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Authors: Roda, Fabrice, and Roda, Jean-Marc

Source: Journal of Vertebrate Biology, 73(23103)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.23103

Journal of Vertebrate Biology
Open Access
J. Vertebr. Biol. 2024, 73: 23103
DOI: 10.25225/jvb.23103
RESEARCH PAPER

Signs of foraging by wild boar as an indication of disturbance to ground-nesting birds

Fabrice RODA[1]* and Jean-Marc RODA[2]

[1] *Parc National de Port-Cros, Hyères Cedex, France; e-mail: roda_fabrice@yahoo.fr*
[2] *CIRAD, Southeast Asia, Jakarta, Indonesia; e-mail: roda@cirad.fr*

Received 1 November 2023; Accepted 15 December 2023; Published online 22 March 2024

Abstract. Wild boar (*Sus scrofa*) population increases have been spectacular in many countries, including France. Wild boar can substantially affect many ecosystem components, including birds, but indicators to monitor such effects are currently lacking. We examined the usefulness of monitoring wild boar foraging traces resulting from rooting behaviour to evaluate wild boar disturbance on ground-nesting birds and developed a simple indicator of kilometric foraging (Ikf). This study measured the effect of wild boar on bird abundance, taking into account vegetation characteristics. Using standardised spot counts, we found ground-nesting bird abundances negatively correlated with Ikf. Our results showed a significant decrease of 45% in ground-nesting bird abundance in areas strongly foraged and disturbed by wild boar. By contrast, the abundance of birds depending on ground or trees for food resources but nesting out of reach of wild boar were not correlated to rooting behaviour traces. Thus, we conclude that Ikf may be a simple and suitable indicator that managers can use on a large scale to monitor wild boar potential disturbance and ecological footprint on ground-nesting birds and other taxa. Further studies are needed to test and validate this new indicator in areas other than the Sainte-Baume Regional Park.

Key words: population control, ungulate management, bird conservation

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Introduction

In recent decades, the decline of temperate bird species in Western Europe and North America has attracted concern (Julliard et al. 2004a, Fuller et al. 2007, Gregory & Van Strien 2010). The causes of the observed decline of temperate songbirds are complex. Habitat quality loss may be responsible for the observed decline of forest (Fuller et al. 2007, Gregory et al. 2007, Quine et al. 2007) and farmland songbirds (Chamberlain et al. 2000, Voříšek et al. 2010). In addition, climate change may pose a threat to some bird species (Julliard et al. 2004b, Jiguet et al. 2007, Gregory et al. 2009).

In parallel to the decline of temperate songbirds, wild ungulate population increases have been spectacular in many regions of North America (Côté et al. 2004) and Western Europe (Massei et al. 2015). The main causes proposed for wild ungulate over-abundance (as defined by Côté et al. 2004) are increased plant growth resulting from climate change, the local extermination of natural predator species such as wolves (but note that wolves are slowly recolonising ancient territories in Western Europe), supplementary feeding, and changes in agricultural, sylvicultural and game management practices (Flueck 2000, Milner et al. 2006, Massei et al. 2015). For example, wild boar (*Sus scrofa*) populations in Europe have

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* *Corresponding Author*

reached historical peaks (Massei et al. 2015). The impact of over-abundant wild boar on conservation and economic interests includes the spread of diseases to livestock and people, vehicle collisions, and damage to crops, as well as reduction in plant and animal abundance and richness (Bourcet et al. 2003, Massei & Genov 2004, Barrios-García & Ballari 2012). As wild boar populations increase in many European countries (Massei et al. 2015), mitigating wild boar impacts on the environment and economic interests will present a significant challenge. What are the known consequences of large ungulate over-abundance on ecosystems? Numerous studies focus on the effects of high deer density on habitats. Deer over-abundance strongly affects plant communities, vegetation structure, and the abundance of many invertebrate taxa (Joys et al. 2004, Allombert et al. 2005a, Stockton et al. 2005). Such changes in the woodland ecosystem affecting food and safe nesting availability are responsible for the adverse cascading effects on songbird abundance and biodiversity (Allombert et al. 2005b, Holt et al. 2011). As omnivorous mammals, wild boar can have a substantial environmental effect and may affect many ecosystem components (Massei & Genov 2004). Their rooting activity can remove the herbaceous cover (Howe et al. 1981, Carpio et al. 2014a), cause a decrease in tree regeneration (Gomez et al. 2003), and facilitate seed dispersion (Barrios-García & Ballari 2012). Wild boar negatively affects rodents by direct predation on juveniles and/or competition for food resources (Focardi et al. 2000, Carpio et al. 2014a). Wild boar over-abundance has cascading effects on threatened predators such as wildcats (*Felis silvestris*) by reducing rodent prey availability (Lozano et al. 2007). Previous studies on wild boar and bird interactions in their native range focused mainly on game bird species predated by wild boar (Massei & Genov 2004). Wild boar predated capercaillie (*Tetrao urogallus*) and hazel grouse (*Tetrastes bonasia*) nests (Saniga 2002, 2003) and simulated nests of red-legged partridge (*Alectoris rufa*; Carpio et al. 2014b). As over-abundant wild boar prey on everything on the ground, their negative effects in their native and introduced range are thus well established (Barrios-García & Ballari 2012).

To manage the ecological impacts of wild ungulates, it is necessary to measure their effects precisely through

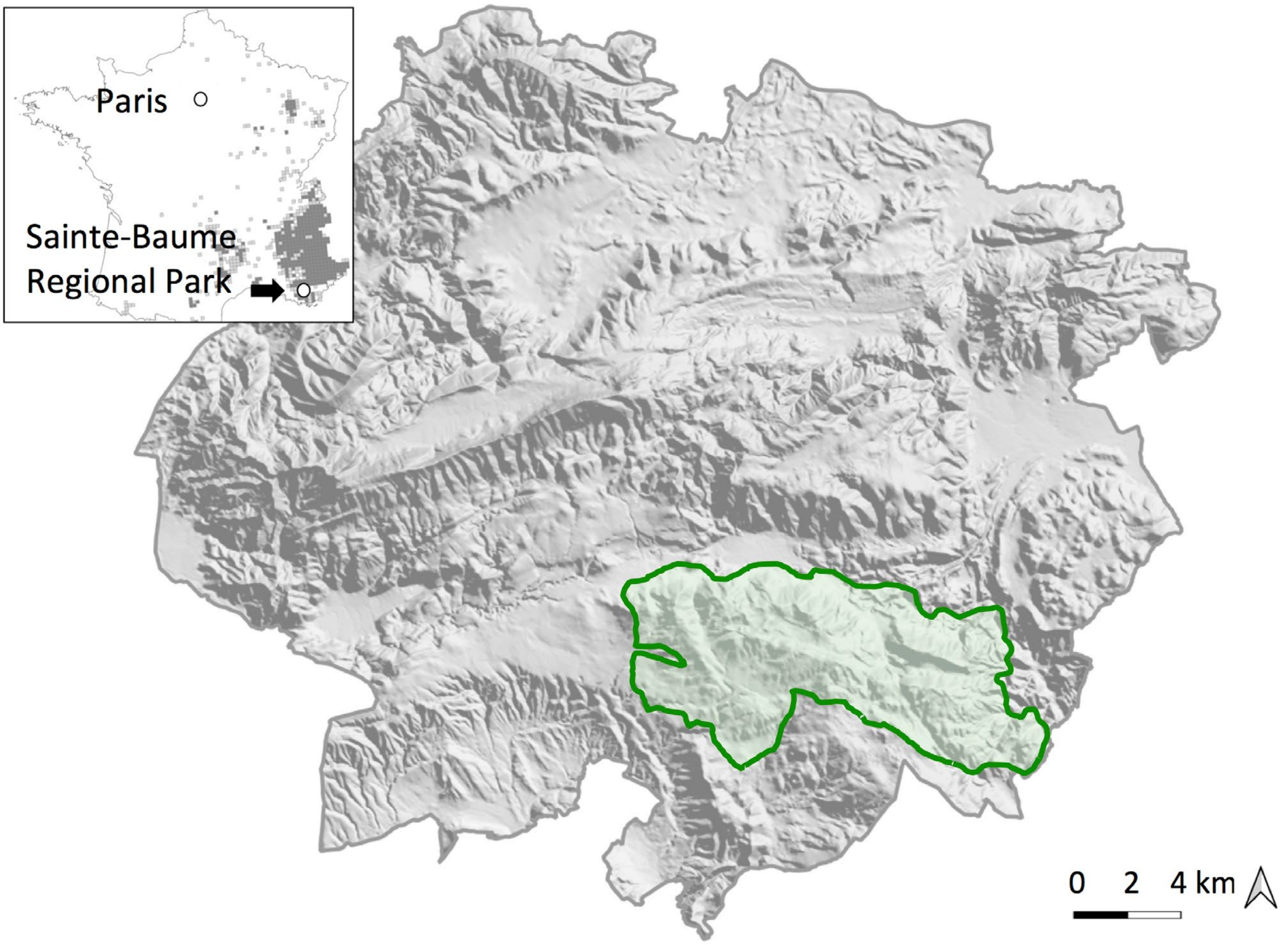

Fig. 1. Location of the Sainte-Baume Regional Park (south-eastern France), showing layout of forest massif of Siou Blanc/Morières (green), corresponding to the study area.

environmental indices. Monitoring changes in these indices provides a basis for setting management objectives (Morellet et al. 2007). Large herbivore populations are usually controlled through hunting in Europe as top predators are slowly recovering but not keeping pace with the increases in ungulates (Milner et al. 2006, Massei et al. 2015). Researchers have recently developed tools for managing ungulate populations based on monitoring a set of ecological change indicators ('IEC'; Cederlund et al. 1998, Morellet et al. 2007). An IEC is an easily measured parameter sensitive to changes in the relationship between the population and its resources and habitat (Cederlund et al. 1998). Acevedo et al. (2007) developed a method describing wild boar abundance based on the frequency of faecal droppings. However, IECs describing wild boar impacts on fauna, flora, biodiversity and habitat are currently lacking. The main objective of this study was thus to find such an IEC to monitor the effect of wild boar on avifauna.

In this study, we propose the hypothesis that H1) wild boar predatory activity should disturb ground-nesting birds and thus decrease their abundances in highly foraged areas. Tree-nesting birds are out of reach of wild boar, so we hypothesised that H2) tree-nesting bird abundances should not negatively correlate with wild boar rooting activity. As wild boar may affect birds through food competition, we investigated H3) the impact of wild boar on birds depending on ground foraging for food resources but nesting out of reach of wild boar.

Material and Methods

Study area

The forest massif of Morières/Siou Blanc is situated in southeastern France in the boundaries of the Sainte-Baume Regional Park (43°32 N, 5°83 E; 8,638-ha forest area; altitude 500-650 m; Fig. 1), in an area with low human density, within which, there are only a few isolated houses. The Sainte-Baume Regional Park map is available at https://inpn.mnhn.fr/espace/protégé/FR8000053. The climate of Morières/Siou Blanc is Mediterranean, with hot and dry summers, mild winters and moderately rainy autumns and springs (mean maximal temperature in July = 27.6 °C; mean minimal temperature in July = 19.4 °C; maximal annual mean = 18.8 °C; minimal annual mean = 12.1 °C; mean precipitation in July = 5.6 mm; annual mean 613.4 mm) (Météo France 2015). The forest massif exhibits Mediterranean vegetation, typical of southeastern France. It displays various profiles of vegetation according to forest management stages. It is a coppice forest with holm oak (*Quercus ilex*), downy oak (*Quercus pubescens*) and a large diversity of shrubs. Some areas are dominated by various pines (*Pinus* spp.) and xeric species of shrubs (*Salvia rosmarinus*, etc.). Numerous stands contained a mix of pines and oaks.

Sport hunting is mainly focused on big game species, especially wild boar. Wild boar abundance varies significantly throughout the massif, with high numbers harvested (6.3 wild boar killed/km^2/year). In contrast, roe deer (*Capreolus capreolus*) are scarcer (0.9 animals killed/km^2/year). A small herd of approximately 50-100 fallow deer (*Dama dama*) and red deer (*Cervus elaphus*) has been recently introduced by game managers (Krammer 2016, Roda 2016). Livestock animals are absent in the prospected area. There were no established wolf packs in the Sainte-Baume Regional Park when this study was conducted. The first wolf reproduction occurred in 2020 (Poulard et al. 2021), and wolf colonisation of the Sainte-Baume Regional Park occurred after the present study (Roda et al. 2020, 2022).

Sampling protocol

The study area was divided into 4 ha numbered blocks; twenty-six stations were selected by randomly drawing a number. Stations were spread over the whole forest massif, without prior knowledge of the vegetation structure or bird communities. Ground visits were organised during the winter season, and the positions of the stations were recorded using GPS to allow their subsequent identification. The stations were in the main body of the forest of Morières/Siou Blanc and were surrounded by woodland. Around each station, a 1 km survey transect was set up to search for wild boar foraging traces resulting from rooting activity. The survey routes were along pre-existing paths or forest roads of 1-5 m in width (allowing cars or people to enter the different areas).

Each survey route was divided into 100 m-length segments, yielding ten segments per transect. In each segment, the presence of wild boar foraging traces resulting from rooting activity was recorded, which allowed the derivation of a simple indicator of kilometric foraging (Ikf, a continuous variable), that is, the number of segments with wild boar foraging traces/ten segments. This methodology gives an index derived from the frequency of occurrence (see a similar methodology based on faecal droppings in Acevedo et al. 2007). The segments were considered positive when signs of rooting activity were seen and occupied a contiguous ground area larger than

2 m². Stations with Ikf ranging from 0 to 0.5 were considered low wild boar traces (Ikf–). Stations with Ikf from 0.6 to 1 were considered high wild boar traces (Ikf+). This two-level factor was used for GLM analysis (see below, statistics section). Two measures of Ikf were made during spring for each station, between 1st April and 30th May 2012. We measured Ikf on the same days as bird surveys. We found 25 counts with low densities of wild boar foraging traces (Ikf–) and 27 counts with high wild boar foraging traces (IkF+).

Along each survey route, we measured variables related to habitat structure, tree cover, density of shrub cover, and average tree and shrub heights. Based on the results of previous bird studies (see below 'Vegetation data' section), we expected these variables to play an important role.

Bird survey

Spot counts were all performed by the same observer (F. Roda). Counts were carried out in each plot during two visits in spring 2012; point-count times were separated by an interval of at least four weeks to detect both early and late breeding birds (1st-15th April and 15th-30th May), following the recommendations of the French Breeding Bird Survey of the National Museum of Natural History (Jiguet et al. 2012). Counts were performed within 1-4 h after sunrise. Stations (n = 26) were positioned a minimum of 500 m apart to avoid overlap of bird counts. Two spot-counts were realised at each station, resulting in 52 spot-counts. To minimise a potential edge effect (Ries & Sisk 2004), the centres of all study plots were situated at least 100 m from the edge of forest alleys. We used 100 m fixed-radius point counts that lasted 5 min to estimate relative bird abundances, following the methodology detailed in Blondel et al. (1970) and Jiguet et al. (2012). Repeating point-counts throughout the breeding season improved estimation of species richness and relative abundances of birds (Bonthoux & Balent 2012). Points were recorded in reverse order during the second count to avoid introducing temporal bias between different stations. Since all of the plots were located in core forest habitats with low visibility, birds were mainly detected through their song. Individuals could be distinguished when several birds continuously sang at different locations in the plot.

We excluded observations of raptors, i.e. golden eagle (*Aquila chrysaetos*), Bonelli´s eagle (*Aquila fasciata*), short-toed snake eagle (*Circaetus gallicus*), peregrine falcon (*Falco peregrinus*), common kestrel (*Falco tinnunculus*), Eurasian sparrowhawk (*Accipiter nisus*), corvids (*Corvus corax* and *Corvus corone*), common cuckoo (*Cuculus canorus*), and Eurasian woodcock (*Scolopax rusticola*) as these species were poorly surveyed by the method used and/or have life cycles that make them irrelevant to the objective of the study. Game birds (*A. rufa* and *Phasianus colchicus*) were not recorded since their presence in a particular station may have been due to game releases in the area.

In accordance with the hypothesis that wild boar predatory activity should disturb ground-nesting birds, we predicted that ground-nesting bird abundance should decrease in highly foraged areas. To test this prediction, we established a classification system that grouped the bird species encountered during the study into two guilds according to the nesting habitat (i.e. ground-nesting *vs.* tree/shrub-nesting birds). In accordance with the hypothesis that wild boar may impact birds through food competition, we predicted that ground-gleaning (for food resource) birds should negatively correlate to wild boar foraging traces resulting from rooting activity. To test this prediction, birds were grouped into two guilds according to ground dependence for food gleaning (i.e. ground-gleaning *vs.* tree-gleaning birds). Ground-nesting birds were separated from ground-gleaning (for food resources) and tree-gleaning guilds to avoid potential overlap of effects (i.e. predation/disturbance and food competition). Locations of the nest sites were taken from the literature (Gregory et al. 2007, Flitti et al. 2009) and our own observations (see Table 1). Four indicators were derived: an indicator for ground-nesting birds (GN, n = 201 birds), an indicator for tree-nesting birds (TN, n = 339 birds), an indicator for ground-gleaning birds (GG, n = 234 birds) and an indicator for tree-gleaning birds (TG, n = 105 birds).

We used species diversity as an indicator of bird community structure. We wanted to obtain a relative comparison among stations (and not evaluate the quality of the ecosystem). As all the stations belonged to the same forest stand (same ecosystem), species diversity was calculated using the Shannon index. The Shannon index reflects the number of species in a community and simultaneously considers how evenly the individuals are distributed among those species (Lyashevska & Farnsworth 2012). The Shannon index was measured at a local scale (the sampling area).

Table 1. Classification of species in relation to gleaning behaviour and nesting dependence.

Species acronym	Species name	Ground or Tree/shrub dependence		Migration strategy
		Nesting	Gleaning	
(a) Species				
Cya cae (n = 55)	Eurasian blue tit (*Cyanistes caeruleus*)	Tree/shrub	Tree/shrub	Partial migrant
Eri rub (n = 69)	robin (*Erithacus rubecula*)	Ground	Ground	Partial migrant
Fri coe (n = 111)	Eurasian chaffinch (*Fringilla coelebs*)	Tree/shrub	Ground	Partial migrant
Lus meg (n = 51)	nightingale (*Luscinia megarhynchos*)	Ground	Ground	Long migrant
Par maj (n = 50)	great tit (*Parus major*)	Tree/shrub	Tree/shrub	Partial migrant
Phy bon (n = 81)	Western Bonelli´s warbler (*Phylloscopus bonelli*)	Ground	Tree/shrub	Long migrant
Syl atr (n = 43)	Eurasian blackcap (*Sylvia atricapilla*)	Tree/shrub	Ground	Partial migrant
Syl mel (n = 26)	Sardinian warbler (*Sylvia melanocephala*)	Tree/shrub	Ground	Partial migrant
Tur mer (n = 34)	blackbird (*Turdus merula*)	Tree/shrub	Ground	Partial migrant
(b) Guilds	Species name			
Ground Nesting (GN, n = 201)	nightingale; robin; Western Bonelli's warbler			
Tree Nesting (TN, n = 339)	blackbird; Eurasian chaffinch; great tit; Eurasian blackcap; Eurasian blue tit; Sardinian warbler			
Ground Gleaning (GG, n = 234)	blackbird; Eurasian chaffinch; Eurasian blackcap; Sardinian warbler			
Tree Gleaning (TG, n = 105)	great tit; Eurasian blue tit			

Vegetation data

This study measured the effect of wild boar on birds, controlling for vegetation characteristics (shrub density, time since last coppicing). Vegetation data were collected during spring 2012, after each bird count session. Measurements were taken at three sampling areas at each point-count station, thus resulting in 78 sampling points. One was located at the point-count station itself, the other two at random distances from the station (< 50 m). Mean values were calculated for each variable listed. Shrub layer density of vegetation layer (0-1 m) was estimated using a pole graduated into 10 cm sections and a protocol adapted from Holt et al. (2011). The number of sections obscured by vegetation was recorded when viewed from a distance of 10 m. An index of shrub density (S, a continuous variable) was derived using the number of segments obscured/10 segments, from 0 to 1. We used these scores to define two classes of shrub layer density: values equal to or smaller than 0.5 were considered as 'low density' (S–), those equal to or greater than 0.6 as 'high density' (S+); this two-level factor was used for GLM analysis (see below, statistics section). As avian community structure is largely determined by the growth stage and associated structural characteristics of vegetation (Fuller et al. 1989), vegetation age was controlled in each plot using local forest management archives. Time since last coppicing (Cut) was used as a continuous variable for statistical purposes (see below, statistics section).

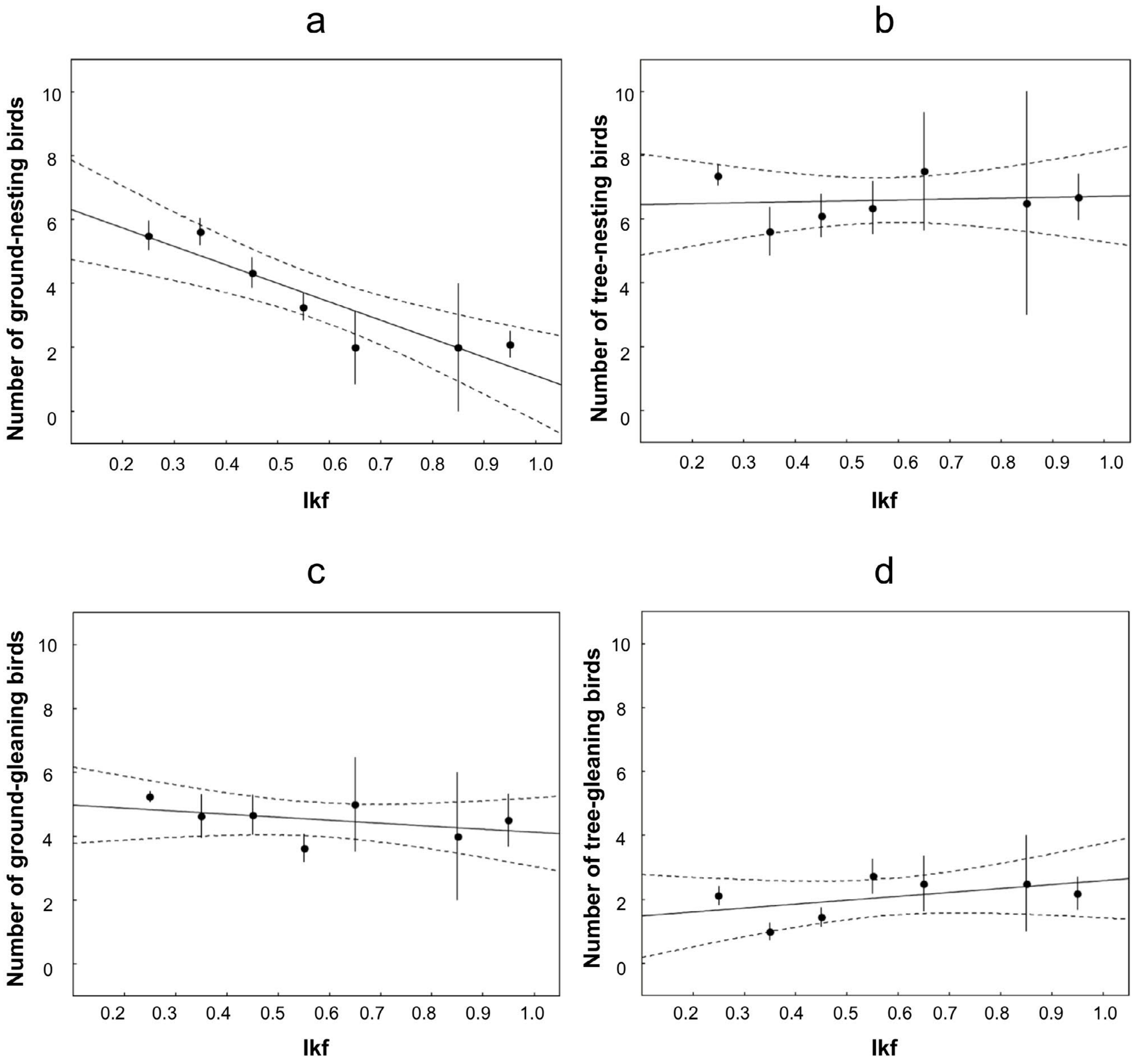

Fig. 2. Variations of forest bird mean abundances in relation to wild boar foraging (Ikf). Predicted trends are presented as black lines with 95% confidence intervals (dashed lines). Bars indicate the standard error of mean. a) ground-nesting (GN) birds b) tree-nesting (TN) birds c) ground-gleaning (GG) birds d) tree-gleaning (TG) birds.

Table 2. Candidate models explaining ground-nesting bird abundance, with the Akaike Information Criterion values (AIC) and the selected variables: wild boar foraging (Ikf), timing of spot-count (Tim), shrub density (S), time since last coppicing (Cut), tree-nesting bird abundance (TN), ground-gleaning bird abundance (GG), tree-gleaning bird abundance (TG). The interactions between wild boar foraging and timing (IkF*Tim), wild boar foraging and shrub density (IkF*S), wild boar foraging, timing and shrub density (IkF*Tim*S) were also tested but gave higher AIC scores (data not shown). Bold characters indicate the selected model.

Guild	Selected variables							AIC	SS Residual
	Ikf	Tim	S	Cut	TN	GG	TG		
Ground Nesting (GN)									
	x	x	x	x	x	x	x	161.7	52.1
	x	**x**	**x**					**164.1**	**52.2**
	x	x	x	x				165.1	51.8
	x	x						183.4	81.5
	x		x					187.9	83.0
	x			x				196.8	109.7
	x							197.7	115.3
		x						208.7	161.7
			x					214.3	167.4
						x		221.6	197.9
					x			221.9	199.7
							x	222.1	200.4
				x				222.0	200.4

As cervids are known to have an impact on birds (see Allombert et al. 2005b, Holt et al. 2011), signs of browsing were carefully searched in each sampling area. We considered only shrub species or woody plants because we could not, with herbaceous species, distinguish deer browsing from that of lagomorphs present in the study area. We recorded the browsing pressure by assessing the number of eaten twigs versus all available twigs at a height < 1.80 m, following a methodology similar to those described elsewhere (Picard 1988, Chevrier et al. 2012). A 'browsing sign' is one bite by the animal on the tree, being evident as a fresh cut on the twigs. As the browsing pressure was < 1 % in all the sampled plots, the impact of cervids on the avifauna was considered negligible in this study. All the assessments were conducted by the same person (F. Roda).

Statistics

We tested for the effects of 1) wild boar foraging (Ikf), 2) shrub cover (S), 3) timing of spot count (Tim) and 4) time since last coppicing (Cut) (the factors of variation) on bird abundances, and species diversity (the dependent variables) using general linear models (GLM). For the count data (bird abundances), each model was tested assuming normal (Gaussian) and Poisson error. We selected the best model using the Akaike Information Criterion (AIC). However, when the AIC of two competing models differed by less than two, we examined the residual sum of squares and retained the simplest model in line with the rules of parsimony. We checked for homoscedasticity and normality of residuals. Raw data were not transformed, and actual bird counts were used throughout the paper. The timing of spot count was entered as a two-level factor (early *vs.* late) in all the models. Wild boar foraging and shrub cover were entered as two-level factors (Ikf– *vs.* Ikf+; and S– *vs.* S+, respectively) to investigate potential interactions between factors. Including wild boar foraging and shrub cover as continuous covariates led to the same conclusions. Time since last coppicing was entered as a continuous covariate (Cut) in all models. Birds were grouped into functional guilds (see Table 1). We fitted several models, including Ikf, S, Tim and Cut interaction effects. As a control of potential bias in our study, we tested the effects of 1) S and 2) Tim (the factors of variation) on Ikf (the dependent variable) using GLM. Statistical analysis was performed with the 'Statistica' software using the 'GLM' function.

At least nine bird species were observed in one-third of point counts and were included in the statistical analysis. All results are expressed as mean ± standard error (SE). Differences were considered significant at $P < 0.05$.

Results

General results

Wild boar foraging signs resulting from rooting behaviour were observed in all surveyed transects. The maximum value of the wild boar indicator of kilometric foraging (Ikf) was 1 with a high mean value of 0.60 ± 0.03, indicating relatively intense wild boar foraging pressure in the study area as a whole. Twenty-five spot counts showed few wild boar traces (Ikf–), and 27 showed many traces (Ikf+, see Methods section). A GLM showed no relationships between Ikf and timing of spot counts (Tim) or shrub cover (S) (adjusted $R^2 = 0.02$; $F = 1.31$; $P = 0.28$). We analysed the abundance of nine bird species and 520 individuals (Table 1). Counts led to an average of 3.9 ± 0.3 SE ground-nesting birds (range 0-8); 6.5 ± 0.3 SE tree-nesting birds (range 3-13); 4.5 ± 0.3 SE ground-gleaning birds (range 1-9); and 2.0 ± 0.2 SE tree-gleaning birds per spot (range 0-7).

Wild boar impact on birds

We tested the effects of Ikf, Tim, S and Cut on the abundance of ground-nesting birds. Abundances of TN, GG and TG birds were also tested as supplementary variables. The best model included the variables Ikf, S and Tim; Cut, TN, GG and TG were rejected as explanatory variables (Table 2).

The observed changes were explained by the GLM and were highly significant (adjusted $R^2 = 0.70$; $F = 17.89$; $P < 0.001$). We found that the abundance values of GN birds were negatively correlated with Ikf (Fig. 2a).

Entering IkF as a two-level factor showed that there was a significant decrease of 44.7 % in ground-nesting bird abundances in areas strongly foraged by wild boar (Fig. 3). The GLM indicated the role of Ikf as being the main factor driving bird abundance changes, and Tim and S as being secondary factors, in this order (Table 3).

Interaction terms for categorical variables were not significant (Table 3). The effect of Tim demonstrated that birds were more numerous in late spring. We observed that the negative effect of wild boar on bird abundance was slightly greater in early spot counts than in late ones, but this result was not statistically significant. Shrub cover was positively correlated to ground-nesting bird abundance. The negative effect of Ikf on bird abundance was marginally greater in S– than in S+ areas, but this result was not statistically significant (Fig. 4). Mean values of GN birds in relation to hypothesis decomposition are summarised in Table 4.

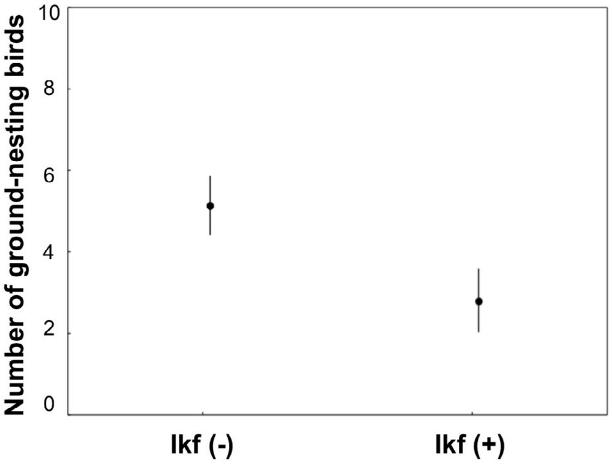

Fig. 3. Mean abundances of ground-nesting (GN) in relation to wild boar foraging. Ikf(–) areas moderately foraged by wild boar; Ikf(+) areas strongly foraged by wild boar. Lines indicate standard error of mean. Results are highly significant (*P* < 0.001); see Table 2 and statistical analysis.

We tested the effects of Ikf, Tim, S and Cut on the other guilds. The results of model selection are summarised in Table 5. In contrast to ground-nesting birds, the abundance of birds belonging to tree-nesting (Fig. 2b) or ground-gleaning (Fig. 2c) guilds were not well explained by IkF or the other variables; the observed changes were not statistically significant (adjusted $R^2 = 0.05$; $F = 1.4$; $P = 0.24$; Adjusted $R^2 = 0.01$; and $F = 1.1$; $P = 0.40$, respectively). The best model describing tree-gleaning bird abundance included Ikf and Tim as explanatory variables (Table 5), but the observed

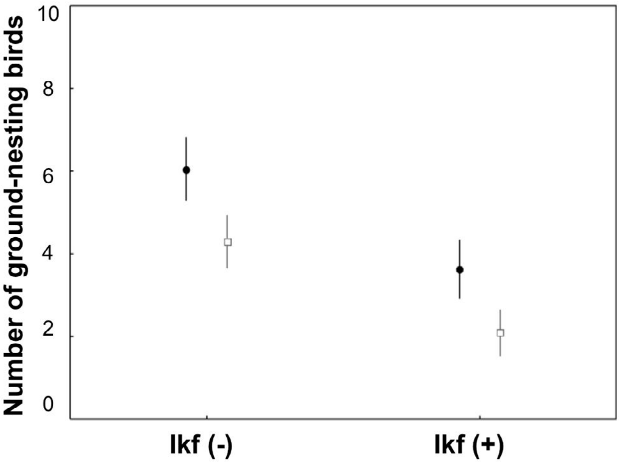

Fig. 4. Mean abundances of ground-nesting (GN) in relation to wild boar foraging and shrub density. IkF(–) areas moderately foraged by wild boar; IkF(+) areas strongly foraged by wild boar. Black filled circles indicate areas with high density of shrubs. Open grey squares indicate areas with light shrub density. Lines indicate standard error of mean. Results are highly significant (*P* < 0.001); see Table 2 and statistical analysis.

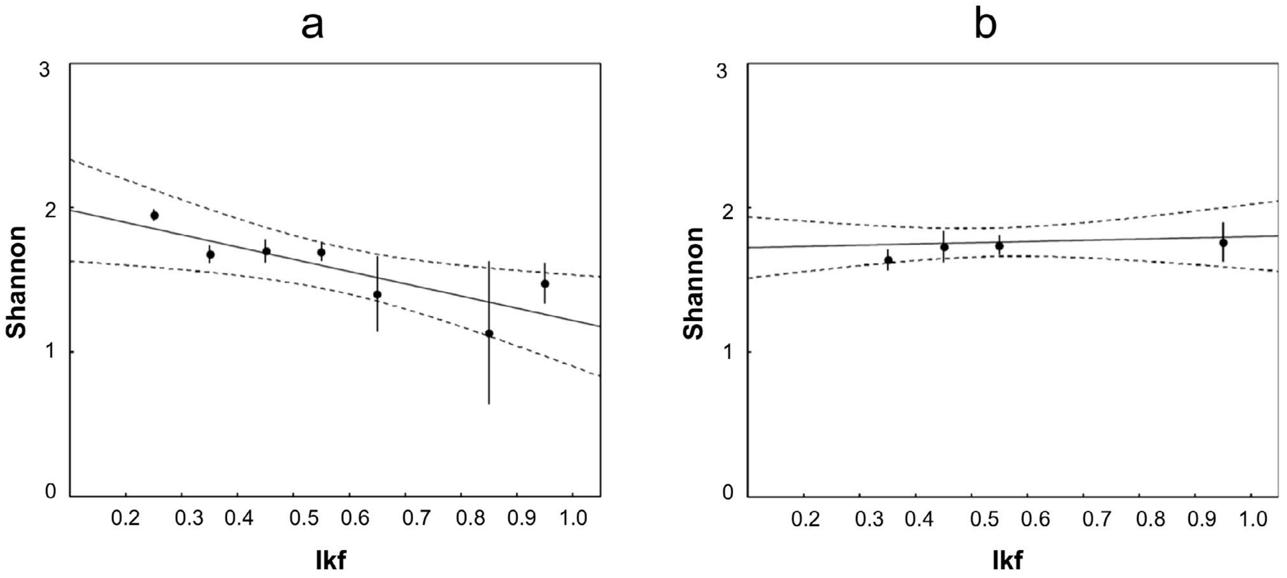

Fig. 5. Variations of bird species diversity (Shannon) in relation to wild boar foraging (Ikf) and shrub density. Predicted trends are presented as black lines with 95% confidence intervals (dashed lines). Bars indicate the standard error + mean. a) bird species diversity in areas with low shrub cover. b) bird species diversity in areas with dense shrub cover.

Table 3. β coefficients and statistical parameters of the most parsimonious GLM model to explain ground-nesting (GN) bird abundance using wild boar foraging signs resulting from rooting activity (Ikf), timing (Tim) and shrub density (S) as predictors. Bold characters indicate statistically significant results.

Estimates (sigma-restricted parameterisation)								
Effect	Level of effect	Column	GN param.	±SE	GN t	GN p	GN β	±SE
Intercept		**1**	**4.0**	**0.2**	**24.2**	**0**		
IkF	(–)	**2**	**1.2**	**0.2**	**7.0**	**0**	**0.59**	**0.08**
Tim	early	**3**	**–0.8**	**0.2**	**–4.8**	**0.000018**	**–0.41**	**0.08**
S	(+)	**4**	**0.8**	**0.2**	**4.9**	**0.000012**	**0.41**	**0.08**
IkF*Tim	1	5	0.1	0.2	0.6	0.581136	0.05	0.08
IkF*S	1	6	0.1	0.2	0.3	0.74449	0.03	0.08
Tim*S	1	7	0.1	0.2	0.3	0.753062	0.03	0.08
IkF*Tim*S	1	8	0.0	0.2	0.2	0.831509	0.02	0.08

Table 4. Mean values of GN birds in relation to hypothesis decomposition. Hypothesis decomposition: wild boar foraging signs resulting from rooting activity (Ikf), timing (Tim) and shrub density (S).

Abundances of GN birds and hypothesis decomposition								
Cell number	IkF	Tim	S	GN means	GN ± SE	GN –95% conf. Int.	GN +95% conf. Int.	n
1	(–)	early	(+)	5.4	0.4	4.6	6.3	7
2	(–)	early	(–)	3.5	0.5	2.4	4.6	4
3	(–)	late	(+)	6.7	0.6	5.4	7.9	3
4	(–)	late	(–)	5.1	0.3	4.4	5.8	11
5	(+)	early	(+)	2.8	0.5	1.7	3.8	4
6	(+)	early	(–)	1.2	0.3	0.5	1.8	11
7	(+)	late	(+)	4.5	0.4	3.6	5.4	6
8	(+)	late	(–)	3.0	0.4	2.1	3.9	6

Table 5. Effects of Ikf (wild boar foraging), Tim (timing), S (shrub density) and Cut (time since last coppicing) on the other guilds and results of model selection. Bold characters indicate the selected model.

Guild	Selected variables							
	Ikf	Tim	S	Cut	Tim*S	Ikf*Tim*S	AIC	SS Residual
Tree Nesting (TN)								
					x	**x**	**220.9**	**225.5**
	x						223.6	273.8
		x					222.9	269.3
			x				223.4	272.4
				x			223.7	274.4
Ground Gleaning (GG)								
					x	**x**	**215.3**	**158.2**
					x		215.8	171.6
	x						217.5	179.4
		x					218.7	184.9
			x				218.7	184.9
				x			218.7	185.0
Tree Gleaning (TG)								
	x	**x**	**x**				**169.5**	**77.9**
	x	x					169.2	82.7
	x						169.6	91.0
		x					173.5	98.6
			x				174.8	101.2
				x			175.3	102.4

Table 6. Model selection for species diversity. Bold characters indicate the selected model.

	Selected variables							
	Ikf	Tim	S	Cut	Ikf*S	Tim*S	AIC	SS Residual
Species diversity								
		x			**x**	**x**	**20.7**	**3.5**
	x	x	x	x	x	x	21.7	3.5
			x		x		25.6	
	x							
		x	x			x	25.1	4.2
					x		28.3	4.4
		x					30.3	5
	x						32.6	5.3
			x				38.1	5.9
				x			38.6	6

effects were marginally non-significant (adjusted $R^2 = 0.12$; $F = 2.0$; $P = 0.07$). However, though we noted that tree-gleaning birds tended to be slightly more numerous in areas strongly foraged by wild boar, the result was non-significant (Fig. 2d).

We further tested the effects of Ikf, Tim, S and Cut on bird species diversity. The best model describing species diversity included the variables Tim, IkF*S, Tim*S; Cut was rejected as an explanatory variable (Table 6). The observed changes in species diversity

Table 7. β coefficients and statistical parameters of the most parsimonious GLM to explain species diversity using wild boar foraging signs resulting from rooting activity (Ikf), timing (Tim) and shrub density (S) as predictors. Bold characters indicate the main factor (S*Ikf) affecting species diversity and its intercept.

Estimates (sigma-restricted parameterisation)								
Effect	Level of effect	Column	Sp. div. param.	±SE	Sp. div. t	Sp. div. *P*	Sp. div. β	±SE
Intercept		**1**	**1.7**	**0**	**38.4908**	**0**		
Tim	early	2	–0.1	0	–1.92837	0.060277	–0.24	0.13
S	(+)	3	0.1	0	1.27066	0.210526	0.16	0.12
IkF	(–)	4	0.1	0	1.33765	0.187885	0.17	0.13
Tim*S	1	5	0.1	0	1.91937	0.061437	0.24	0.13
Tim*IkF	1	6	0	0	0.63077	0.531456	0.08	0.13
S*IkF	1	**7**	**–0.1**	**0**	**–2.34528**	**0.023587**	**–0.30**	**0.13**
Tim*S*IkF	1	8	0	0	0.51398	0.609837	0.06	0.12

were statistically significant (adjusted $R^2 = 0.33$; F = 4.6; $P < 0.001$). When two models had similar AIC and SS Residual scores, the most parsimonious model was chosen (see Methods). We found that the main factor affecting bird species diversity was the interaction of IkF*S (Fig. 5, Table 7).

In accordance with the hypothesis that wild boar predatory activity should disturb ground-nesting birds, the prediction that GN birds should be less abundant in areas strongly foraged by wild boar (Fig. 2a) was supported. In addition, the prediction that TN bird abundance should not be affected by wild boar foraging was also supported by the model (Fig. 2b). In relation to the hypothesis that wild boar may impact birds through food competition, the prediction that GG birds should negatively correlate with wild boar foraging traces resulting from rooting activity was not supported (Fig. 2c).

Discussion

This study is the first to correlate bird abundance with an index based on the frequency of wild boar foraging signs resulting from rooting activity. Understanding and measuring the environmental effects of wild ungulates in forest ecosystems remains a challenge for researchers and wildlife managers. Wildlife population trends are often assessed by species counts; surveillance monitoring frequently requires several years to amass enough data to provide strong evidence of a decline in state before action is taken. Species sampling methods remain labour-intensive and time-consuming and may be subject to bias (Kéry & Schmidt 2008). As a result, there is an increasing demand from policymakers to improve management by incorporating relevant indicators that are simple, reliable and rapidly assessed. By recording a set of IECs, the aim is to achieve management objectives, rather than deliver routine surveillance monitoring (Cederlund et al. 1998, Morellet et al. 2007). With a set of IECs, one can envisage an adaptive management program (as defined by Nichols & Williams (2006)) of wild boar game harvest that is compatible with bird conservation. Thus, a key challenge is to find a mix of measures that give easily identified signals and can be used to track the ecological conditions at reasonable cost. Our indicator of wild boar foraging meets these criteria, and thus provides managers with a rapid diagnostic index of potential wild boar environmental impact on avifauna.

Our results showed a significant decrease of 44.7 % in ground-nesting bird abundances in areas strongly foraged by wild boar; in contrast, tree-nesting birds (out of reach of large ungulates) were not affected by wild boar gleaning. This result was expected since ground-nesting birds are highly impacted by other over-abundant ungulates (Allombert et al. 2005b, Holt et al. 2011), and wild boar are known to be highly opportunistic mammals that prey on anything near the ground: depredations on birds and nests (Saniga 2002, 2003, Carpio et al. 2014b, Oja et al. 2017), reptiles and amphibians (Jolley et al. 2010, Ballouard et al. 2021), small mammals (Lozano et al. 2007, Wilcox & van Vuren 2009), and other fauna and flora communities are substantial (see for review Barrios-García & Ballari 2012). The general assumption that all clutches of birds that nest on the ground represent potential prey for wild boar is probably true. This predation effect may explain the observed changes in bird distribution, as predation risk is known to influence the use of space by birds (Thomson et al. 2006, Cresswell 2008). We noted an interaction effect of wild boar foraging and habitat on birds, i.e. the effects of wild boar foraging on species diversity were more important in areas with low shrub cover. Other studies have pointed out that the density of potential nests and predation rates is dependent on vegetation structure complexity and that foliage density near the nest may reduce predation impact (Martin 1988, Chalfoun & Martin 2009). In addition to resource competition, predation risk is an important factor determining the spatial distribution of birds (Suhonen 1993) and offspring success (Martin 1996, Thomson et al. 2006, Chalfoun & Martin 2007). Interestingly, GN bird abundances were influenced by the timing of spot count. As two of the three species comprising the GN bird guild are long-migrant species, this result is unsurprising as these birds are late nesting. Further research is needed to investigate the potential interactions between migration strategy and wild boar impact, i.e. if long-migrant birds are more impacted than partial migrants.

We then explored the hypothesis that wild boar may compete with ground-gleaning birds for food resources. Previous studies showed that wild boar negatively impacted rodent populations due to direct competition for seeds (Focardi et al. 2000) or legumes (Carpio et al. 2014a). Although wild boar are omnivorous and prey on invertebrates, their diet consists mainly of plant matter, including above-ground green material (Baubet et al. 2004). The most apparent direct effect of rooting by wild boar is the reduction in plant cover (Massei & Genov 2004). Surprisingly, ground-gleaning birds in our study were not statistically affected by wild boar foraging. This finding supports the idea that wild boar-mediated effects in this study resulted mainly from direct predation on birds and nests or increased predation risk rather than food competition. In a remarkable long-term study, Wesolowski et al. (2009) showed that wood warbler (*Phylloscopus sibilatrix*) abundance in the Białowieża Forest was inversely correlated with small mammal predator densities and was only weakly correlated with caterpillar abundance; the nomadic behaviour of wood warblers appears to be a consequence of their attempts to breed in safe places. Although most studies focused on the direct adverse effects of wild ungulates on habitat alterations and invertebrate availability, large herbivores may affect many species of plants and animals through indirect effects (Suominen & Danell 2006, Barrios-García & Ballari 2012). Large ungulate concentrations may have both positive and negative effects on insectivorous birds, positive effects probably being mediated by nutrient input through the ecosystem (Mathisen & Skarpe 2011, Mathisen et al. 2012). This type of complex interaction may explain the observation in our study that tree-gleaning birds showed modest increases in areas strongly foraged by wild boar.

Surprisingly, the use of foraging traces as an indicator of wild boar impacts on ground-nesting birds has hitherto never been tested (Massei & Genov 2004, Barrios-García & Ballari 2012). We found that wild boar foraging traces provided a simple indicator of ground-nesting bird disturbance. Our results provide evidence for the utility of this method since it was highly correlated with GN bird abundances but not with other avian guilds (tree-nesting or ground-gleaning birds). The protocol described in this study has numerous advantages. First, the measurements do not depend on biological experts for bird species determination; in other words, anyone can perform an inventory of wild boar foraging signs resulting from rooting activity. Wild boar rooting signs are easily detected, and the probability of detection is likely constant among different observers using a standardised protocol. Second, wild boar rooting signs can be rapidly measured, which may prove helpful in monitoring programs designed to track annual changes in wild boar environmental impact on ground ecosystems at large spatial scales. Finally, monitoring wild boar impacts on the avifauna does not require previous knowledge of wild boar population size.

We thus conclude that Ikf may be a simple and suitable indicator that can be used at large scales to monitor wild boar potential disturbance on ground-nesting birds and negative or positive effects on other taxa. Further studies are needed to test and validate this new indicator in areas other than the Sainte-Baume Regional Park.

Acknowledgements

We thank Gilles Cheylan and Philippe Orsini for fruitful discussions and exchanges. We are grateful to the anonymous reviewers who helped us to improve the manuscript. We thank Florence Cheong (native English speaker) and Alice Cheylan (native English speaker) for reviewing the English version.

Author Contributions

F. Roda conceptualised and designed the experiments. F. Roda and J.-M. Roda analysed the data. J.-M. Roda contributed analysis tools. F. Roda wrote the paper. All authors agree with the contents of the manuscript and its submission to *the journal. Neither the manuscript nor any parts of its contents are currently under consideration or published in another journal. All authors disclose any potential conflict of interest with other people or organisations that could inappropriately influence their work.*

Data Availability Statement

The data supporting this study's findings are available in the FigShare Digital Repository: https://figshare.com/account/articles/25099805.

Literature

Acevedo P., Vicente J., Höfle U. et al. 2007: Estimation of European wild boar relative abundance and aggregation: a novel method in epidemiological risk assessment. *Epidemiol. Infect. 135: 519.*

Allombert S., Gaston A. & Martin J. 2005b: A natural experiment on the impact of over-abundant deer on songbird populations. *Biol. Conserv. 126: 1–13.*

Allombert S., Stockton S. & Martin J. 2005a: A natural experiment on the impact of over-abundant deer on forest invertebrates. *Conserv. Biol. 19: 1917–1929.*

Ballouard J.-M., Kauffmann C., Besnard A. et al. 2021: Recent invaders in Small Mediterranean Islands: wild boar impact snakes in Port-Cros National Park. *Diversity 13: 498–511.*

Barrios-García M. & Ballari S. 2012: Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biol. Invasions 14: 2283–2300.*

Baubet E., Bonenfant C. & Brandt S. 2004: Diet of the wild boar in the French Alps. *Galemys 16: 101–113.*

Blondel J., Ferry C. & Frochot B. 1970: La méthode des indices ponctuels d'abondances (IPA) ou des relevés d'avifaune par stations d'écoutes. *Alauda 38: 55–71.*

Bonthoux S. & Balent G. 2012: Point count duration: five minutes are usually sufficient to model the distribution of bird species and to study the structure of communities for a French landscape. *J. Ornithol. 153: 491–504.*

Bourcet J., Bracque P., De Nonancourt P. & Sapor C. 2003: Evaluation des risques liés à l'augmentation des densités des sangliers sauvages en France. *Inspection générale de l'environnement, rapports publics. https://medias.vie-publique.fr/data_storage_s3/rapport/pdf/034000731.pdf*

Carpio A., Guerrero-Casado J., Ruiz-Aizpurua L. et al. 2014a: The high abundance of wild ungulates in a Mediterranean region: is this compatible with the European rabbit. *Wildl. Biol. 20: 161–166.*

Carpio A., Guerrero-Casado J., Tortosa F.S. & Vicente J. 2014b: Predation of simulated red-legged partridge nests in big game estates from south central Spain. *Eur. J. Wildl. Res. 60: 391–394.*

Cederlund G., Duncan P., Bergqvist J. et al. 1998: Managing roe deer and their impact on the environment: maximising the net benefits to society. *The European Roe Deer: the Biology of Success, Scandinavian University Press, Oslo, Norway: 337–372.*

Chalfoun A.D. & Martin T.E. 2007: Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *J. Appl. Ecol. 44: 983–992.*

Chalfoun A.D. & Martin T.E. 2009: Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. *J. Anim. Ecol. 78: 497–503.*

Chamberlain D., Fuller R. & Bunce R. 2000: Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J. Appl. Ecol. 37: 771–788.*

Chevrier T., Said S., Widmer O. et al. 2012: The oak browsing index correlates linearly with roe deer density: a new indicator for deer management. *Eur. J. Wildl. Res. 58: 17–22.*

Côté S., Rooney T., Tremblay J. & Dussault C. 2004: Ecological impacts of deer over-abundance. *Annu. Rev. Ecol. Evol. Syst. 35: 113–147.*

Cresswell W. 2008: Non-lethal effects of predation in birds. *Ibis 150: 3–17.*

Flitti A., Kayser Y., Kabouche B. & Olioso G. 2009: Atlas des oiseaux nicheurs de Provence-Alpes-Côte d'Azur. *Delachaux et Niestlé, Paris, France.*

Flueck W. 2000: Population regulation in large northern herbivores: evolution, thermodynamics, and large predators. *Z. Jagdwiss. 46: 139–166.*

Focardi S., Capizzi D. & Monetti D. 2000: Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. *J. Zool. 250: 329–334.*

Fuller R., Smith K., Grice P. et al. 2007: Habitat change and woodland birds in Britain: implications for management and future research. *Ibis 149 (Suppl. 2): 261–268.*

Fuller R., Stuttard P. & Ray C. 1989: The distribution of breeding songbirds within mixed coppiced woodland in Kent, England, in relation to vegetation age and structure. *Ann. Zool. Fenn. 26: 265–275.*

Gomez J., García D. & Zamora R. 2003: Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. *For. Ecol. Manag. 180: 125–134.*

Gregory R. & Van Strien A. 2010: Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithol. Sci. 9: 3–22.*

Gregory R.D., Voříšek P. & Strien A. 2007: Population trends of widespread woodland birds in Europe. *Ibis 149 (Suppl. 2): 78–97.*

Gregory R.D., Willis S.G., Jiguet F. et al. 2009: An indicator of the impact of climatic change on European bird populations. *PLOS ONE 4: e4678.*

Holt C.A., Fuller R.J. & Dolman P.M. 2011: Breeding and post-breeding responses of woodland birds to modification of habitat structure by deer. *Biol. Conserv. 144: 2151–2162.*

Howe T.D., Singer F.J. & Ackerman B.B. 1981: Forage relationships of European wild boar invading northern hardwood forest. *J. Wildl. Manag. 45: 748–754.*

Jiguet F., Devictor V., Julliard R. & Couvet D. 2012: French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. *Acta Oecol. 44: 58–66.*

Jiguet F., Gadot A., Julliard R. et al. 2007: Climate envelope, life history traits and the resilience of birds facing global change. *Glob. Change Biol. 13: 1672–1684.*

Jolley D.B., Ditchkoff S.S., Sparklin B.D. et al. 2010: Estimate of herpetofauna depredation by a population of wild pigs. *J. Mammal. 91: 519–524.*

Joys A.C., Fuller R.J. & Dolman P.M. 2004: Influences of deer browsing, coppice history, and standard trees on the growth and development of vegetation structure in coppiced woods in lowland England. *For. Ecol. Manag. 202: 23–37.*

Julliard R., Jiguet F. & Couvet D. 2004a: Common birds facing global changes: what makes a species at risk. *Glob. Change Biol. 10: 148–154.*

Julliard R., Jiguet F. & Couvet D. 2004b: Evidence for the impact of global warming on the long-term population dynamics of common birds. *Proc. R. Soc. Lond. B Biol. Sci. 271 (Suppl. 6): S490–S492.*

Kéry M. & Schmidt B. 2008: Imperfect detection and its consequences for monitoring for conservation. *Community Ecol. 9: 207–216.*

Krammer M. 2016: Le Daim européen. In: LPO PACA, GECEM & GCP (eds.), Les mammifères de Provence-Alpes-Côte d'Azur. *Biotope, Mèze, France: 210–211.*

Lozano J., Virgós E., Cabezas-Díaz S. & Mangas J.G. 2007: Increase of large game species in Mediterranean areas: is the European wildcat (*Felis silvestris*) facing a new threat. *Biol. Conserv. 138: 321–329.*

Lyashevska O. & Farnsworth K. 2012: How many dimensions of biodiversity do we need. *Ecol. Indic. 18: 485–492.*

Martin T.E. 1988: Habitat and area effects on forest bird assemblages: is nest predation an influence. *Ecology 69: 74.*

Martin T.E. 1996: Fitness costs of resource overlap among coexisting bird species. *Nature 380: 338–340.*

Massei G. & Genov P. 2004: The environmental impact of wild boar. *Galemys 16: 135–145.*

Massei G., Kindberg J., Licoppe A. et al. 2015: Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Manag. Sci. 71: 492–500.*

Mathisen K.M., Pedersen S., Nilsen E.B. & Skarpe C. 2012: Contrasting responses of two passerine bird species to moose browsing. *Eur. J. Wildl. Res. 58: 535–547.*

Mathisen K.M. & Skarpe C. 2011: Cascading effects of moose (*Alces alces*) management on birds. *Ecol. Res. 26: 563–574.*

Météo France 2015: French national meteorogical service (period 1981-2010). *Accessed on December 2015. http://www.meteofrance.com*

Milner J., Bonenfant C., Mysterud A. et al. 2006: Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *J. Appl. Ecol. 43: 721–734.*

Morellet N., Gaillard J., Hewison A. et al. 2007: Indicators of ecological change: new tools for managing populations of large herbivores. *J. Appl. Ecol. 44: 634–643.*

Nichols J. & Williams B. 2006: Monitoring for conservation. *Trends Ecol. Evol. 21: 668–673.*

Oja R., Soe E., Valdmann H. & Saarma U. 2017: Non-invasive genetics outperforms morphological methods in faecal dietary analysis, revealing wild boar as a considerable conservation concern for ground-nesting birds. *PLOS ONE 12: 1–9.*

Picard J. 1988: Evaluation de la charge en gibier par analyse floristique. *Rev. For. Fr. 40: 77–84.*

Poulard F., Dietrich R., Nasi N. & Roda F. 2021: Suivi d'une meute de loups au coeur de la Provence à l'aide d'un chien de détection et de pièges photographiques: prédation, utilisation de l'espace, et comportement de marquage par les loups en fonction des saisons. *Faune PACA Publication 108: 1–27.*

Quine C., Fuller R., Smith K. & Grice P. 2007: Stand management: a threat or opportunity for birds in British woodland. *Ibis 149: 161–174.*

Ries L. & Sisk T. 2004: A predictive model of edge effects. *Ecology 85: 2917–2926.*

Roda F. 2016: Le Cerf élaphe. In: LPO PACA, GECEM & GCP (eds.), Les mammifères de Provence-Alpes-Côte d'Azur. *Biotope, Mèze, France: 206–207.*

Roda F., Poulard F., Ayache G. et al. 2022: How do seasonal changes in wolf defecation patterns affect scat detection probabilities of trained dog surveys. *J. Vertebr. Biol. 71: 22043.*

Roda F., Sentilles J., Molins C. et al. 2020: Wolf scat detection dog improves wolf genetic monitoring in new French colonised areas. *J. Vertebr. Biol. 69: 20102.*

Saniga M. 2002: Nest loss and chick mortality in capercaillie (*Tetrao urogallus*) and hazel grouse

(*Bonasa bonasia*) in West Carpathians. *Folia Zool. 51: 205–214.*

Saniga M. 2003: Ecology of the capercaillie (*Tetrao urogallus)* and forest management in relation to its protection in the West Carpathians. *J. For. Sci. 49: 229–239.*

Stockton S., Allombert S., Gaston A. & Martin J. 2005: A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests. *Biol. Conserv. 126: 118–128.*

Suhonen J. 1993: Predation risk influences the use of foraging sites by tits. *Ecology 74: 1197–1203.*

Suominen O. & Danell K. 2006: Effects of large herbivores on other fauna. In: Danell K., Bergström R., Duncan P. & Pastor J. (eds.), Large herbivore ecology, ecosystem dynamics and conservation. *Cambridge University Press, Cambridge, UK: 383–412.*

Thomson R.L., Forsman J.T., Sardà-Palomera F. & Mönkkönen M. 2006: Fear factor: prey habitat selection and its consequences in a predation risk landscape. *Ecography 29: 507–514.*

Voříšek P., Jiguet F. & Van Strien A. 2010: Trends in abundance and biomass of widespread European farmland birds: how much have we lost. *BOU Proceedings – Lowland Farmland Birds III., Leicester, UK. http://www.bou.org.uk/bouproc-net/lfb3/vorisek-etal.pdf*

Wesolowski T., Rowinski P. & Maziarz M. 2009: Wood warbler *Phylloscopus sibilatrix*: a nomadic insectivore in search of safe breeding grounds. *Bird Study 56: 26–33.*

Wilcox J. & Van Vuren D. 2009: Wild pigs as predators in oak woodlands of California. *J. Mammal. 90: 114–118.*