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RESEARCH ARTICLE

Impact of hunting modality on social contacts in wild boar populations across Europe

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Abstract

1. Variation in animal social interactions emerges from individual responses to social and physical environments and plays a key role in shaping pathogen transmission, gene flow and information transfer. Although hunting can induce changes in contact patterns through disruption of the social environment, the non-consumptive effects of hunting have not received much attention compared to demographic effects of harvest.
2. We examined the effects of hunting activities on contact rates in wild boar, a species particularly exposed to social disruptions owing to its high sociality and intense management. Using GPS-telemetry data from 21 populations across Europe (435 unique dyads), we analysed how hunting activities impact social contacts within and between wild boar groups while accounting for confounders potentially shaping contact heterogeneity (e.g. habitat productivity, population density, predation, seasonality, individuals' sex and spatial proximity).
3. We found that drive hunts, but not individual hunts, lowered contact rates within wild boar groups. Contact rates tended to be negatively related to drive hunts' frequency.
4. We did not observe the effect of hunting mode on contact rates between members of different groups, which was mainly shaped by a positive relationship with spatial proximity. Contact probability among females from different groups was lower compared to male–male or mixed-sex dyads.
5. *Synthesis and applications*. Our study showcases how hunting disturbance influences social contact rates in a group-living wild mammal. Along with other biotic and abiotic drivers, hunting modality plays a significant role in shaping intra-group, but not inter-group, contacts. Reduced group cohesion induced by

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drive hunts could negatively impact survival, foraging efficiency, and resource utilization. Hunting management could mitigate those negative impacts by spatially spreading driven areas throughout the season and targeting different groups each time. Our results suggest that hunting disturbances should not enhance disease spread through increased inter-group contacts. Yet, hunting-induced escape movements could still pose a risk of transmission into new areas. Inter-group connectedness appeared to be maintained predominantly by males which could be targeted if disease transmission was a major management objective. Spatial proximity between individuals can be a reliable index of the amount of direct contacts within wild boar populations.

KEYWORDS
disturbance, Euroboar, GPS-telemetry, *Sus scrofa*, wildlife management

1 | INTRODUCTION

Animal societies are characterized by variation in contact patterns, underlying key population processes, such as pathogen transmission (Altizer et al., 2003; Bansal et al., 2007), gene flow (Altmann et al., 1996; Archie et al., 2008) and information transfer (Aplin et al., 2015; McComb et al., 2001). This heterogeneity in animal contacts arises from social preferences and spatial decisions of individuals in a population. Individual interactions with their social and spatial environment shape the emerging contact structure which is inherently dynamic owing to the nature of social and ecological processes (Webber et al., 2023). From the ecological side, contact rates can be impacted by the distribution and phenology of resources (Karczmarski et al., 2005; Peignier et al., 2019), habitat structure (Leu et al., 2016) and predation risk (Groenewoud et al., 2016; Kelley et al., 2011). From the social side, contact patterns can be shaped by kinship (Archie et al., 2006; Podgórski, Lusseau, et al., 2014), reproductive behaviour (Edenbrow et al., 2011), population-level factors, such as density and spatial distribution of conspecifics (Vander Wal et al., 2014) and individual-level characteristics, such as sex and age (Rushmore et al., 2013; Rushmore et al., 2023), personality (Wolf & Krause, 2014), reproductive status (Rushmore et al., 2013) and social preferences (Gero et al., 2015).

Among the many factors shaping contact patterns, landscape of fear—including anthropogenic disturbances—can significantly affect the social environments of individuals. Activities such as hunting and fishing, by directly removing individuals (i.e. consumptive effect), disrupt group cohesion and composition, altering social connectivity and reducing foraging efficiency (Maldonado-Chaparro et al., 2018) and survival (Bond et al., 2021; Busson et al., 2019). Selective harvesting of specific age and sex classes or key group members can, for example, lead to the loss of habitat and social knowledge (McComb et al., 2001), increased infanticide (Swenson et al., 1997), induced abortion (Berger, 1983), disease spread (Carter et al., 2007) and ultimately lower vital rates (Milner et al., 2007). Hunting may also exert non-consumptive effects on animal behaviour triggering changes in habitat use, temporal activity and antipredator strategies (i.e. landscape of fear), especially when hunting activity is spatially and temporally unpredictable (Cromsigt et al., 2013; Potratz et al., 2024). Ecotourism, intensive recreational activities and hunting disturbances are suspected to have equally detrimental impacts as direct harvesting (Montgomery et al., 2022). Yet, non-consumptive effects of hunting disturbances on social interactions have not received much attention compared to direct removal and their potential effects remain poorly understood (Slovikosky & Montgomery, 2024).

One species particularly exposed to such social disruptions through hunting and intensive management (Massei et al., 2015) is the wild boar (*Sus scrofa*), a highly social species. Indeed, wild boar hunting was shown to exert evolutionary pressure on life history traits (Gamelon et al., 2011) and induce behavioural responses (Keuling & Massei, 2021). The latter include temporary displacements (Olejarz et al., 2024; Tolon et al., 2009), changes in home range size (Scillitani et al., 2010), habitat use (Drimaj et al., 2021; Saïd et al., 2012) and activity patterns (Johann et al., 2020). However, evidence for the effects of hunting on wild boar behaviour remains somewhat ambiguous with results often confounded by seasonality (Brivio et al., 2017; Keuling et al., 2008; Keuling & Massei, 2021). Intensive hunting practices (e.g. drive hunts) could potentially disrupt strong social and spatial structuring of wild boar populations (Podgórski et al., 2018) by inducing escape movements and unnatural groupings. A relatively weak kin structure observed in a heavily hunted population in Italy was suggested to have arisen from random associations of the hunting survivors (Iacolina et al., 2009). Despite these observations, the effects of hunting on wild boar social behaviour and structure remain largely unstudied. Filling this knowledge gap could help us better understand and manage the epizootic of African swine fever (ASF) which is currently spreading throughout the species' geographic range (EFSA et al., 2024; Jiang et al., 2022). More broadly, a better understanding of how hunting affects the social behaviour and structuring of common game species is essential for ensuring sustainable management that does not introduce artificial selection pressures or exacerbate human–wildlife conflicts.

Here, we examine the effects of hunting on direct contact rates in wild boar using GPS-telemetry data from 21 European populations at two temporal scales: the monthly scale of the hunting season and the daily scale of the hunting event, while accounting for confounders arising from life history, social behaviour, distribution of individuals in space, population density, predation and habitat which potentially shape contact heterogeneity. Specifically, we tested the effect of two contrasting hunting modes: driven hunts, which involve large, coordinated group efforts to make animals flee, and individual hunting, where a single hunter selectively targets individuals. We hypothesized that hunting modes would interact with social structure and have a differential impact on social contacts within and between wild boar groups. We expected that during drive hunting months and events (i) within-group contacts would decrease due to disturbance-related escape movements and group fission, and (ii) between-groups contacts would increase due to regrouping and random associations. We expected that individual hunts would not have the same level of disturbance effect as drive hunts and would not affect contact rates.

2 | MATERIALS AND METHODS

2.1 | Data

We used GPS data of wild boar tracked across Europe in 2007–2022 using the Euroboar database, which is part of Euromammals, a collaborative scientific network that aims to understand large-scale mammalian movement ecology (Urbano et al., 2021). We selected study areas (i.e. populations) with at least two individuals tracked simultaneously for at least 1 month (herein defined as a dyad) which was a basic temporal unit of the subsequent analyses. The dataset consisted of 1610 unique dyad-months from 21 study areas, 9 European countries, 289 GPS-marked individuals (Figure 1; Table S1, see Table S2 for sex/age structure). Mean (±SD) tracking period of a pair of individuals was 3.7 months ± 2.63 (min–max: 1–16).

Initially, GPS sampling rates ranged from 5 to 60 min across study areas. To maintain consistency, sampling rates were equalized to 60-min intervals across all study areas. We used the simple ratio index (SRI) of dyadic association (Cairns & Schwager, 1987; Hoppitt & Farine, 2018) to quantify inter-individual contacts. SRI is defined as the number of observations of two individuals together divided by the total number of observations of either of them and corresponds to the proportion of time two individuals spend together. SRI ranges from 0 (two individuals never observed together) to 1 (always together). To ensure unbiased estimation of SRI (He et al., 2022; Hoppitt & Farine, 2018), sampling schedules across pairs of individuals at the study area level were cross-checked to contain only GPS fixes with matching timestamps. We used a spatial threshold of 25 m and a temporal window of 5 min to define contacts. The thresholds were chosen to account for variation in location accuracy and acquisition times of GPS fixes. Association indices were computed with the 'spatsoc' package (Robitaille et al., 2019) of the R environment (R Core Team, 2020).

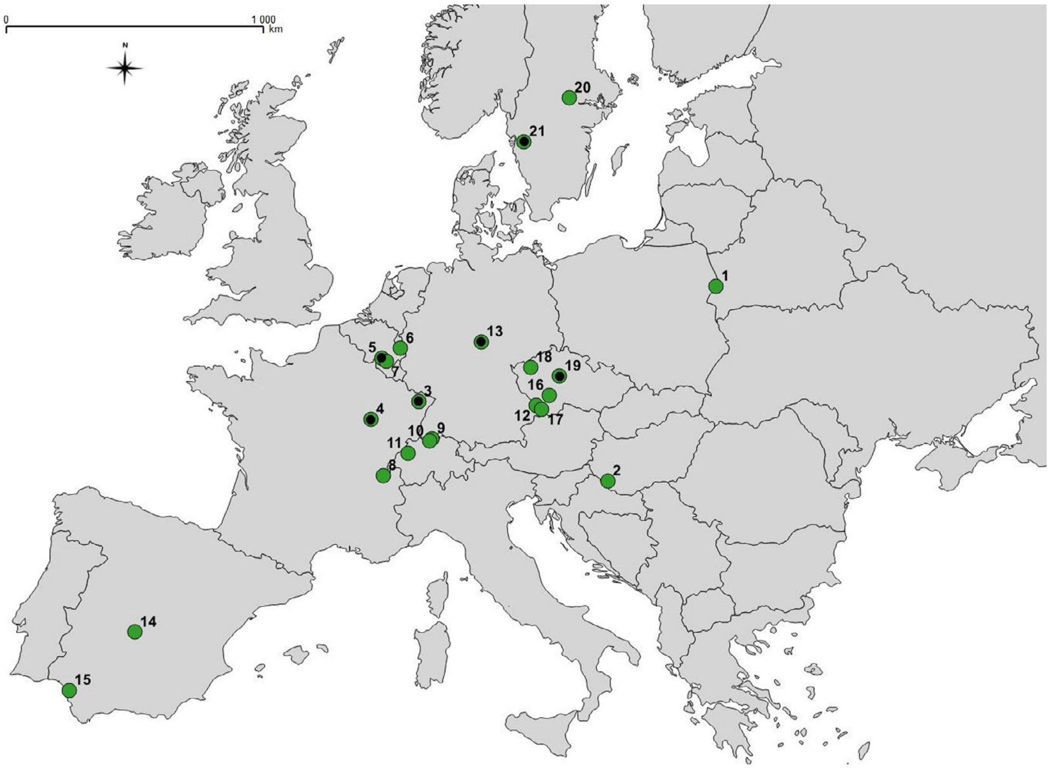

FIGURE 1 Study areas across Europe. Green dots represent areas which provided telemetry and hunting data on the monthly scale, black-filled green dots additionally provided data on a daily scale. Numbers correspond to study area ID, see Table S1 for more detailed information.

Wild boar is a group-living species with contact rates typically higher by an order of magnitude among individuals within groups than between groups (Pepin et al., 2016; Podgórski et al., 2018). Therefore, we decided to analyse within- and between-group contacts separately due to their different dynamics, scales and underlying processes. To determine the group membership of individuals at the study area level, we calculated six social cohesion indices (Table S3) for each dyad based on GPS location data using the WildlifeDI package (Long et al., 2022). Next, we performed a clustering analysis based on social cohesion indices using the k-means clustering algorithm as implemented in the 'cluster' package (Maechler et al., 2022). The number of clusters (*k* parameter) was set to 2 ('within-group' and 'between-group') with 25 runs to optimize the partitioning of the dataset. Clustering analysis divided the dataset into 243 and 1367 within- and between-group dyads, respectively. Monthly spatial overlap for each pair of individuals was calculated using the volume of intersection (VI) index (Fieberg & Kochanny, 2005) using the 'adehabitatHR' package (Calenge, 2006). The VI index method measures the similarity of two kernel utilization distributions (UD) and ranges between 0 (no overlap) and 1 (identical UDs). Only dyads with monthly spatial overlap >0 were included in the analysis. Pairwise spatial overlap was used as one of the covariates in the models explaining variation in contact rates to account for the spatial distribution of individuals.

Information on hunting management practices was collected at the monthly scale for each study area, that is population. Specifically, we focused on hunting modalities as they are likely to influence contact rates. Categories of hunting modalities included no hunting, individual hunts and drive hunts (see Tables S4 and S5 for sample sizes). Drive hunts have been shown to elicit stronger spatial response (flight) compared to individual hunts (Keuling et al., 2008; Thurfjell et al., 2013) and the response increased with higher frequency of drive hunts (Olejarz et al., 2024). The individual hunts (one person, silent) category included months with single hunts only, mainly hunting from hides but also stand-stalking. The frequency of individual hunts averaged 14 hunting days per month (min–max: 6–20, data from 6 areas; see Table S6 showing temporal distribution across the year). The drive hunts (collective hunts, multiple people and dogs) category included months with drive hunts only as well as months when drive and individual hunts were performed simultaneously. We merged the two modalities here due to the assumed stronger disturbing effect of drive hunts. The frequency of drive hunts averaged 3.5 days per month (min–max: 1–10, data from 12 areas) with two drives per hunting day involving 30 people and dogs (data from 9 areas).

For six study areas, we could obtain information on drive hunts at the daily scale (53 hunting days; Figure 1). To accurately capture the potential effects of the hunt on contact rates, we selected dyads in which both individuals overlapped spatially with the driven area during the same hunt. The overlap between the driven area and a particular dyad was calculated as the percent overlap of the hunting polygon and the daily home range of each individual of the dyad. Only if both individuals of the pair showed overlap with the driven area during the hunting day, were they considered for further analysis. We computed daily SRI for the drive hunt day and for four randomly chosen non-hunting days (one per week within the same month), separated by at least 3 days from the hunting event, as a control group. We chose 4 days as a balanced number to maintain a sufficient temporal distance from the hunting event while ensuring all comparisons remained within the same month for consistency. This resulted in a dataset of 230 dyad days (Table S7). Two types of models were fitted to within- and between-group contact data due to inherent differences in data structure (Figure S1).

2.2 | Statistical analyses: Within-group contacts

Within-group contacts had SRI >0 in all of the analysed months and days with large variation (median $=0.41$, interquartile range (IQR) $=0.33$ and median $=0.36$, IQR $=0.24$, respectively; Figure S1) and were thus modelled as a continuous response variable. Variation in monthly and daily contacts within groups was examined with generalized linear mixed-effects models with a beta distribution and 'logit' link function.

For variation in monthly contacts, we tested the effect of hunting modality (categorical predictor; drive hunts, individual hunts, no hunts) while accounting for confounding variables potentially influencing contact rates. We included (1) the phase of the wild boar biological cycle (categorical; mating: Nov.–Jan., farrowing: Feb.–Apr., summer: May–Aug., autumn: Sep.–Oct.); (2) sex (categorical; male dyad, female dyad, mixed dyad); and (3) spatial overlap, to account for proximity between each pair of individuals (continuous; proportion of overlapping home range, exponentially transformed following preliminary data exploration). We also considered predictors reflecting heterogeneity in environmental conditions across study areas and potentially underpinning contact rate dynamics and spatial behaviour, namely (4) wolf occurrence in the study area (categorical; present, absent), to account for the presence of the wild boar's main predator; (5) wild boar relative abundance index, as a proxy for wild boar density (continuous; number of individuals culled/km^2), (6) mean annual net primary productivity, to account for food availability (continuous; g C/m^2), (7) mean annual temperature, as a proxy for climate severity (continuous; °C). Additionally, (8) drive hunts frequency (average monthly number of drive hunts in the study area) was added to a separate model fitted to a limited subset of data for which this variable was available. Details on the rationale for and compilation of the above variables are reported in Supporting Information.

For variation in daily contacts, only the effect of the drive hunt was tested by fitting a binary predictor (categorical; presence of drive hunt, absence of drive hunt) to the daily data. Models for the daily scale were reduced because their main purpose was to contrast the effects of drive hunts at the hunting event scale and because limited sample size precluded including other predictors. Spatial overlap (transformed as above) was also fitted as a continuous predictor.

Random effects initially included pair ID nested in the study area. However, the variance of the 'study area' was estimated at zero leading to a singular fit of the within-group models, and thus only 'pair ID' was retained. The initial random structure was retained for between-group models.

2.3 | Statistical analyses: Between-group contacts

Between-group pairs of individuals had SRI = 0 (i.e. no contact) in 64% of months and 78% of days which produced an excess of zeros in this subset of data (Figure S1). Additionally, the monthly SRI distribution was highly skewed with little variation (median = 0, IQR = 0.0008) even in the positive-only subset of data, that is SRI > 0 (median = 0.002, IQR = 0.007). Between-group contacts were thus modelled as a binary process for improved model fit and with negligible loss in data resolution. SRI values were converted into a binary response variable (0: no contact, i.e. SRI = 0; 1: contact, i.e. SRI > 0). The probability of monthly and daily contact between groups was examined using zero-inflated models (Brooks et al., 2017). The conditional part of the model (i.e. examining variation in the response) was fit with the binomial family and 'logit' link, including, along with hunting modality, the same confounding variables as the model on within-group contact (predictors 1–7), as well as the pair ID nested within the study area as random intercepts. The zero-inflated part of the model (i.e. examining the probability of observing extra zeros) was fit with the default binomial distribution and 'logit' link and allowed the probability of producing zero to vary with spatial overlap because we assumed a positive relationship between proximity and contact, that is individuals from far-away groups are unlikely to associate, thus producing an excess of zeros. A separate model was fitted to the limited subset of data with added information on the frequency of drive hunts.

Similarly to the within-group contacts daily model, the model for between-group contacts based on daily data only included a binary predictor of drive hunt, and the zero-inflation part of the model allowed the probability of producing zero to vary with spatial overlap.

2.4 | Statistical analyses: Inference

In all models, we tested support for the effect of hunting modality by comparing the full model against an identical model excluding the hunting modality (null model), using the likelihood ratio test. Then, for models at the monthly timescale, we assessed differences between the effect of hunting modality (drive hunts vs. individual hunts vs. no hunts) on contact rates by performing Tukey's post hoc comparisons. In each full model, the interactive effects of sex and hunting modality were initially tested but eventually not retained as the likelihood ratio tests showed no support for the models including the interaction terms (within-groups models: $\chi^2 = 2.05$, $p = 0.727$, between-groups models: $\chi^2 = 6.17$, $p = 0.187$).

Analyses were run in R version 3.6.1. Statistical models were fitted using the 'glmmTMB' package (Brooks et al., 2017), likelihood ratio tests were conducted using the 'lmtest' package (Zeileis & Hothorn, 2002), and Tukey's post hoc comparisons were performed using the 'multcomp' package. Model diagnostics were performed using the 'DHARMa' package (Hartig, 2020), and multicollinearity was checked using the 'performance' package (Lüdecke et al., 2021). The diagnostics included testing for residual heterogeneity and dispersion, and model overfitting. No significant issues were detected. Model predictions were generated with the R package 'ggeffects' (Lüdecke, 2018) by holding non-target variables constant at their means.

3 | RESULTS

3.1 | Contact rates

Individuals within groups associated at a monthly rate of mean SRI = 0.42, CI 95%: 0.39–0.45 (Figure S1a), while between-group interactions were much less frequent at mean SRI = 0.007, CI 95%: 0.005–0.009 (Figure S1b).

3.2 | Hunting effects

We found that within-group contacts were less frequent during months when drive hunts were performed compared to months without hunting or with individual hunts only (Figure 2a). Specifically, SRI during months with drive hunts, as predicted by the model, averaged (mean [CI 95%]: 0.22 [0.15–0.33]), which was significantly lower than in months with no hunting (0.45 [0.31–0.60]) or with only individual hunts (0.44 [0.32–0.58]) (Table 1). Decreased contact rates at drive hunts were also observed on a daily scale within drive hunt months (Figure 2b). On average, predicted SRI during drive hunt days (0.18 [0.08–0.36]) was significantly lower compared to non-hunting days (0.38 [0.22–0.56]; Table 2; Figure 2). Likelihood ratio tests between the full and the null models showed strong support for the effect of hunting modality at a monthly scale ($\chi^2 = 28.94$, $p < 0.001$) and the effect of drive hunts at a daily scale ($\chi^2 = 8.65$ $p = 0.003$) on contact rates within groups. The full model fitted to the subset of data containing information on the frequency of drive hunts showed a tendency for lower contact rates with more frequent drive hunts (likelihood ratio test $\chi^2 = 3.70$, $p = 0.054$; Table S8). Predicted SRI decreased from 0.32 [0.11–0.64] at one drive hunt/month to 0.11 [0.02–0.45] at 10 drive hunts/month.

Predicted contact probabilities among individuals from different groups did not differ across months with individual hunts (0.44 [0.26–0.64]), drive hunts (0.47 [0.29–0.66]), or without hunting (0.46 [0.27–0.67]) (Figure 2c; Table 3). On a daily scale, contact probability during non-hunting days (0.03 [0.00–0.26]) tended to be slightly higher compared to drive hunts days (0.00 [0.00–0.13]) (Figure 2d;

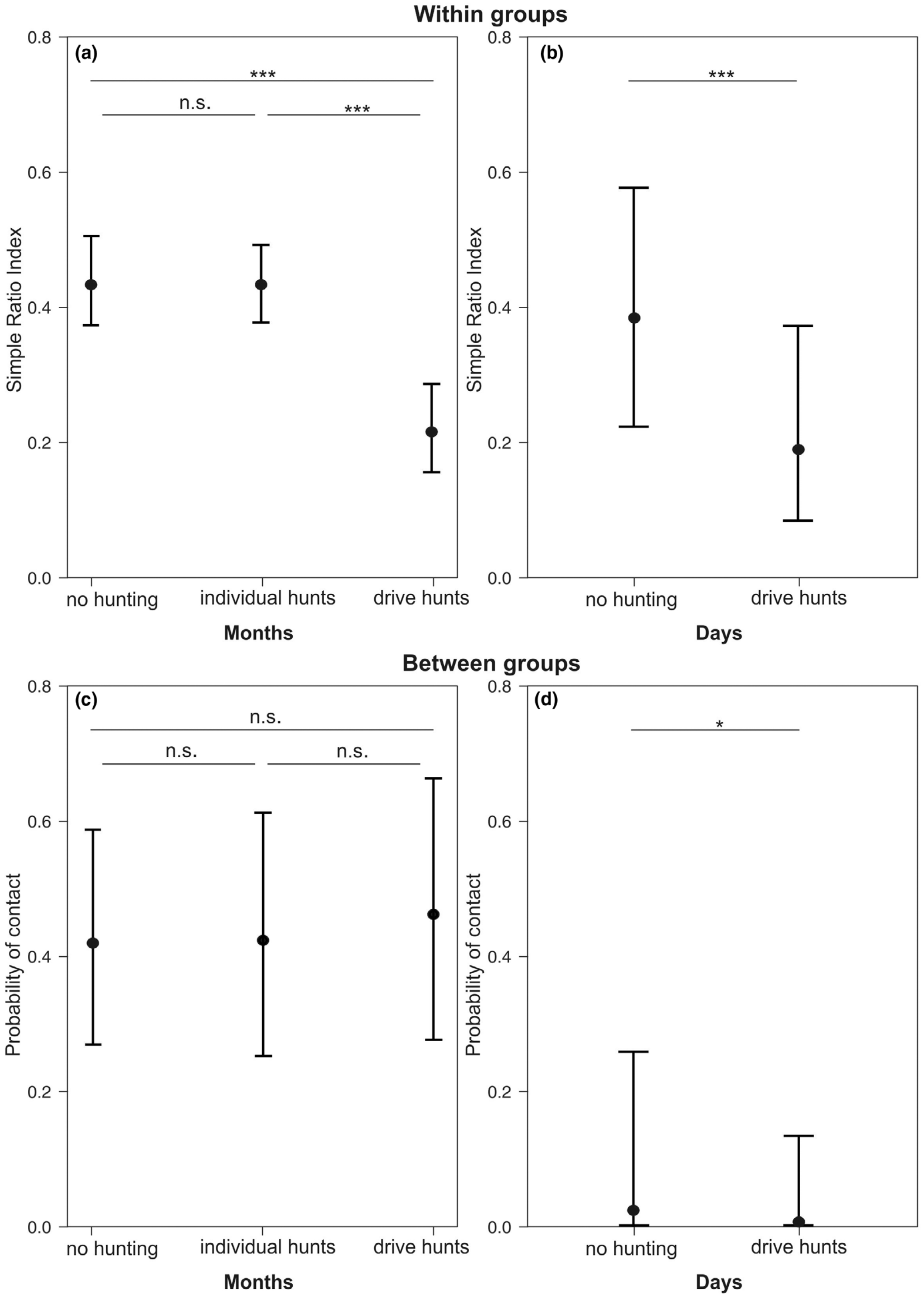

FIGURE 2 Model predictions for the effects of monthly hunting modality and daily drive hunts on contact rates within (a, b) and between (c, d) wild boar groups. Statistical significance of the differences: n.s. $p>0.1$, *$0.1<p>0.05$, ***$p<0.0.1$.

Table 4). Likelihood ratio tests showed no support for the effect of hunting modality at a monthly scale ($\chi^2=0.28$, $p=0.873$) and a marginal support for the effect of drive hunts at a daily scale ($\chi^2=3.78$, $p=0.052$) on contact probability between groups. We found no effect of the frequency of drive hunts on the between-group contact probability (likelihood ratio test $\chi^2=2.36$, $p=0.125$; Table S9).

3.3 | Spatial, sex-related and seasonal effects

Our analyses also supported the effects of some confounding variables in driving social contact rates in wild boar. Distributions of spatial overlap of monthly and daily ranges showed opposing patterns within (left-skewed) and between (right-skewed) groups (Figure S2).

TABLE 1 Results of the generalized mixed-effect models for contact rates (simple ratio index) within wild boar groups at a monthly scale.

Predictors	Estimates	SE	*p*
(Intercept)	−0.22	0.271	0.409
Hunting mode (no hunt—individual)	0.03	0.185	0.887
Hunting mode (drive—no hunt)	−1.04	0.240	**<0.001**
Hunting mode (drive—individual)	−1.01	0.193	**<0.001**
Relative abundance index	−0.061	0.257	0.813
Productivity index	0.09	0.273	0.740
Mean annual temperature	−0.03	0.272	0.740
Wolf presence (yes)	−0.14	0.534	0.788
Season (farrowing—mating)	−0.20	0.190	0.719
Season (summer—mating)	−0.71	0.203	**0.002**
Season (autumn—mating)	−1.10	0.194	**<0.001**
Season (autumn—farrowing)	−0.90	0.200	**<0.001**
Season (summer—farrowing)	−0.51	0.145	**0.002**
Season (autumn—summer)	−0.39	0.180	0.135
Sex (males—mixed)	0.61	0.293	**0.037**
Sex (females—mixed)	0.54	0.222	**0.016**
Sex (males—females)	0.07	0.243	0.957
Home range overlap	0.35	0.058	**<0.001**
Random effects			
σ^2	0.05		
$\tau_{00\text{pair\_ID}}$	0.27		
ICC	0.85		
$N_{\text{pair\_ID}}$	58		
Observations	243		
Marginal R^2/conditional R^2	0.523/0.931		

Values in bold indicate statistical signifance (*p*-values < 0.05).

TABLE 2 Results of the generalized mixed-effect models for contact rates (simple ratio index) within wild boar groups at a daily scale.

Predictors	Estimates	SE	*p*
(Intercept)	−3.42	0.709	**<0.001**
Drive hunt day (yes)	−1.02	0.312	**0.002**
Home range overlap	3.88	0.698	**<0.001**
Random effects			
σ^2	0.02		
$\tau_{00\text{pair\_ID}}$	0.53		
ICC	0.96		
$N_{\text{pair\_ID}}$	4		
Observations	17		
Marginal R^2/conditional R^2	0.682/0.987		

Values in bold indicate statistical signifance (*p*-values < 0.05).

Dyadic monthly overlap among animals from the same group averaged 0.77 [0.75–0.80] while between-group overlap averaged 0.18 [0.17–0.19]. Spatial overlap played a major role in shaping contact rates among individuals within and between the groups across the dataset (Tables 1–4; Figure 3). Within groups, monthly contact rates ranged from SRI = 0.22 [0.13–0.36] to 0.50 [0.37–0.63] across a range of home overlap (min-max: 0.0004–0.948) (Figure 3). The predicted probability of contact between groups within a month increased from 0.18 [0.07–0.38] to 0.99 [0.97–1.00] across an overlap range of 0.0 to 0.9, respectively (Figure 3).

Sex of interacting individuals had a moderate effect on the contact rates within and between groups (Tables 1 and 3; Figure 4a,c). Within groups, predicted female–female and male–male associations occurred at a similar rate (SRI = 0.58 [0.45–0.70] and 0.60 [0.44–0.73], respectively), while mixed associations of males and females were less frequent (SRI = 0.44 [0.32–0.58]; Table 1; Figure 4a). The probability of between-group contact was similar in mixed-sex dyads (0.42 [0.22–0.65]) and males-only dyads (0.40 [0.20–0.65]), while females-only dyads showed a lower probability of contact (0.29 [0.13–0.51]) compared to mixed-sex dyads (Table 3; Figure 4c).

Seasonality in contact rates among individuals within groups was stronger than between groups (Tables 1 and 3; Figure 4b,d). Within groups, contact rates during mating and farrowing (SRI = 0.44 [0.32–0.58] and 0.40 [0.27–0.54], respectively) were similar but significantly higher than in summer and autumn (SRI = 0.28 [0.18–0.41] and 0.21 [0.13–0.31], respectively) (Table 1; Figure 4b). Between groups, on the other hand, monthly contact probabilities were comparable across seasons (Table 3; Figure 4d), ranging from 0.42 [0.22–0.65] during mating, 0.42 [0.23–0.63] in autumn, 0.54 [0.30–0.76] in summer, to 0.56 [0.32–0.78] during farrowing.

4 | DISCUSSION

In this study, we demonstrated how different modes of hunting impact contact rates in wild boar populations. Specifically, we found that contacts within wild boar groups were affected by drive hunts but not by individual hunts, while we did not observe the effect of hunting mode on contact rates between members of different groups. Drive hunts, which involve coordinated disturbance by hunters, beaters and dogs, are known to trigger strong behavioural responses in wild boar, for example increased movement, nocturnality and temporal shifts in habitat use (Chassagneux et al., 2020; Scillitani et al., 2010; Thurfjell et al., 2013; Tolon et al., 2009). Our results suggest that these responses also include reduced within-group contacts.

This decline in within-group contacts during drive hunt days could result from the direct chasing and the temporal scattering of group members by dogs and beaters. Reduced group cohesion suggests that the response to hunting disturbance is individual rather than collective. Notably, the effect was short-lived and within several

TABLE 3 Results of the zero-inflated mixed-effect models for contact probability between wild boar groups at a monthly scale.

Predictors	Estimates	SE	*p*
Count model			
(Intercept)	−0.32	0.481	0.506
Hunting mode (no hunt—individual)	−0.01	0.341	0.980
Hunting mode (drive—no hunt)	0.17	0.387	0.898
Hunting mode (drive—individual)	0.16	0.337	0.880
Relative abundance index	−0.19	0.308	0.532
Productivity index	−0.08	0.264	0.753
Mean annual temperature	−0.19	0.253	0.446
Wolf presence (yes)	−0.17	0.891	0.849
Season (farrowing—mating)	0.56	0.388	0.459
Season (summer—mating)	0.47	0.381	0.590
Season (autumn—mating)	−0.02	0.302	0.999
Season (autumn—farrowing)	−0.58	0.328	0.274
Season (summer—farrowing)	−0.09	0.252	0.984
Season (autumn—summer)	−0.49	0.306	0.360
Sex (males—mixed)	−0.08	0.283	0.959
Sex (females—mixed)	−0.60	0.238	**0.012**
Sex (males—females)	0.52	0.332	0.257
Home range overlap	1.21	0.139	**<0.001**
Zero-inflated model			
(Intercept)	−5.28	1.810	**0.004**
Home range overlap	−6.58	1.938	**0.001**
Random effects			
σ^2	3.29		
$\tau_{00\text{pair\_ID}}$	0.71		
$\tau_{00\text{area\_name}}$	1.01		
ICC	0.34		
$N_{\text{pair\_ID}}$	378		
$N_{\text{area\_name}}$	20		
Observations	1367		
Marginal R^2/conditional R^2	0.248/0.506		

Values in bold indicate statistical signifance (p-values <0.05).

TABLE 4 Results of the zero-inflated mixed-effect models for contact probability between wild boar groups at a daily scale.

Predictors	Estimates	SE	*p*
Count model			
(Intercept)	−23.75	9.732	**0.015**
Drive hunt day (yes)	−5.14	2.959	0.082
Home range overlap	16.89	6.977	**0.016**
Zero-inflated model			
(Intercept)	0.33	1.170	0.779
Overlap	−4.27	2.401	0.075
Random effects			
σ^2	3.29		
$\tau_{00\text{pair\_ID}}$	0.20		
$\tau_{00\text{area\_name}}$	13.79		
ICC	0.81		
$N_{\text{pair\_ID}}$	37		
$N_{\text{area\_name}}$	6		
Observations	213		
Marginal R^2/conditional R^2	0.642/0.932		

Values in bold indicate statistical signifance (p-values <0.05).

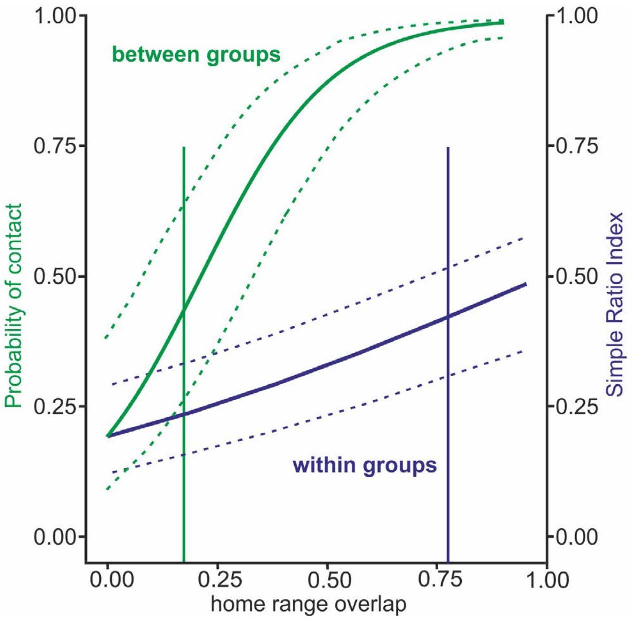

FIGURE 3 Relationships between home range (kernel utilization distribution) overlap and monthly contact rates (±95% CI) among individuals within and between wild boar groups. Vertical lines correspond to the mean overlap across the dataset.

days contact rates returned to levels comparable to the non-hunting season. This pattern is consistent with the known short duration and small spatial scale of flight responses to human (Wielgus et al., 2024) and hunting (Keuling et al., 2008; Olejarz et al., 2024; Scillitani et al., 2010) disturbances. While the disruptive effect of drive hunting events was short-lived, its repetitiveness (on average 3.5 drive hunt days per month) resulted in decreased contact rates during months with drive hunts. Group fission through disturbances can have various negative consequences. It can make group members more vulnerable to predation (Podgórski et al., 2016; Pulliam, 1973) and reduce their foraging efficiency (Maldonado-Chaparro et al., 2018; Rieucau & Giraldeau, 2011) by limiting the transfer of social cues, lower group coordination and suboptimal resource utilization (Rieucau & Giraldeau, 2011). Whether hunting-induced disruptions

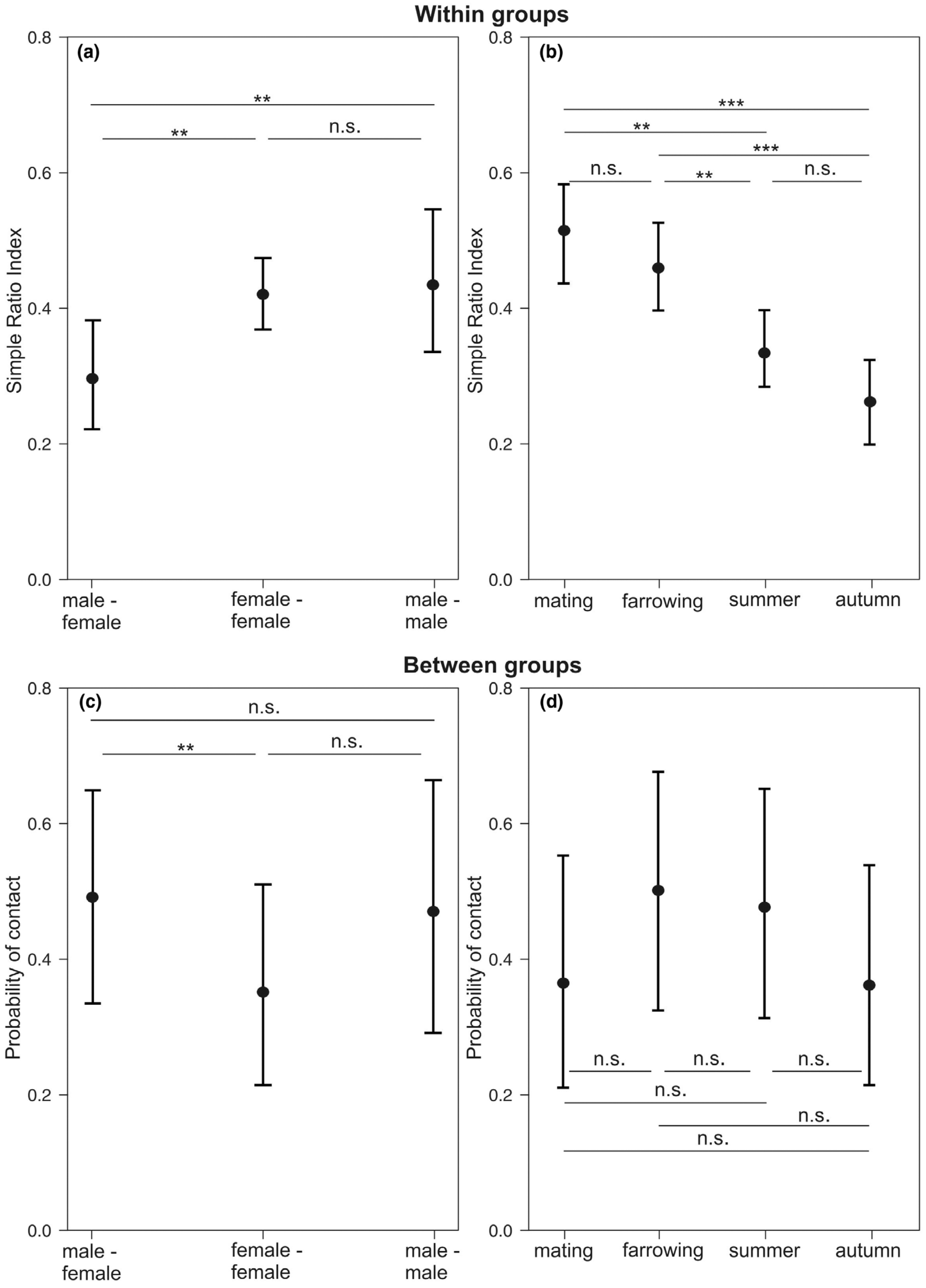

FIGURE 4 Model predictions for the effects of season and sex on monthly contact rates within (a, b) and between (c, d) wild boar groups. Statistical significance of the differences: n.s. $p > 0.1$, $^{**}0.05 < p > 0.01$, $^{***}p < 0.0.1$.

in wild boar lead to similar outcomes remains to be tested with appropriate data in the future. In any case, hunting management could diversify the location of driven areas throughout the hunting season and thus target different groups each time, mitigating disturbance and alleviating potentially detrimental effects.

Contrary to our prediction, we found no effect of hunting on the between-group contacts, neither at the scale of the individual hunting event nor across the hunting season. Thus, we found no evidence to support the previous hypothesis by Iacolina et al. (2009) that individuals from different groups regroup or form random associations in response to hunting disturbance. Given that interactions between groups can play a particularly important role in pathogen transmission (Drewe, 2010; VanderWaal et al., 2016), our finding does not provide support for the role of hunting disturbances in facilitating the spread of directly transmissible diseases. However, escape movements triggered by drive hunts (Keuling & Massei, 2021; Olejarz et al., 2024; Scillitani et al., 2010; Tolon et al., 2009) can still pose a risk of transmission into new areas. Compared to hunting, home range overlap was a much stronger predictor of between-group contact rates. This is in line with the previously reported negative relationship between spatial distance and contact rates (Pepin et al., 2016; Podgórski et al., 2018). While social structure with a strong spatial clustering is not conducive to the rapid spread of infectious diseases (Pepin & VerCauteren, 2016), spatial proximity was shown to be a significant predictor of pathogen transmission, as demonstrated for ASF in wild boar (Podgórski et al., 2022), chronic wasting disease in white-tailed deer (Grear et al., 2010). Low-density wild boar population can thus be expected to maintain low inter-group contact rates and limit both density- and frequency-dependent disease transmission. Interestingly, we did not detect an effect of population density on contact rates, either within or between groups, despite the adequate, yet not exhaustive, range of densities considered (0.2–5.4 inds/km^2; see data at https://doi.org/10.5061/dryad.v41ns1s6p). Evidence for density–contact relationships in mammals remains mixed and may depend on species-specific social structures and the range of densities studied (Ramsey et al., 2002; Sanchez & Hudgens, 2015; Vander Wal et al., 2012). Perhaps those two factors, pending further studies, contributed to the absence of the effect of population abundance in our study. It is possible that contact rates do not scale with population densities in wild boar owing to strong social structuring in this species (Podgórski et al., 2018). Additionally, our metric of relative population abundance did not account for hunting effort, potentially introducing bias across study areas (Pettorelli et al., 2007), which could further mask the density effect. Interestingly, the effect of home range overlap on contact rates was also detected within groups. However, the effect was weaker (Figure 3) and likely driven by a small fraction of dyads with low overlap (Figure S2) or periods of low group cohesion, for example drive hunt months. Nevertheless, our results indicate that spatial proximity between individuals can be a reliable index of the amount of direct contacts between groups within wild boar populations and could thus be used as an actionable metric in management and epidemiological contexts.

As expected, sex differences in the frequency of between-group contacts aligned with the matrilineal social system of wild boar. Females from different groups interacted less frequently than male–male or mixed-sex dyads, suggesting that males predominantly facilitate between-group interactions. Wild boar social structure is based on matrilineal groups of which the core is composed of a few related females maintaining long-lasting, multiyear relationships while adult males join groups temporarily for brief (few days) periods of time (Podgórski, Lusseau, et al., 2014). Young males remain in their natal groups until dispersal, which starts around 10 months of age (Keuling et al., 2010; Podgórski, Scandura, & Jędrzejewska, 2014; Truve & Lemel, 2003). The higher probability of inter-group contacts in mixed-sex dyads observed in our study could result from adult males moving between groups during mating season and interactions with mating competitors. Inter-group connectedness appeared to be maintained predominantly by males which could be targeted if disease transmission was a major management objective. The lower frequency of interactions between females from different groups underlines strong social bonds in matrilineal groups and suggests a low frequency of group fusion events. Thus, targeted removal of males could potentially be used in management to reduce rates of disease spread in the population. Surprisingly, we found a slight sexual segregation in contact rates within groups. Same-sex dyads showed higher contact rates than mixed-sex ones. High contact rates among females reinforce previous observations of female philopatry (Kaminski et al., 2005; Podgórski, Scandura, & Jędrzejewska, 2014; Poteaux et al., 2009) and indicate potential inclusive fitness benefits (Armitage & Schwartz, 2000). Male–male associations within groups could be a part of the pre-dispersal process of subadult male bonding prior to separation from the groups.

We found seasonality in contact rates to be strong within groups and weak between groups. Social dynamics often respond to changes in the physical environment, for example distribution of resources and food availability (Henzi et al., 2009; Peignier et al., 2019). While we did not find the impact of site-specific habitat productivity on contact rates, this metric did not account for temporal changes in the environment and resource distribution. In the forest–agricultural landscapes, wild boar shifts seasonally between woodland (winter) and crop fields (summer) (Keuling et al., 2009; Thurfjell et al., 2009). Different spatial strategies individuals adopt during the crop season, that is none, partial or total shift (Keuling et al., 2009), could be partially responsible for the lower group cohesion in summer–autumn observed in our study. On the other hand, higher within-group contact rates during the farrowing period could be related to more uniform habitat use in spring. Alloparental care is likely to be present in wild boar groups where reproduction is synchronized (Delcroix et al., 1990), litters are large (Servanty et al., 2007), and mothers are related to each other (Podgórski, Scandura, & Jędrzejewska, 2014). Kin-directed cooperative behaviours can improve the inclusive fitness of group members (Focardi et al., 2015; West et al., 2007), and this could be reflected in strong social bonds during the piglet weaning period in spring. Between-group contact frequency was relatively even throughout the year. Higher inter-group contact rates could be expected during the mating season when adult males move between groups. Yet, the frequency of those mating interactions has not been quantified previously and perhaps they are not frequent enough to change the seasonal pattern. Our results may also indicate that social structure is resilient to ecological conditions throughout the year. However, more evidence is needed to elucidate the drivers of social dynamics in this species.

There are, inevitably, limitations in any analysis aiming at identifying the role of hunting on a complex etho-ecological phenomenon such as contact rates between individuals. A more even distribution of hunting events throughout the annual cycle would have improved our investigation. For example, data on non-hunted populations or with temporal restrictions on hunting could have allowed a better evaluation of seasonal vs. hunting modality effects. However, the hunting season for wild boar, and particularly drive hunts, is mainly concentrated throughout autumn–winter across European countries (Apollonio et al., 2011, p. 92). Therefore, although future studies in other continents would be needed, we can reasonably assume that our data are representative of the general European context. Moreover, our evaluation could have been improved by considering additional hunting characteristics as a proxy for hunting intensity, such as numbers of hunters and dogs per daily hunt and the extent of the driven area. Unfortunately, similar metrics were not available and are often difficult to obtain for multi-site studies, especially at fine spatio-temporal scales. One important perspective would be to combine the lethal and non-lethal effect of hunting on social structure, that is disentangling whether contact rates vary with successful hunting events vs. unsuccessful hunting events within the group. This would require highly detailed data, linking hunted individuals to the group of origin where some other individuals are tracked. Hence, studies considering fine-scale spatial variations in hunting intensity, as well as a wider range of hunting intensities, are still needed to elucidate possible effects on contact rates. Additionally, fine-scale data on hunting effort would also help us calibrate the population abundance index for a more robust evaluation of population density effects on contact rates (Imperio et al., 2010; Kahlert et al., 2015; Pettorelli et al., 2007). Finally, we did not consider the age of individuals in our analysis due to inconsistencies in age estimation methods across study areas but believe it to be a potentially important driver of social interactions which should be included in future studies. In any case, however, the models employed here well predict social contact rates in wild boar (within-group contact: $R^2=0.93$; between-group contact: AUC=0.90), suggesting that our investigation was able to disentangle the role of hunting modality from that of other drivers.

AUTHOR CONTRIBUTIONS

Tomasz Podgórski conceived the ideas. Niccolò Fattorini, Stefano Focardi, Francesca Cagnacci, Kevin Morelle and Tomasz Podgórski designed the methodology; Tomasz Podgórski, Evelina Augustsson, Eric Baubet, Christian Fiderer, Claude Fischer, Marco Heurich, Milos Ježek, Petter Kjellander, Alisa Klamm, Alain Licoppe, András Náhlik, Sonia Said, Stefan Suter, Tamás Tari, Joaquin Vicente collected the data; Niccolò Fattorini, Kevin Morelle, Eveline Nivois, Astrid Olejarz and Tomasz Podgórski analysed the data; Tomasz Podgórski led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.v41ns1s6p (Podgórski et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Study areas and respective datasets used in the study.

Table S2: Sex and age (determined at trapping) structure of the animals used in the study.

Table S3: Description of the coefficients of cohesion measured at the dyadic level.

Table S4: Sample size of various subsets of monthly-scale data used in the study.

Table S5: Sample sizes of dyads in each month and study area used in the analysis.

Table S6: Temporal distribution of hunting seasons across the study areas.

Table S7: Sample size of various subsets of daily-scale data used in the study.

Table S8: Results of the generalized mixed-effect models for contact rates (simple ratio index) within wild boar groups at a monthly scale for a subset of data containing information on the frequency of drive hunts.

Table S9: Results of the zero-inflated mixed-effect models for contact probability between wild boar groups at a monthly scale for a subset of data containing information on the frequency of drive hunts.

Figure S1: Distributions of Simple Ratio Index (SRI) of inter-individual contacts within and between wild boar groups at a monthly (a, b) and daily (c, d) resolution, i.e. hunting season and hunting event scale, respectively.

Figure S2: Distributions of pairwise home range overlap within and between wild boar groups at a monthly (a, b) and daily (c, d) resolution, i.e. hunting season and hunting event scale, respectively.

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