al., 2012). In our case study, "closed" and "garrigue" territory types are composed of dense vegetation (as green oak stands) reducing visibility to a few meters and thus the ability to shoot. In contrast, open deciduous forests offer greater visibility, increasing the probability of catching a wild boar (Curtis, 1971; Brinkman et al., 2009; Lebel et al., 2012). However, visibility is not the only criteria which influences the probability of catching an individual: practicability of the hunting territory is also a constitutive element of catchability (Peterson and Unit, 1969; Andersen and Kaltenborn, 2013; Poinsot, 2012). For example, in our case study, "mountain" and "slope" territory types constrain hunterś movements. Another element is the change in the landscape over time: visibility and practicability criterion may change over the hunting season (e.g. leaves fall or harsher climatic conditions). Likewise, hunterś behavior can change over the hunting season (Hilborn, 1985; Oostenbrugge et al., 2008): they may gain experience and thus become more efficient over the hunting season (Maunder et al., 2006; Milner-Gulland and Rowcliffe, 2008; Diekert et al., 2016). Accordingly, catchability increased until December in our case study, whatever the territory types, and then reached a plateau that can be explained by hunters acquiring a maximum of skills in the middle of the hunting season. It is also possible that the length of the hunting season leads to tiredness and weariness especially when wild boar quotas are reached, thus translating to a decrease in catchability (see e.g. "open" territory type in Ardèche).

From a management point of view, the hunting effort can be manipulated to manage populations and reach management goals (Vajas et al., 2020). This can be measured across several metrics such as hunt duration, number of hunters-days during a given period, distance walked, etc. (Sirén et al., 2004; Brøseth and Pedersen, 2000; Rist et al., 2008). In our case, we chose to measure the hunting effort by the total number of hunters participating to a hunt during a hunting day, which is consistent with previous studies (Vajas et al., 2020). If the management goal is to decrease population size, the hunting effort should increase through an increase in the number of hunters participating to the hunt during hunting days, and/or in the number of hunting days and/or in the length of the hunting season. Manipulating each of these three components can be possible, but not equivalent, to reach a management goal. In our case study, the strategy has been to increase the number of hunters by stimulating hunterś invitation and thus keep a high hunting effort. Information on temporal trends in population size for each hunting season and management unit might allow managers to adapt their future hunting effort based on these past trends. Thus, our model offers promising perspectives. For instance, during the hunting season (at mid-season), managers may assess the hunting effort already invested, the resulting effects on the number of individuals culled, as well as provide an intermediate estimate of the hunting pressure (hunting mortality rate) and abundance. This intermediate assessment may then be used to make recommendations for the end of the season. An exciting next step would therefore be to propose a predictive tool to help hunters and managers reach their management goals.

Although wild boar is an opportunistic omnivore, mast seeding is widely preferred when present (Massei et al., 1996; Servanty et al.,

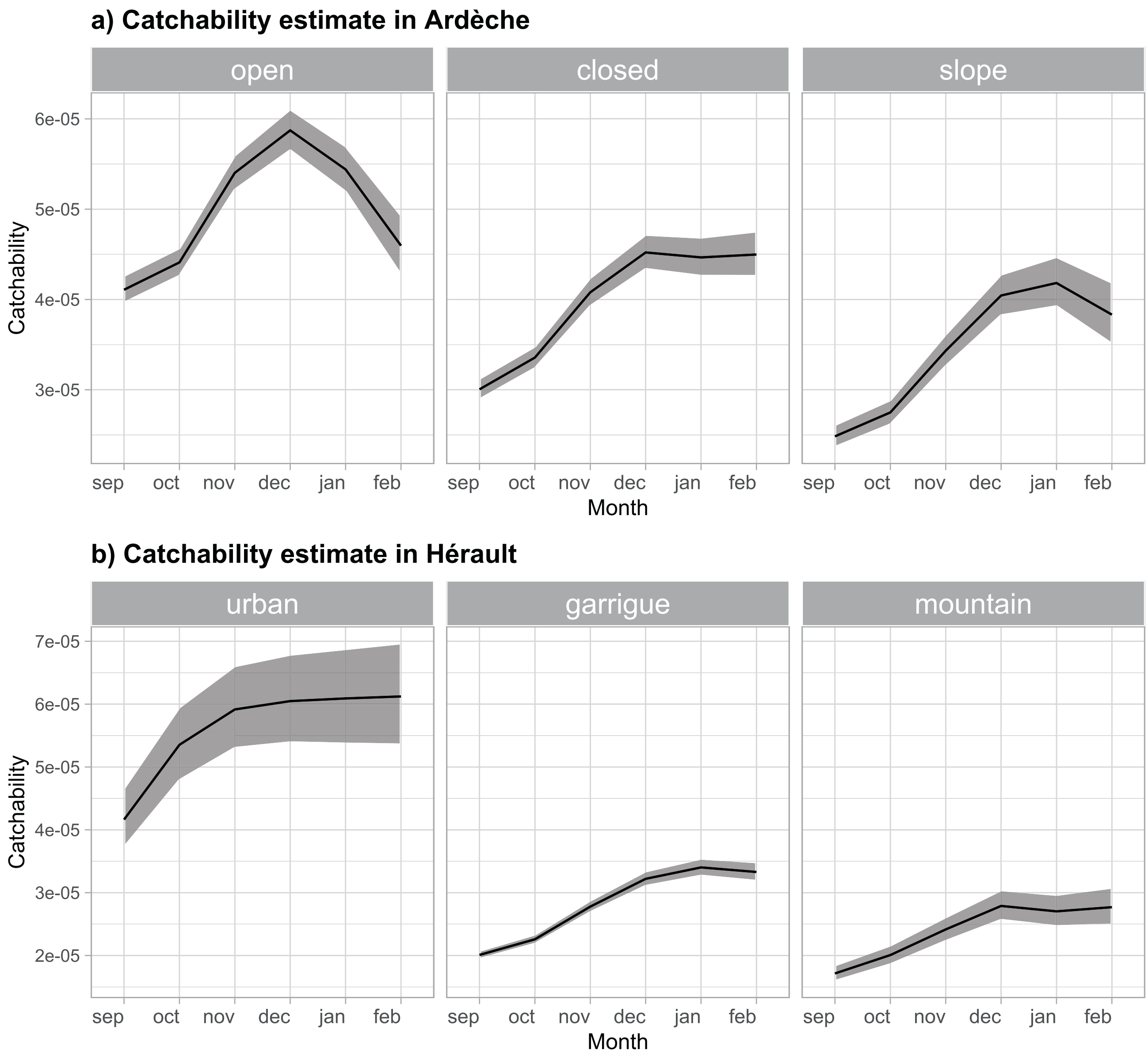

Fig. 5. Posterior distributions of median (black line) and 90% credible interval (grey) of catchability estimates for the different territory types of territories over the hunting season in Ardèche (a) and Hérault (b).

2009). Previous work has shown that acorn production (i.e. oak mast seeding) positively influences breeding probability for females (Servanty et al., 2009; Gamelon et al., 2017, 2020; Touzot et al., 2020) and population growth rates (Bieber and Ruf, 2005; Touzot et al., 2020; Gamelon et al., 2020). In the current context of global warming, mast seeding frequency is expected to increase over the next century in temperate oak forests in response to warmer springs (Caignard et al., 2017; Schermer et al., 2019). Accordingly, we found an increase in population size in MUs, both in Ardèche and in Herault, with rich habitats. For instance, in the East and South-East Ardèche and the East Herault, are characterized by holm oak trees, populations increase whereas further North Ardeche in mixed forests (mixture of deciduous and coniferous trees) and North North-West Herault in coniferous trees, populations remain stable (Thurfjell et al., 2009; Torres-Porras et al., 2015).

5. Conclusion

Our model addresses many challenges. It responds to strong societal demands about the sustainable management of overabundant species such as wild boar by making efficient use of hunting logs dataset integrated in a simple conceptual framework directly accessible to practitioners. This framework can be used both on a large scale (e.g. management unit) and on a smaller scale (e.g. forest). In our case study, the catchability was estimated for drive hunting, independently of our two study departments. However, as soon as the hunting removed enough individuals from the population during one season, the hypotheses on catchability could be adapted to other hunting conditions and hunting practices. Thus, this approach through more detailed hunting logs allows additional information to be gained from conventional studies using hunting bags alone (Acevedo et al., 2014). Furthermore, this approach locally allows managers and hunters to adapt management policies in the light of new information provided by the model (increase or decrease hunting effort to adjust hunting pressure). In this sense, our framework allows passive adaptive management (Parma, 1998) that could become active by experimenting different hunting effort levels, under different conditions and on populations with contrasting demographic status (Parma, 1998). This is particularly

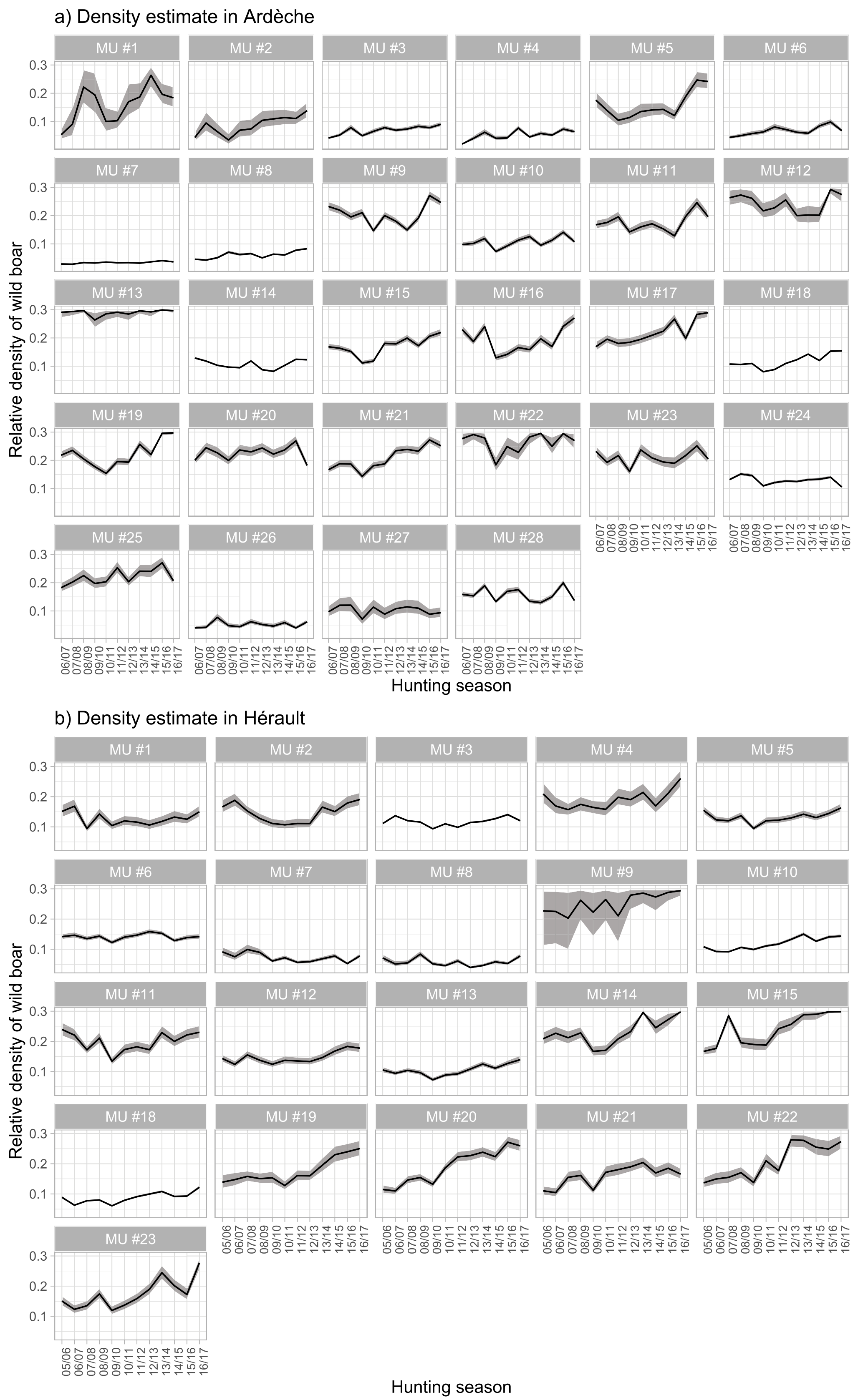

Fig. 6. Posterior distributions of median (black line) and 90% credible interval (grey) of density estimates for the different management units MUs over years for Ardèche (a) and Hérault (b). See Fig. 1 for the correspondence between numbers and location of the MUs.

relevant since in a context of technological advancement, smartphone applications already in use, enable hunting logs to be available in real-time during the hunting season and thus make it possible to estimate the stock assessment and the hunting pressure exerted on the population in real time.

CRediT authorship contribution statement

Pablo Vajas: Conceptualization, Software, Formal analysis, Data curation, Visualization, Writing - original draft. **Clément Calenge:** Conceptualization, Methodology, Software, Formal analysis, Writing - review & editing. **Marlène Gamelon:** Writing - review & editing. **Fabrice Girard:** Resources, Data curation. **Olivier Melac:** Resources, Data curation. **Charlette Chandosne:** Resources, Data curation. **Emmanuelle Richard:** Writing - review & editing. **Sonia Said:** Writing - review & editing. **Eric Baubet:** Supervision, Writing - review & editing.

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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