Spatio-temporal dynamics of attacks around deaths of wolves: A statistical assessment of lethal control efficiency in France

Oksana Grente*[1,3], Thomas Opitz[2], Christophe Duchamp[3], Nolwenn Drouet-Hoguet[4], Simon Chamaillé-Jammes[1], Olivier Gimenez[1]

[1] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[2] Biostatistics and Spatial Processes, INRAE, 228 Route de l'Aérodrome, Avignon, 84914, France
[3] Office Français de la Biodiversité, Direction de la Recherche et Appui Scientifique, Micropolis La Bérardie 05000 Gap, France
[4] Office Français de la Biodiversité, Direction de la Recherche et Appui Scientifique, ZI Mayencin 38610 Gières, France

*Corresponding author
Correspondence: oksana.grente@gmail.com

Abstract

The lethal control of large carnivores is criticized regarding its efficiency to deter hotspots of attacks on livestock. We evaluated the effects of wolf lethal removals on the distribution of attack intensities in the French Alps between 2011 and 2020, using a BACI approach with retrospective data. We built an original framework combining both continuous spatial and temporal scales and a 3D kernel estimation. We compared the attack intensities observed before and after 278 legal killings of wolves on a period of 90 days and on a range of 10 km, and with control situations where no removal occurred. The analysis was also corrected for livestock presence, and explored different subsets of removals in relation to their locations, seasons and proximity to other removals. This method provided efficient visual charts and trends of attack intensity variations before and after removals. A moderate decrease of attack intensity was the most common outcome after a lethal removal. Analysis scale modulated this general pattern, with decreases being generally amplified at a small spatio-temporal range. Contextual factors (*e.g.*, geographical or seasonal variations) could also lead to deviations from this general pattern, with outcomes of subsets ranging from important decreases to moderate increases. Thus, between 2011 and 2020, lethal control of wolves in France generally contributed to manage livestock attacks but did not eliminate it, even though mainly implemented alongside non-lethal measures. Our results highlight the importance of accounting for scale in such assessments and suggest that the evaluation of the effectiveness of lethal removals in reducing livestock predation might be more relevant in a local context. As a next step, we recommend to move forward from patterns to mechanisms by linking the effects of lethal control on wolves to their effects on attacks through analysis of fine-scaled data on wolves and livestock.

Keywords: Before-After Control Impact, *Canis lupus*, culling, depredation, French Alps, kernel density estimation, removal, sheep

1. Introduction

Lethal control of large carnivores aims to reduce damages on livestock by decreasing the encounter risk with livestock or by removing individuals inclined to predation on livestock (Lennox et al., 2018). The side effects of these management practices are often claimed to undermine the efficiency of lethal control or even to create more damages (Elbroch and Treves, 2023). In the specific case of social canids like wolves, studies have mostly pointed out additive human-caused breeder loss as a risk for increasing damages on livestock (Jędrzejewska et al., 1996; Žunna et al., 2023). Social instability can indeed cause multiple reproduction (Ausband et al., 2017) or pack disruption (Cassidy et al., 2023), although their effects on damages have not been assessed.

Implementing randomized controlled experiments to evaluate the efficiency of lethal control of large carnivores is extremely difficult, considering the involved large spatial and temporal scales. To date, no experimental study has been conducted for this matter (Treves et al., 2016, 2019). Only Allen (2014) conducted a controlled experiment to evaluate dingo's baiting efficiency but using the number of lactation failures as a proxy for calves lost to predation instead of direct cases of predation.

Also, retrospective studies have been conducted to answer the question of lethal control efficiency. The data they used were not collected within a scientific frame but generally through management (*e.g.* damages from compensation schemes). Most of retrospective studies on social canids (gray wolves *Canis lupus*, dingoes *Dingo dingo*, coyotes *Canis latrans*) were correlative and tested for a relationship between the number of livestock damages and the number of killed predators (Šuba et al., 2023; Fernández-Gil et al., 2016; DeCesare et al., 2018; Conner et al., 1998; Allen, 2015; Kutal et al., 2023). However, the ability of this approach to infer causality is being debated (Arif and MacNeil, 2022; Nichols and Cooch, 2025). The approach is also subject to analytical variability (Gould et al. 2023). For example, three correlative studies which used the same dataset concluded differently on the effect of lethal removals of wolves on livestock damages (Kompaniyets and Evans, 2017; Poudyal et al., 2016; Wielgus and Peebles, 2014).

A smaller number of retrospective studies used a comparative approach. Harper et al. (2008), Bradley et al. (2015), Santiago-Avila et al. (2018) and Wagner and Conover (1999) compared situations where lethal control was used and situations where it was not (*i.e.* inter-site comparison). Bjorge and Gunson (1985) and Blejwas et al. (2002) compared the situation before and after the implementation of lethal control within the same site (*i.e.* intra-site comparison). While the inter-site comparison is more susceptible to possible spatial confounding factors but minimizes temporal confounding factors, the opposite is true for the intra-site comparison. Kutal et al. (2023) was the only study to mix inter-site and intra-site comparisons, by combining comparisons before and after hunting season and between sites with and without hunted wolves (*i.e.* Before-After Control-Impact, BACI). The BACI study design showed a better performance to estimate the effect of an impact in a simulated ecological dataset than intra-site or inter-site comparisons (Christie et al., 2019), and performed even better than the randomized controlled experiment still considered as gold-standard of scientific inference (Treves et al., 2019).

Five of these seven comparative studies on social canids showed that lethal control significantly decreased damage recurrence, whereas Santiago-Avila et al. (2018) and Kutal et al. (2023) found no significant effect of lethal control on damages. Yet, results suggested variability in the efficiency of lethal control. For example, Harper et al. (2008) detected that only the death of an adult wolf male was significantly efficient, whereas Bradley et al. (2015) did not detect sex or age conditions on efficiency. Variability could also result from the study designs themselves, as these studies used

different spatial and temporal scales to evaluate lethal control efficiency. Thus, small scale (*e.g.* 4 km in Harper et al. (2008)), medium scale (*e.g.* pack territory in Bradley et al. (2015)) or large scale (*e.g.* 711 km² in Kutal et al. (2023)) could be used for space, sometimes within the same study (*e.g.* Santiago-Avila et al., 2018). Time scale could also be disparate, going from several days or months (*e.g.* Blejwas et al. (2002)) to two years (*e.g.* Kutal et al., 2023) or more (*e.g.* Bjorge and Gunson (1985)). Most importantly, none of the mentioned retrospective studies have both used continuous spatial and temporal scales, making it difficult to identify potential gradients of lethal control effects, as those suggested in Santiago-Avila et al. (2018). Finally, only two of the seven comparative studies have controlled for livestock presence or abundance (Blejwas et al., 2002; Wagner and Conover, 1999), yet the primary factor structuring damage risk and the highest risk of confounding factor.

The aim of our study was to evaluate the effects of the lethal control applied for gray wolves in France on the intensity of attacks on sheep. We used the data collected by the French administrations for the period 2011-2020. Given the retrospective nature of our study, we attempted to fill the gaps identified in the previously mentioned retrospective studies on the subject. For that purpose, we used the study designs of intra-site comparison and of BACI, used continuous spatial and temporal study scales and corrected for livestock presence through an original framework of kernel estimation.

2. Methods

2.1 Management context and study area

After historical campaigns of destruction, gray wolves disappeared from France at the beginning of the twentieth century, despite being present on the whole metropolitan territory at the end of the eighteenth century (de Beaufort, 1987). From the 1970s, the combination of protective legislation and the increase of forested habitat allowed the recovery of the species in Europe (Chapron et al., 2014). In the 1990s, wolves from the Apennines population in Central Italy dispersed and settled into the south-western Alps, straddling Italy and France (Linnell and Cretois, 2018; Fabbri et al., 2007; Poulle et al., 1997). From there, a wolf population progressively established in the area. On the French side, the population has expanded but has until now remained mainly restricted to the south-eastern corner of France, except for a few reproductive packs outside of this area (Louvrier et al., 2018). The spatial growth reflected a demographic growth that has been exponential. In the first twenty years of the recovery, the population size progressively increased and reached approximately 200 estimated individuals in 2013 (Réseau Loup-Lynx, 2024). Then, the growth rate accelerated, and the population more than doubled in five years, with more than 500 estimated individuals in 2018 (Office National de la Chasse et de la Faune Sauvage, 2019). This sustained growth has continued at least up to 2022, with a population size approaching 800 estimated individuals (Réseau Loup-Lynx, 2024).

South-eastern France is characterized by a variety of landscapes, including high altitude mountains, Piedmont plains, hills and garrigue lands, where mountain and Mediterranean climates converge. Livestock farming is generally extensive. Herds of cow are principally present in the north of the region, while those of sheep are present in the whole area (Dobremez et al., 2016). The pastoral practice of transhumance, consisting in moving all or part of herds from low to high altitude pastures during summer and vice versa during winter, is still important. Duration of grazing season increases following a north-south gradient, with some herds from low altitudes in the south grazing outside all year round (Grente et al., 2022). Livestock owners can share pastures, and even gather their herds to limit the cost of transport for transhumance and of herding. In the Alps, herds of cows are generally not mixed with flocks of sheep, but the latter can be occasionally mixed with goats. Mean size of

transhumant flocks of sheep varies greatly between alpine departments and ranges between less than 250 sheep up to 2000 sheep (Agreste, 2021).

To prevent attacks, France subsidies non-lethal measures for protecting flocks of sheep or goat through livestock guarding dogs, fences and additional shepherds. In situations where attacks persist despite non-lethal measures, France authorizes lethal removals of wolves by ground shooting since 2004, based on the article 12 of the Directive Habitats. Other forms of removals (*e.g.* trapping, aerial shooting) are prohibited. Conditions of application of ground shooting are defined by ministerial decrees (*e.g.* Ministère de la Transition Ecologique et Solidaire, 2018) and depend on the implementation of non-lethal protective measures and on the recurrence of attacks. If the conditions are met, the administration assigns the derogation to the livestock owner for a duration between two months and five years. The owner itself or a mandated hunter can shoot wolves during an attack on its livestock (hereafter 'simple defense'). When attacks still remain, governmental agents or special volunteers who are trained may support owners in protecting their livestock (hereafter 'reinforced defense'). Eventually, if the level of attacks escalates in an area, the administration can decide to shoot a specific number of wolves under game hunting conditions (hereafter 'hunting'). Between 2004 and 2018, the number of wolves that could be annually killed if required was prevented from exceeding between 10 and 12% of the annual estimated wolf population size, in order to avoid threatening the recovery of the species. Throughout this period, the number of killed wolves followed the increases of both the wolf population size and the attack occurrences, and from 2011, wolves have been legally removed every year (Grente, 2021). Since 2019, considering that the wolf population reached a satisfying demographic conservation status, France has increased the possible number of lethal removals to 21% of the annual population size estimate (Ministère de la Transition Ecologique et Solidaire, 2020).

Because wolves were removed sporadically between 2004 and 2010 (range: 0-2 wolves per year), we started our study period in 2011, until 2020 included. Within the study period, only three lethal removals were outside south-eastern France and concerned lone wolves which dispersed far and whose territories were very isolated. Their deaths could only lead to an absence of attacks. This context was totally different from the one in the Alpine range where the wolf population was settled. Therefore, we restricted our study area to the two south-eastern regions, Provence-Alpes-Côte-d'Azur in its entirety and Auvergne-Rhône-Alpes restricted to its five most south-eastern departments, Ardèche, Drôme, Isère, Savoie and Haute-Savoie (Figure 1).

2.2 Datasets

2.2.1 Lethal removals

We used the records of deaths of wolves from 2011-2020 compiled by the regional French administrations. We used the 362 records of wolves killed by legal shootings and that were geolocated within the study area. Dates of lethal removals were recorded, but not the hour. The number of lethal removals increased over time and could be divided into three periods, 2011-2014, 2015-2018 and 2019-2020, that represented respectively 8%, 44% and 48% of the dataset, for annual means of 7 (standard deviation, hereafter '±', 6), 40 (± 6) and 87 (± 3) lethal removals respectively.

Almost half of the records were cases of reinforced defense (48%), while simple defense and hunting cases represented respectively 27% and 25% of the dataset. There were 58 records (16%) for which no wolf body was found after the shooting, but they were considered as killed because there was enough evidence for lethal injuries. For the remaining 304 records, information from the necropsy

reports was available on the sex and the estimated age class (pup, subadult or adult) of the killed wolves and on the annual reproductive status for females.

2.2.2 Attacks on sheep

We used the claims of attacks on livestock from 2010-2020 compiled by the French administration and for which wolf responsibility could not be discarded. We used the 23 645 claims that were geolocated within the study area. We then restricted the dataset to the 21 936 claims on sheep. Each claim corresponded to one or several dead or wounded sheep.

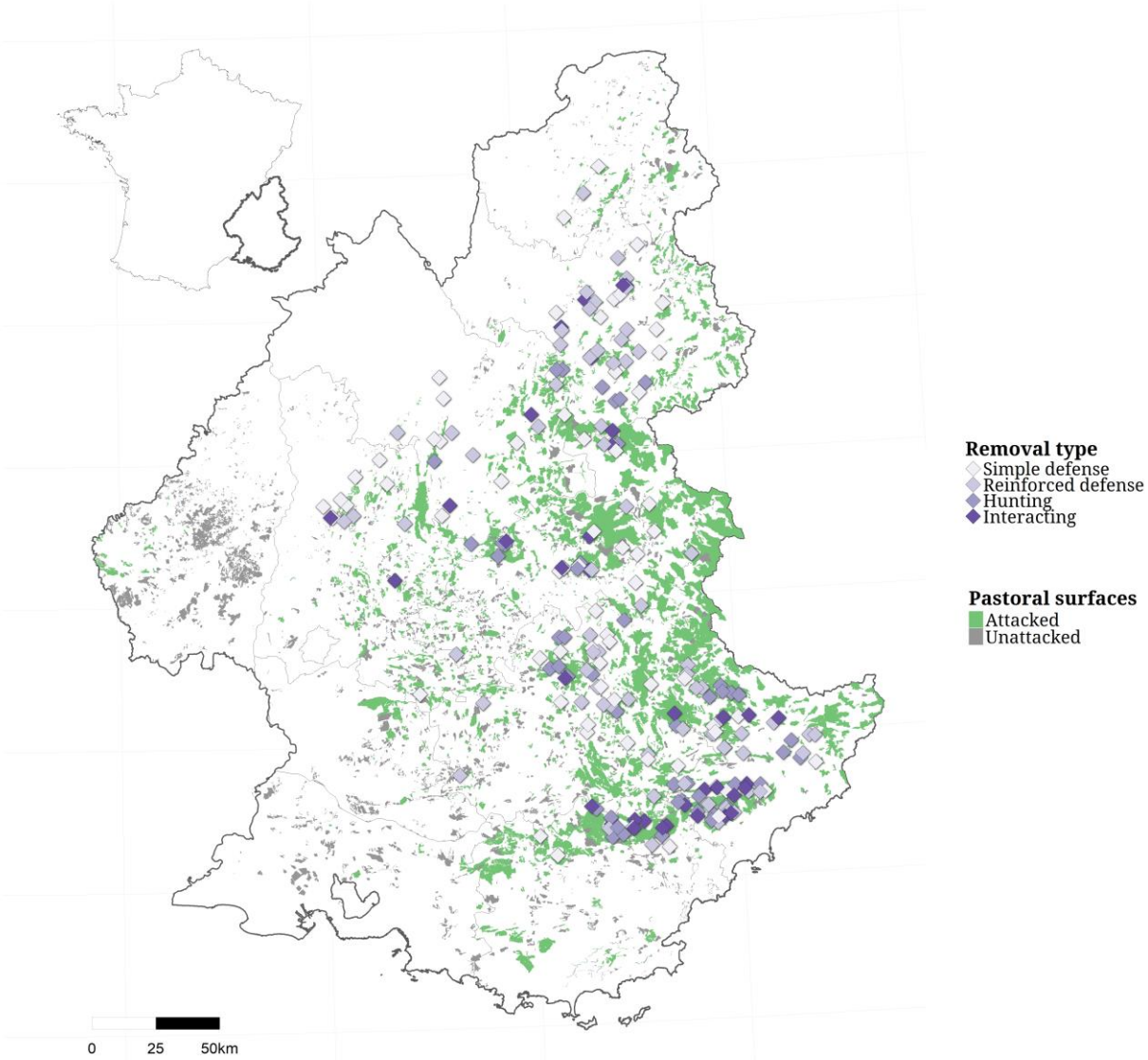

Figure 1. Study area and location within France. Purple points represent locations of the 196 analyzed lethal removals of wolves, colored according to the three types of shooting implementation (simple defense, reinforced defense, hunting) and of the centroids of the 36 groups of 'interacting' lethal removals of wolves that were combined for analysis (darkest color). Pastoral units with or without attacks are shown in green and grey, respectively, after correction for inconsistencies between the pastoral and attack datasets (see part 2.2.4).

Apart very few specific cases, all claims were checked in the field by trained public agents. They followed a standardized procedure to estimate the date of the attack and if wolf responsibility could be discarded or not. Compensation was attributed regardless of non-lethal measures up to 2019. From 2020, compensations after two compensated attacks depended on the implementation of

protective measures, with conditions of implementation varying locally according to the level of attacks of municipalities. Protective measures are widely implemented in south-eastern France (Meuret et al., 2020). We have therefore confidence in the level of reports of attacks noticed by breeders.

2.2.3 Spatio-temporal sheep distribution

We used the data from the pastoral census of the two south-eastern regions Provence-Alpes-Côte-d'Azur and Auvergne-Rhône-Alpes conducted by the National Research Institute for Agriculture, Food and the Environment (Dobremez et al., 2016). The census indexed and delimited for the period 2012-2014 the pastoral units at medium or high altitude used by flocks, as well as the pastoral zones at lower altitudes. Given the relative stability of the use of the pastoral units and zones over time (Grente et al., 2022), we assumed the information of the pastoral census was valid for our entire study period. Pastoral units and zones delimited the spatio-temporal area where attacks could have occurred. Therefore, our analysis was restricted to the pastoral area delimited by this census, in order to correct for livestock presence.

We used the 3176 units and 8184 zones within the study area. We restricted the dataset to units and zones that were used for grazing sheep, regardless of the other livestock. The annual number of grazing sheep was on average 955 (± 764) for units (range 2-6000) and 412 (± 411) for zones (range 1-3600). The months for which the area was grazed were known for each pastoral unit. Only the seasons in use were available for pastoral zones. Therefore, we attributed to the pastoral zones the months corresponding to the seasons for which they were grazed (spring: March to May, summer: June to August, fall: September to November, winter: December to February). The annual number of grazed months was on average 6.9 (range 1-12). The total size of our final dataset of pastoral units and zones (hereafter 'pastoral units') was 4987 (Figure 1).

2.2.4 Attributing attacks to pastoral units

The attack dataset showed 59% of consistency with the dataset of pastoral units, meaning that 59% attacks were within pastures that were in use according to the pastoral census. The other attacks could be outside pastoral units, or could have occurred in months for which pastoral units were not supposed to be in use according to the pastoral census. These mismatches could result from changes in the spatial or temporal use of pastoral units, from errors during the attack record (*e.g.* geolocation approximation), or because attacks occurred in non-indexed pastoral units.

When attacks were within pastures and when difference between the month of their dates and the sets of grazed months of their pastures did not exceed three months (9% of total attack dataset), we only updated the pastoral census by adding the months of the attacks to the corresponding pastures. Otherwise, we relocated attacks to their closest pastures within a 500 meters radius by favoring pastures with the smallest difference between their sets of grazed months and the months of the attacks. When these differences exceeded 3 months, or if no pastoral unit could be found within a 500 meters radius around the attacks, we excluded these attacks (13% of total attack dataset). Relocations were done at the closest point of the pastoral units to the original attack locations (19% of total attack dataset). When necessary, we added the months of the relocated attacks to the sets of grazed months of their new pastoral units. The final dataset of attacks had 19 302 events.

Contrary to attacks, lethal removals did not require to be located within pastoral units, as hunting did not necessarily occur within pastoral units.

2.3 Analysis

Apart from being precisely geolocated, our data about attacks and lethal removals were very unbalanced in favor of attacks (19 302 attacks against 362 lethal removals). Consequently, we could adopt an original approach consisting in choosing removals as focal points through the use of 3D-buffers (for geographic space and time), and in computing attack intensities over continuous spatial and temporal scales.

2.3.1 Construction of 3D-buffers

We attributed to each lethal removal a spatio-temporal 'observed buffer', which can be visualized as a cylinder centered on the lethal removal event (Figure 2.A). The circle base of the cylinder corresponded to the spatial dimensions (X, Y) and had the role to scan for attacks within the pastoral space around the lethal removal. The height of the cylinder corresponded to the temporal dimension, the left and right parts scanning for attacks that had occurred before or after the lethal removal, respectively.

The observed buffer was composed solely of the pastoral units where attacks could occur. Therefore, the buffer was sparse, and remained empty where there was no used pastoral unit around the removal event according to the pastoral census.

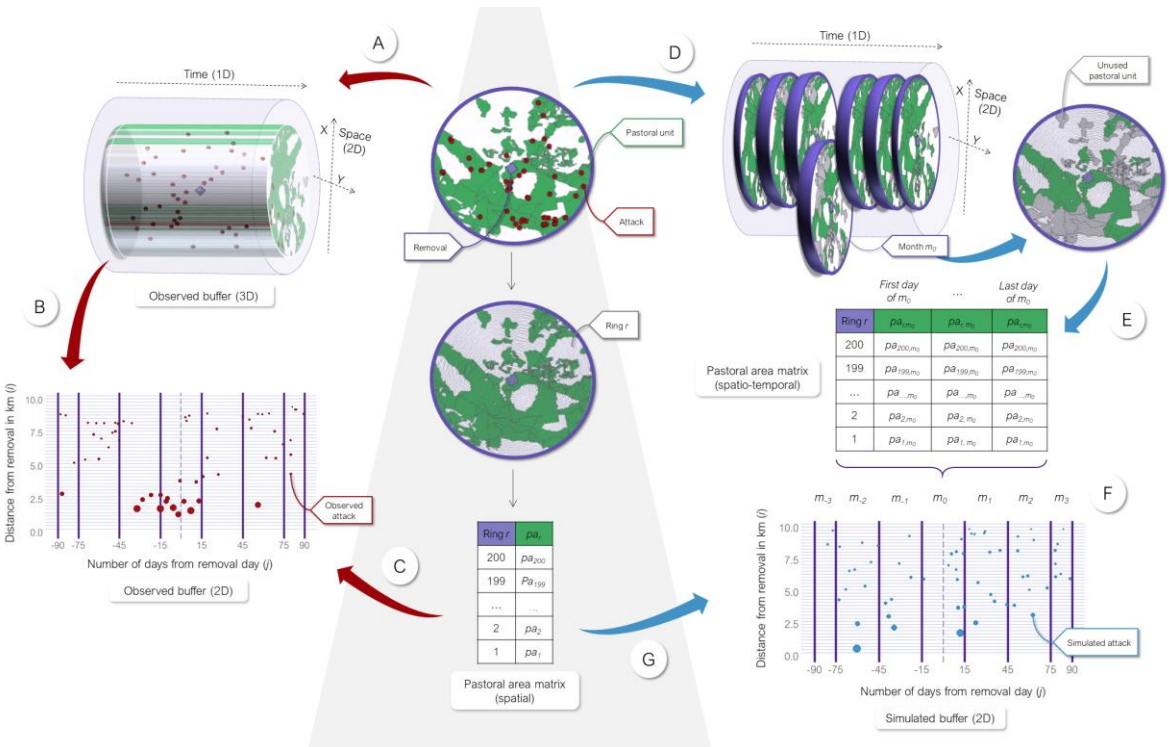

Figure 2. Example of data transformations of observed attacks (red arrows) and simulated attacks (blue arrows) for one lethal removal occurring on the 15th of August 2017. ***A.*** *Attribution of the observed 3D-buffer to the removal (purple point) of 10 km radius and 90 days around the removal. Attacks in the buffer have 3 coordinates: 1 temporal (day), and 2 spatial (x,y).* ***B.*** *Reduction of the spatial coordinates of the observed attacks, through the Euclidian distance to the removal (spatial coordinate i, time coordinate j).* ***C.*** *Spatial correction $1/pa_r$ showed as the size of the observed attacks. The pastoral area pa_r is calculated for each of the 200 rings r of the spatial buffer.* ***D.*** *The seven monthly slices m of the observed 3D-buffer. Months could be complete (from m_{-2} to m_2) or partial (m_{-3} and m_3, here only 15 days each).* ***E.*** *The pastoral area $pa_{r,m0}$ is calculated for each of the 200 rings r of m_0. The unique column of $pa_{r,m0}$ is duplicated into the number of days of m_0. Note that the operation is repeated for each m, and results in a final matrix of 200 x 180 dimensions (not showed here).* ***F.*** *One simulation of coordinates i and j of attacks based on the final matrix of $pa_{r,m}$. The number of simulated attacks (blue points)*

of the simulated 2D-buffer is the same as the number of observed attacks (red points) of the observed buffer. ***G.*** *Spatial correction 1/pa$_r$ showed as the size of the simulated attacks, with the same process as in step C.*

We set the radius of the cylinder at 10 km, in order to encompass more than one wolf territory radius, estimated at 7–8 km in France through telemetry and genetic tracking (Duchamp et al., 2012). Therefore, ripple effects, if any, could be observed up to 10 km from the lethal removal. The pastoral units overlapping the buffer were truncated to the buffer.

We set the height of the cylinder to 180 days, meaning that all attacks occurring 90 days before and 90 days after the lethal removal were part of the buffer. Thus, we analyzed the effect of lethal removal on a full season if the removal event occurred in the middle of the season, or on two successive seasons if not. The day of the removal was not part of the buffer, because we could not know if an attack recorded at the day of the removal occurred after of before the removal, having no information about the hour of both attacks and removals.

Attacks were not homogeneously distributed across space and time (Grente et al., 2022). Increasing the radius or the height of buffers compressed the attack distribution towards the centers of buffers (*i.e.* at small spatial and temporal distances), and prevented an optimal reading of the results.

We ensured that the buffers did not overlap geographic areas or periods without data about attacks. We removed 84 lethal removals occurring at less than 10 km from the terrestrial limits of the study area or occurring after the 1st October 2020, eventually leaving 278 analyzed lethal removals.

Most buffers overlapped in space and in time, with a total of 86% of buffers overlapping with at least another one. However, only few removal events were simultaneously close in space and time (Figure 3), with 82 removals separated by less than 5 km and less than 25 days. In these cases, we considered that the risks of interaction between removals were high. We called these removals, 'interacting removals'. We pooled the interacting removals into 36 groups, with each group corresponding to a set of interacting removals. For the special case where two removals were not interacting, but were both interacting with a third removal, we considered these three removals part of the same group of interacting removals. On average, 2.28 wolves (± 0.45, range 2—3) were killed per group.

We attributed a single observed buffer to each group of interacting removals, of 10 km radius, of 180 days height and centered on the centroid of the interacting removals of the group. To compare the attack intensity before and after each group of interacting removals, we excluded the attacks recorded between the date of the first removal of the group and the date of the last removal of the group. The exclusion period lasted 7.5 days on average (± 8.38, range 0—27). In cases where interacting removals occurred the same day (28% of groups), only the date of the removals was not part of the buffer, as previously.

We ended up with 232 observed buffers, including 36 buffers of groups of interacting removals, corresponding to a total of 6110 attacks (Figure 1). On average, an observed buffer included 26.3 attacks (± 20.7, range 0—100).

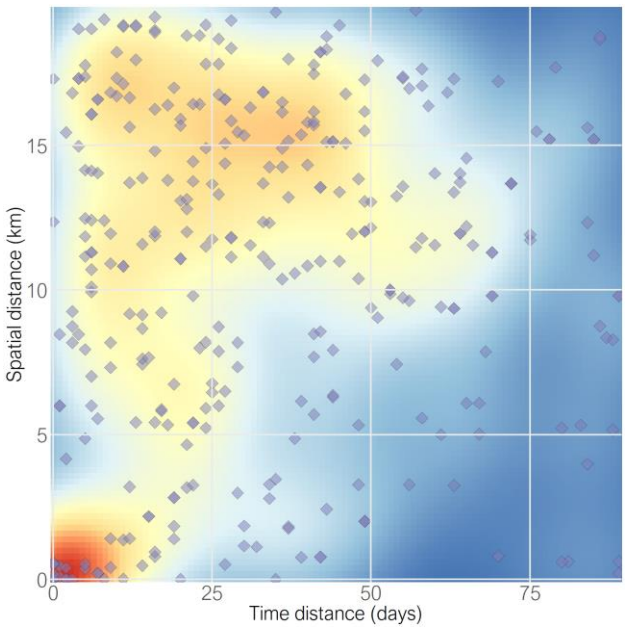

Figure 3. Spatial and temporal distances between the 352 pairs of lethal removals whose buffers overlapped.

2.3.2 Reducing the number of spatial dimensions

Methods for the analysis of interactions of several datasets with three dimensions are yet to be developed and may suffer from the curse of dimensionality (Wikle et al., 2019). Therefore, we followed standard geostatistical practices and reduced the two spatial dimensions of the observed buffers to one, by computing the Euclidian distance of each attack to the center of the buffer. In other words, we converted the spatial circle of buffers to a line. The temporal dimension corresponded to the difference in days between each attack and the date of the removal of the buffer. In the case of interacting removals, we used the first (or last) date of the group if the attack occurred before (or after) the exclusion period. Thus, each attack had then two coordinates *(i, j)* corresponding to the spatial *i* and temporal *j* distances from the center of the observed 2D-buffer (Figure 2.B).

Nevertheless, converting a 2D-circle into a 1D-line always induces a spatial bias that gives more representation of points farther away, simply because the circle perimeter increases linearly with circle radius. Therefore, we should have applied a spatial correction of $1/i$ to each attack of an observed buffer, with *i* the Euclidian distance of the attack to the buffer center. However, the buffers were delimited by pastoral units that were not homogeneously distributed around the buffer center. In other words, the spatial bias did not increase linearly with the radius, but according to the perimeter fraction that intersected with pastoral units. For example, the spatial bias could be low at the furthest distances of the buffers if pastoral units were almost non-existent at these distances.

To incorporate pastoral units to the spatial correction, we sliced up each spatial buffer into 200 rings *r* of width 50 m. We calculated pa_r, the total area of pastoral units of each ring *r*. We then attributed to each attack from the observed 2D-buffer the inverse of the pastoral area of its ring, $1/pa_r$ (Figure 2.C). Because attacks could only be located in pastoral units (part 2.2.4), pa_r of rings containing attacks could not be null.

2.3.3 Correction for livestock presence

For each observed buffer, we corrected for livestock presence by randomly simulating attacks with a distribution defined according to the locations of pastoral units of the buffer and their grazed months. The simulated dataset corresponded to the expected distribution of attacks if they only depended on the livestock presence.

For each month *m* represented in the observed 3D-buffer, we calculated the pastoral area $pa_{r,m}$ that was used per ring *r* during month *m* (Figure 2.D). Because the information about pastoral use was monthly and not daily, we duplicated the unique column of $pa_{r,m}$ into the number of days of this month that were part of the buffer (Figure 2.E). We repeated the same process for the other months of the buffer. This resulted in a matrix of 200 x 180 dimensions (one row per ring, one column per day). The matrix coordinates were similar to the coordinates (*i, j)* of the observed attacks, with a slightly coarser spatial resolution of 50 meters (*i.e.* ring width) and the same temporal resolution of 1 day.

We converted the matrix into a two-dimensional pixel image. We generated a random point pattern, with the pixel image acting as the probability density of the points. We generated the same number of points as the number of observed attacks of the buffer. We extracted the coordinates *(i, j)* of each point (hereafter, 'simulated attack'), corresponding to its spatial and temporal distances to the buffer center (Figure 2.F). We also attributed the spatial correction $1/pa_r$ for each simulated attack, following the same calculations as in 2.3.2 (Figure 2.G). We repeated the simulation 1000 times. Thus, for each observed buffer, we ended up with 1000 2D-buffers of simulated attacks (hereafter, 'simulated buffers').

2.3.4 Compilation of buffers

The generalization of the spatio-temporal pattern of the attacks surrounding the lethal removals required to compile the observed buffers, in order to move on from case-by-case. We first created two primary subsets: the subset of removals that were not interacting ('*Non-interacting*', n = 196 removals), and the subset of groups of interacting removals ('*Interacting'*, n = 36 groups, corresponding to 82 removals).

We also divided the primary subset of *Non-interacting* removals into 18 secondary subsets, according to 4 categories, in order to explore additional effects.

The first category was defined according to removal locations. We delimited zones by using 25 Alpine mountain ranges defined by hydrography and orography (Knopf, 2019) and the limits from OpenStreetMap of the protected area *Parc Naturel Régional des Préalpes d'Azur* (PNRPA) and of the military zone *Canjuers*, both in the south of the study area. We attributed removals to their closest zone to a limit of 15 km. We selected the 8 zones with at least 10 removals (Figure 4): *PNRPA* (n = 33), *Mercantour* (23), *Vercors* (18), *Les Trois-Evêchés* (18), *Vanoise* (15), *Préalpes de Digne* (12), *Ecrins* (12) and *Canjuers* (11).

The second category was defined according to the wolf seasons during which removals occurred (Figure 4): *Winter* (November — January, n = 30), *Reproduction* (February — March, 9), *Denning* (April — June, 35), *Rendez-vous* (July — August, 59) and *Fall* (September — October, 63).

The third category was defined according to the removal administrative types (Figure 1): *Simple defense* (n = 69), *Reinforced defense* (75) and *Hunting* (52).

The fourth category was defined according to the sex of the killed wolf when known: *Male* (n = 83) and *Female* (n = 78). At the necropsy, 7 females of our final dataset of lethal removals were declared as being reproductive at least the year they were killed, which we considered too low to constitute a subset. Annual reproductive status of males was unknown. In addition, we considered that the distribution of lethal removals among the three age classes when known was too unbalanced to investigate a potential effect of age class (177 adults, 24 subadults and 16 pups).

The same primary and secondary subsets were used for the simulated buffers.

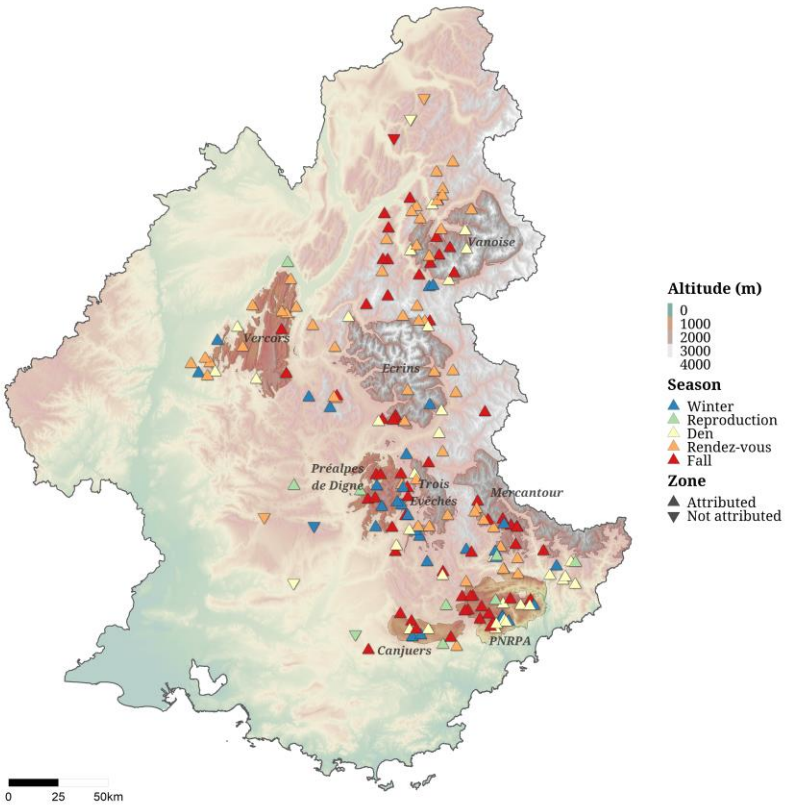

Figure 4. Topography of the study area, with the 8 highlighted zones from the Geographic zone category that were selected for the analyses. Upward and downward triangles represent lethal removals that could be attributed or not to one of the 27 zones, respectively. Colors show their affiliation to the Season category.

2.3.5 Kernel estimates

For each main or secondary subset defined in the previous section 2.3.4, all the observed 2D-buffers of the removals from the subset were combined into a unique 'observed subset buffer' (Figure 5). The point of coordinates $i = 0$ and $j = 0$ of the subset buffer then represented the combined spatial location of all the removals included in the subset, and the day before the removals (*i.e.* the day of the removals was not part of the buffer).

We estimated the observed attack intensities λ_{obs} of the subset buffer by applying an anisotropic Gaussian kernel density estimation. The method consisted in dividing the observed subset buffer into pixels, and in estimating the observed attack intensity of each pixel of coordinate (i, j). We used the same pixel resolution as previously, *i.e.* 50 meters and 1 day. A Gaussian function (*i.e.* 'kernel') was centered over each pixel, and could spread over adjacent pixels. The spread of the kernel was determined by the bandwidth parameters. We used two separate bandwidth parameters for spatial

distance and temporal lag, of 500 meters and 2 days. The choice of the bandwidth parameters was *ad-hoc*, and met the needs of adopting a resolution close to the pixels while smoothing attack intensities enough in order to obtain interpretable results. The attack intensity of a pixel $\lambda_{obs}(i,j)$ was then calculated by summing the value of the attacks within its kernel. The value of an attack was equal to its spatial correction $1/pa_r$, in order to correct for the reduction in the spatial dimensions (section 2.3.2). Thus, the higher the spatial corrections of the attacks within a kernel, the higher the attack intensity estimate of the related pixel, $\lambda_{obs}(i,j)$ (Figure 5).

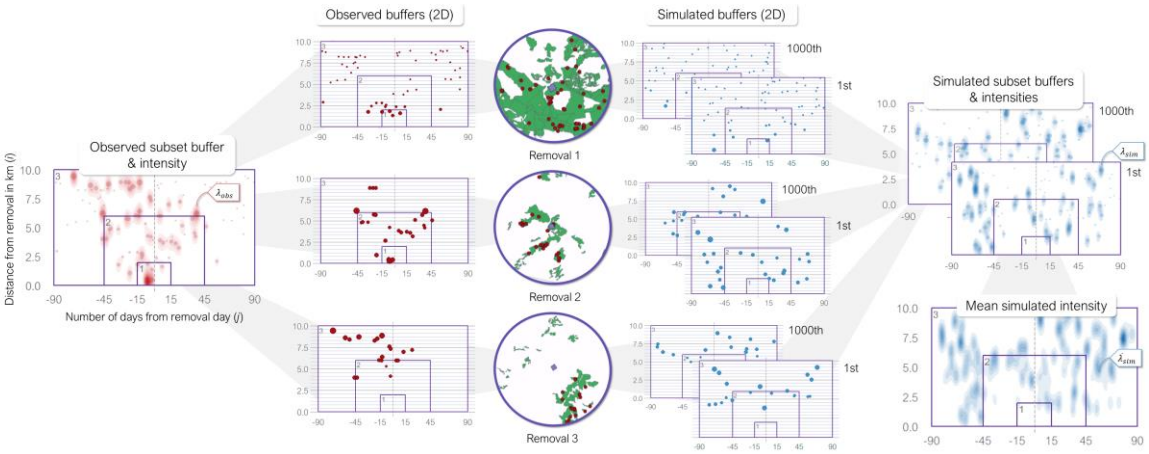

Figure 5. Example of a combination of observed and simulated buffers of three lethal removals, into one observed subset buffer (left) and two simulated subset buffers (right), on which the Gaussian kernel estimation is applied to estimate the observed intensity $\lambda_{obs}(i,j)$ (left) and the simulated intensities $\lambda_{sim}(i,j)$ (right). The mean of the simulated intensities $\bar{\lambda}_{sim}$ is then calculated (bottom right). Only the first and last sets of simulated buffers are showed here. The size of points represents the spatial correction $1/pa_r$ applied similarly for the attacks and simulated attacks of the three lethal removals. Rectangles delimit the three analysis scales s: 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days).

We also considered the spatio-temporal distributions of attacks before removals ($j \in [-90, 0]$ and after removals ($j \in [1, 90]$) as two separate distributions by appropriately right- and left-truncating kernels in the time dimension for pixels occurring before and after the date of removals, respectively. Thus, kernels that were centered before removals could not spread over spatial coordinates located after removals, and vice versa.

We corrected kernel estimates for outliers by capping the estimated observed attack intensities $\lambda_{obs}(i, j)$ to $Q_3 + 1.5\times(Q_3 - Q_1)$, where Q_1 and Q_3 were the first and third quantiles of the whole estimated distribution of λ_{obs} of the subset buffer (Walfish, 2006).

Similarly, we combined one simulated 2D-buffer of all the removals of the subset into a unique 'simulated subset buffer' (Figure 5). We repeated the combination for the 999 other sets of simulated buffers. We estimated the simulated attack intensities $\lambda_{sim}(i,j)$ for each of the 1000 simulated subset buffers. We then calculated the mean estimated simulated attack intensities $\bar{\lambda}_{sim}(i,j)$ which corresponded to the expected attack intensities given pastoral use.

To correct the observed kernel estimation for livestock presence, we calculated the corrected intensities $\lambda_{corr}(i, j)$ as:

$$\lambda_{corr}(i,j) = \bar{\lambda}_{sim}(i,j) - \lambda_{obs}(i,j) \quad (1)$$

Thus, a value of $\lambda_{corr}(i, j)$ lower, equal or higher than zero indicated that the observed attack intensity at coordinates *(i, j)* was lower, equal or higher, respectively, than the attack intensity expected according to pastoral use.

Eventually, we calculated the trends of observed or corrected attack intensities at different spatio-temporal scales *s* as:

$$Y_{\lambda,s} = \frac{\sum_{i=1,j=1}^{i=I,j=J+1} \lambda'(i,j) - \sum_{i=1,j=-J}^{i=I,j=0} \lambda'(i,j)}{I \times (J+1)} \times 100 \qquad (2)$$

where *I* and *J* were the number of rows (spatial distance to removals) and columns (number of days before or after removals) of scale *s*, $\lambda'(i, j)$ was the observed or corrected intensity at the coordinates *(i, j)* rescaled over [0,1] for observed intensity or over [-1,1] for corrected intensity by using the minimum and maximum values of $\lambda_{obs}(i, j)$ or $\lambda_{corr}(i, j)$ over the temporal range *-J*, *J+1*. The rescaling allowed trend comparison between subsets. The division by $I \times (J+1)$ allowed trend comparison between scales *s*. We investigated three spatio-temporal scales *s*: the small scale (*s* = 1) of spatial range 0-2 km and of temporal range ± 15 days (*I* = 40, *J* = 14), the intermediate scale (*s* = 2) of spatial range 0-6 km and of temporal range ± 45 days (*I* = 120, *J* = 44) and the large scale (*s* = 3) of spatial range 0-10 km and of temporal range ± 90 days (*I* = 200, *J* = 89).

In addition, we investigated the potential spatial shift of attack intensities by applying Equation 2 separately for each spatial coordinate *i* of the spatial range 0-10 km ($i \in [1,200]$) and for each of the three temporal ranges (*J* = 14 at *s* = 1, *J* = 44 at *s* = 2, *J* = 89 at *s* = 3). We only adjusted the results by $J+1$ as the spatial range was the same for the three temporal ranges. Namely, we transformed Equation 2 into Equation 3: $Y_{\lambda,s}(i) = \left(\sum_{j=1}^{j=J+1} \lambda'(i,j) - \sum_{j=-J}^{j=0} \lambda'(i,j)\right) / (J+1) \times 100$.

2.3.6 Control events

Lastly, we combined the intra-site comparison performed in the previous section 2.3.5 with an inter-site comparison, *i.e.* we applied a BACI study design. We compared the trends of the spatio-temporal patterns of attacks surrounding lethal removals and surrounding control events where no lethal removal was applied.

Each non-interacting lethal removal and each group of interacting lethal removals received one control event. In the case of a non-interacting lethal removal, we attributed the date of the removal to its control event. In the case of a group of interacting removals, we attributed two dates to its control event: the date of the first removal of the group and the date of the last removal of the group.

Then, we delimited the sampling area where the spatial location of the control event could be randomly sampled. We considered that only the mountain range the removal was within, buffered by 15 km (section 2.3.4), represented a similar environment to the removal. Therefore, we restricted our dataset to removals that could be attributed to a mountain range, giving 188 non-interacting removals (instead of 196) and 35 groups of interacting removals (instead of 36).

However, the attack distribution within the mountain range could be distorted by the lethal removals occurring shortly before or after the control event. Therefore, we removed from the sampling area the 10-km spatial buffer of any known removal occurring less than 90 days from the removal. Compared to section 2.3.1, we therefore defined more strict conditions for the risks of interaction between a removal buffer and a control event buffer (*i.e.*, 90 days and 10 km, instead of 25 days and 5 km).

In addition, some mountain ranges could be close, and their 15-km buffers could overlap. We removed the overlapping buffers of the other mountain ranges from the sampling area. We also removed all the area closer than 10 km from the terrestrial and maritime limits of the study area. The final sampling area for each mountain range can be visualized in Figure 6, as well as the sampling area and the sampled control events for one removal as an example.

The whole analysis process previously described, from section 2.3.1 to 2.3.5, was then repeated for the 223 control events. We then simulated 99 more sets of the 223 control events. On average, the observed buffers of the control events included a total of 3387 attacks (± 173), against 6110 for the observed buffers of removals. Each control buffer included on average 16.7 attacks (± 0.9), against 26.3 (± 20.7) for the removal buffers.

We extracted the mean and the 95% confidence intervals (95-CI) of the trends of observed or corrected attack intensities of the final 100 sets of control events (hereafter, 'control sets'), at the same scales *s* as in section 2.3.5 (Equation 2) and for the same subsets as in section 2.3.4. We considered that the positive or negative trend of a subset of lethal removals was significant for a specific scale *s* if it was higher or lower, respectively, than the 95-CI of the trends of the control sets of the same subset ($\alpha = 0.05$).

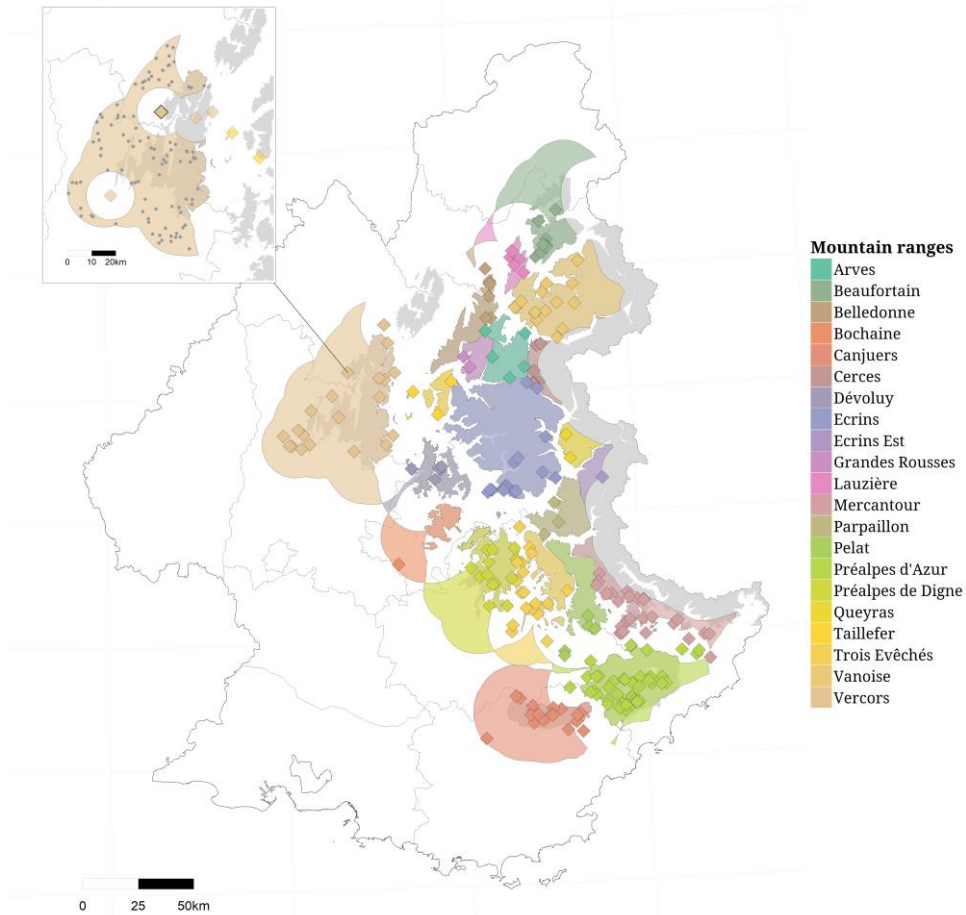

Figure 6. Sampling areas within the mountain ranges for the control events, and the 223 lethal removal locations (colored squares) used for the BACI design. One sampling area corresponds to the 15-km buffer of the mountain range minus the 15-km buffers of the other mountain ranges and minus the area closer than 10 km from the terrestrial and maritime limits of the study area. The inset plot shows the specific sampling area (light brown) of one focal lethal removal (thick square) in the Vercors mountain range, corresponding to the Vercors sampling area minus the 10-km buffers of the other lethal removals (thin squares) occurring less than 90 days from the focal lethal removal; the grey round points represent the locations of the 100 sampled control events of the focal lethal removal.

2.4 Implementation

The analysis was conducted in R 4.4.2 (R Core Team, 2023). We used the R packages *tidyverse 2.0.0* (Wickham et al., 2019), *readxl 1.4.2* (Wickham and Bryan, 2023), and *sf 1.0-12* (Pebesma and Bivand, 2023) to handle the datasets. We used the R package *spatstat 3.2-1* (Baddeley et al., 2015) to simulate point patterns in part 2.3.3. We adapted the function *kde2d.weighted* from *ggtern 3.4.2* (Hamilton and Ferry, 2018) to separate the kernel estimates before and after the removal date in part 2.3.4. We used the package *osmdata 0.2.5* (Padgham et al., 2017) to extract limits of PNRPA and of Canjuers military zone. We used the packages *RColorBrewer 1.1-3* (Neuwirth, 2022), *tidyterra 0.4.0* (Hernangómez, 2023), *geodata 0.5-8* (Hijmans et al., 2023), *scales 1.2.1* (Wickham and Seidel, 2022), *ggfx 1.0.1* (Pedersen, 2022a), *ggnewscale 0.4.9* (Campitelli, 2023), *metR 0.14.1* (Campitelli, 2021), *patchwork 1.1.2* (Pedersen, 2022b) and *ggtext 0.1.2* (Wilke and Wiernik, 2022) for data visualization. The datasets, codes and results are available online (Grente et al., 2025).

3. Results

Trends in the observed and corrected attack intensities after lethal removals are displayed in Table 1 for the subsets of the intra-site comparison, in Table S1.A for the subsets of the BACI and in Table S1.B for the control sets (mean and 95-CI) of the BACI. Distributions of the trends from Table 1 and Table S1 are displayed in Figure 7.

The significance of the trends of lethal removals from the BACI design is displayed in Figure 8. Trends of the intra-site comparison as a function of spatial coordinate *i* are displayed in Figure 9 for the 15-day temporal range, and in Figure S1.A and Figure S1.B for the 45-day and 90-day temporal ranges, respectively. Lastly, heatmaps of observed and corrected kernel estimates are displayed in Figure 10 and Figure S2.

3.1 Trends of attack intensities

The distributions of the trends of attack intensities were mostly within a negative range (Figure 7), indicating a general decrease of attack intensities after lethal removals, regardless of the correction for livestock presence or of the study design (intra-site or BACI). The main modes of these distributions ranged between -21% and -8% (Figure 7). This shift towards negative values was not observed for the distributions of the mean control trends from the BACI design, that were symmetrically centered on zero, and more or less widespread according to scales and livestock correction (Figure 7).

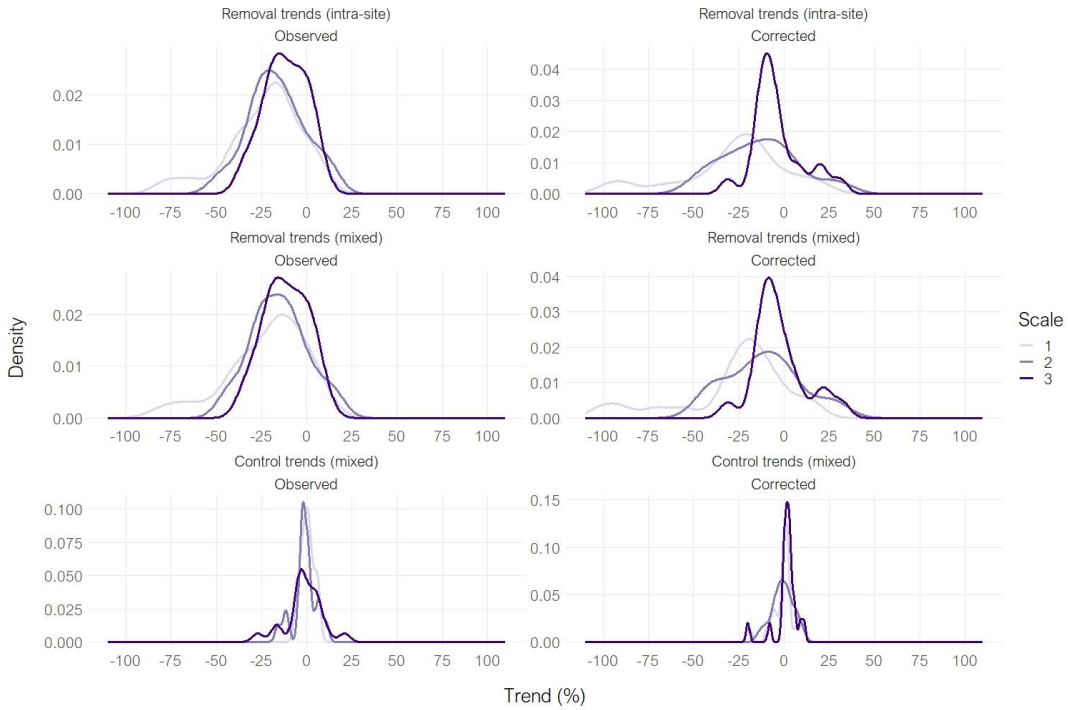

Figure 7. Density distributions of the trends of observed (left) and corrected (right) attack intensities for the 20 subsets of (top) removals from the intra-site comparison, (middle) removals from the BACI design or (bottom) controls sets of removals from BACI design, at the spatio-temporal scales 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days). Data from Table 1, Table S1.A and Table S1.B (mean trends of control sets).

However, this general decrease concealed disparities between subsets. Indeed, we could observe a gradient of possible trends in Table 1 (intra-site comparison) and in Table S1.A (BACI), from important decreases to moderate increases, by way of no changes. The prevalence of decrease was particularly noticeable at s = 1, especially when correction for livestock presence was applied. Only 3

or 2 subsets out of 20, from the intra-site comparison and BACI design respectively, presented increases 15 days after lethal removals within 2 km, when the correction for livestock presence was applied. At the larger scales, the effect of decrease was slightly less prevalent among subsets, but most importantly, the intensities of the decreases within subsets were generally lower than at scale 1. On the contrary, besides being slightly more prevalent, the positive trends had higher intensities at scales 2 and 3, especially when the correction for livestock presence was applied.

Table 1. Trends of observed $Y_{\lambda_{obs},s}$ and corrected $Y_{\lambda_{corr},s}$ attack intensities (%) after the lethal removals used for the intra-site comparison, calculated over three different spatio-temporal scales s, 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days) following Equation 2, separately for each subset. All trends are comparable. Column "Total" indicates the number of lethal removals of each subset, or of groups of lethal removals for the main subset "Interacting". Column "Figure" gives the corresponding figure number of heatmaps. Gradient of colors ranges from dark blue for -100 to dark red for 100, while the middle color in white corresponds to 0.

					Scale 1		Scale 2		Scale 3	
Main subset	Category	Subset	Total	Figure	$Y_{\lambda_{obs},1}$	$Y_{\lambda_{corr},1}$	$Y_{\lambda_{obs},2}$	$Y_{\lambda_{corr},2}$	$Y_{\lambda_{obs},3}$	$Y_{\lambda_{corr},3}$
Non-interacting			196	10.A	-16	-14	-28	-23	-18	-8
	Geographic zone	*PNRPA*	33	10.C	1	-1	-9	-15	-10	-15
		Mercantour	23	S2.D	-39	-54	-27	-23	-21	-10
		Trois Evêchés	18	S2.C	-34	-29	-24	-3	-19	6
		Vercors	18	10.E	-35	-38	11	31	0	19
		Vanoise	15	S2.E	-18	-30	-27	-38	-5	-11
		Ecrins	12	S2.B	-15	-21	0	2	3	9
		Préalpes de Digne	12	10.D	-77	-67	-30	-2	-23	21
		Canjuers	11	S2.A	6	13	2	0	-3	-8
	Season	*Fall*	63	S2.F	-17	-17	-48	-49	-33	-11
		Rendez-vous	59	10.G	-10	-16	12	9	7	-8
		Denning	35	10.F	-62	-96	-26	-42	2	-12
		Winter	30	10.H	-33	-17	-16	25	-23	31
		Reproduction	9	S2.G	-23	-40	-8	-15	-17	-31
	Class	*Reinforced defense*	75	10.J	-14	-15	-8	-3	-11	-6
		Simple defense	69	10.I	-20	-27	-19	-26	0	-3
		Hunting	52	10.K	4	20	-40	-39	-33	-16
	Sex	*Male*	83	S2.H	-21	-25	-19	-12	-14	-3
		Female	78	S2.I	-5	1	-15	-10	-13	-2
Interacting			36	10.B	-44	-88	-14	-28	-7	-13

By comparison, a range of 7-15 subsets of the control sets presented an increase, generally weak, depending on the scale and the livestock correction (Table S1.B). This is why most of negative trends of subsets of lethal removals were significant, with only three or one weakly negative corrected trends not significant at *s* = 1 and *s* = 2, respectively (Figure 8, Table S1.A).

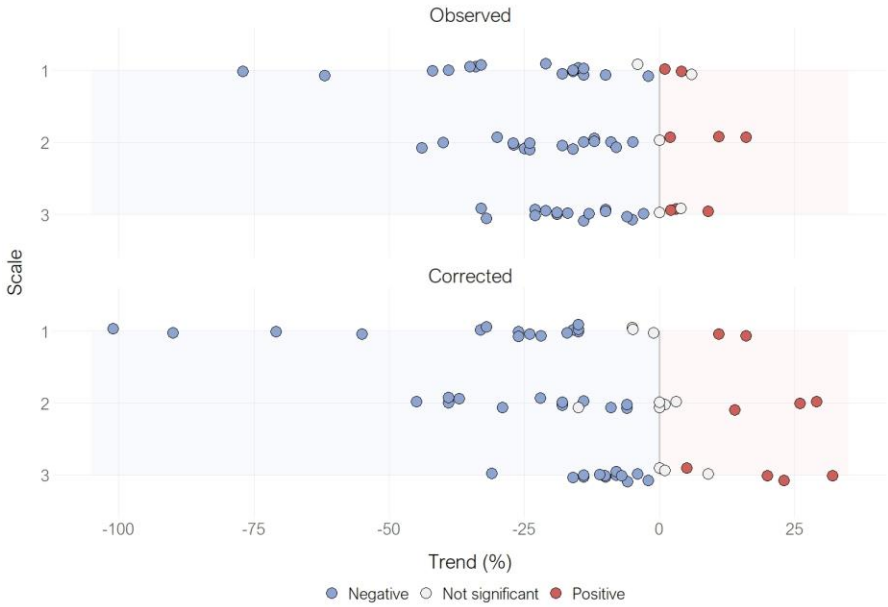

Figure 8. Trends of observed attack intensities $Y_{\lambda_{obs},s}$ (top) and of corrected attack intensities $Y_{\lambda_{corr},s}$ (bottom) after the lethal removals from the BACI design, and calculated over three different spatio-temporal scales s, 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days) separately for each of the 20 subsets. The gray points correspond to the trends of subsets of lethal removals that are within the 95-CI of the corresponding trends of subsets of control sets, and are not considered as significant, as defined in section 2.3.6. Data from Table S1.A.

All subsets that showed positive trends for at least one scale also showed negative trends at the other scales, meaning that one or several shifts from positive to negative trends between scales, or *vice-versa*, could coexist within the same subset (Table 1, Table S1.A). These shifts of trends also occurred along the spatial gradient when setting the temporal scale at 15 days before and after removals (Figure 9). In fact, only one subset (Mercantour) presented a pronounced spatial negative trend shift over all spatial distances. For the other subsets, the null or positive trends could appear from the removal locations (*i.e.* 0 km) or much farther (> 8 km), like in *Fall* and *Hunting*. However, the negative trends were more intense and over larger spatial portions than the positive trends, except for *Vercors*, *Canjuers*, *Rendez-vous* and *Winter*.

When setting the scale at 45 or 90 days (Figures S1.A and S1.B), spatial trend shifts were generally similar to the 15-day scale, despite a rebalancing between the negative and positive trends at these scales. This similarity between temporal scales demonstrated that the shifts of trends between scales 1, 2 and 3 in Table 1 and Table S1.A were more depending on the spatial scale than the temporal scale. In other words, for most subsets, the distribution of the attacks should be first structured by space, with strong spatial aggregations of attacks, and should be subsequently modulated by time.

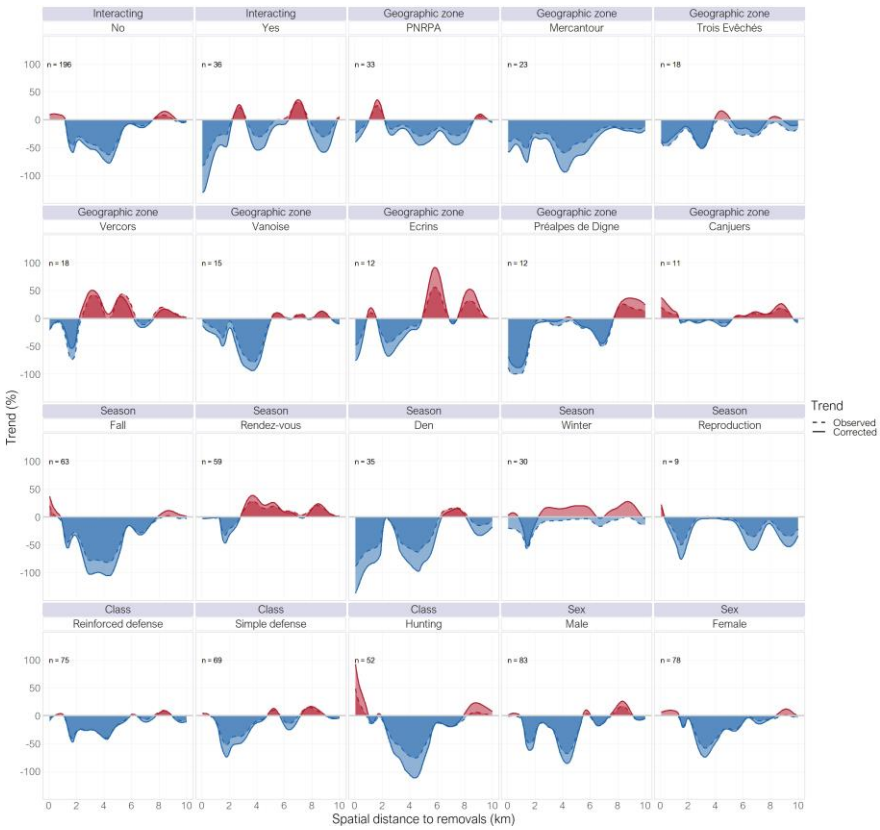

Figure 9. Trends of observed attack intensities $Y_{\lambda_{obs}}$ (dotted line) and of corrected attack intensities $Y_{\lambda_{corr}}$ (solid lines) after the lethal removals used for the intra-site comparison, calculated along the spatial scale of 10 km with a fixed temporal scale of ± 15 days following Equation 3. Top facet strips indicate the main subset or the category, and the bottom facet strips indicate the subset.

3.2 Spatio-temporal distributions of attack intensities

Diversity and shifts between scales *s* in trends were the result of the large diversity in the distributions of attack intensities in time and in space around lethal removals (Figures 10 and S2). For example, some patches of high intensities could be present in a bundled form, such as in *Fall* (Figure S2.F), or in a more fragmented way, such as in *Ecrins* (Figure S2.B). However, we could extract two features common to all subsets. First, removals were generally preceded by high attack intensities at their locations, meaning they were applied in response to attacks, in accordance with French legislation. Second, attacks tended to aggregate below 2 km from removal locations, regardless of time and of other possible aggregation spots. Therefore, the attack process was generally a persistent phenomenon at these locations, although showing possible interruptions in time, even before removals (*e.g.* subset of *Rendez-vous*).

The correction for livestock presence generally provided similar attack distributions to the observed distributions, but for some subsets, differences were noticeable, such as *Préalpes de Digne* (Figure 10.D), *Vercors* (Figure 10.E), *Reinforced defense* (Figure 10.J), *Winter* (Figure 10.H), *Trois Evêchés* (Figure S2.C) or *Female* (Figure S2.I). Yet, not all of these subsets were associated with high differences between observed and corrected trends (Table 1, Table S1.A, *e.g.* 5% for *Reinforced defense* in the intra-site comparison). In the case of *Reinforced defense*, the effect of livestock control was the same before and after removals (Figure 10.J), whereas in the case of *Winter*, the

correction decreased the intensities before removals and increased those after removals (Figure 10.H). These differences laid on the monthly distribution of removals. Corrections varied more greatly along the temporal axis when removals occurred at the limit between an intense and calm grazing period, like removals of the *Winter* subset (Figure 10.H.ii). This is why the larger the scale, the higher the differences between the observed and corrected trends. Hence, 5 subsets presented a different sign between their observed and corrected trends at scale 3, against only 1 at scale 2.

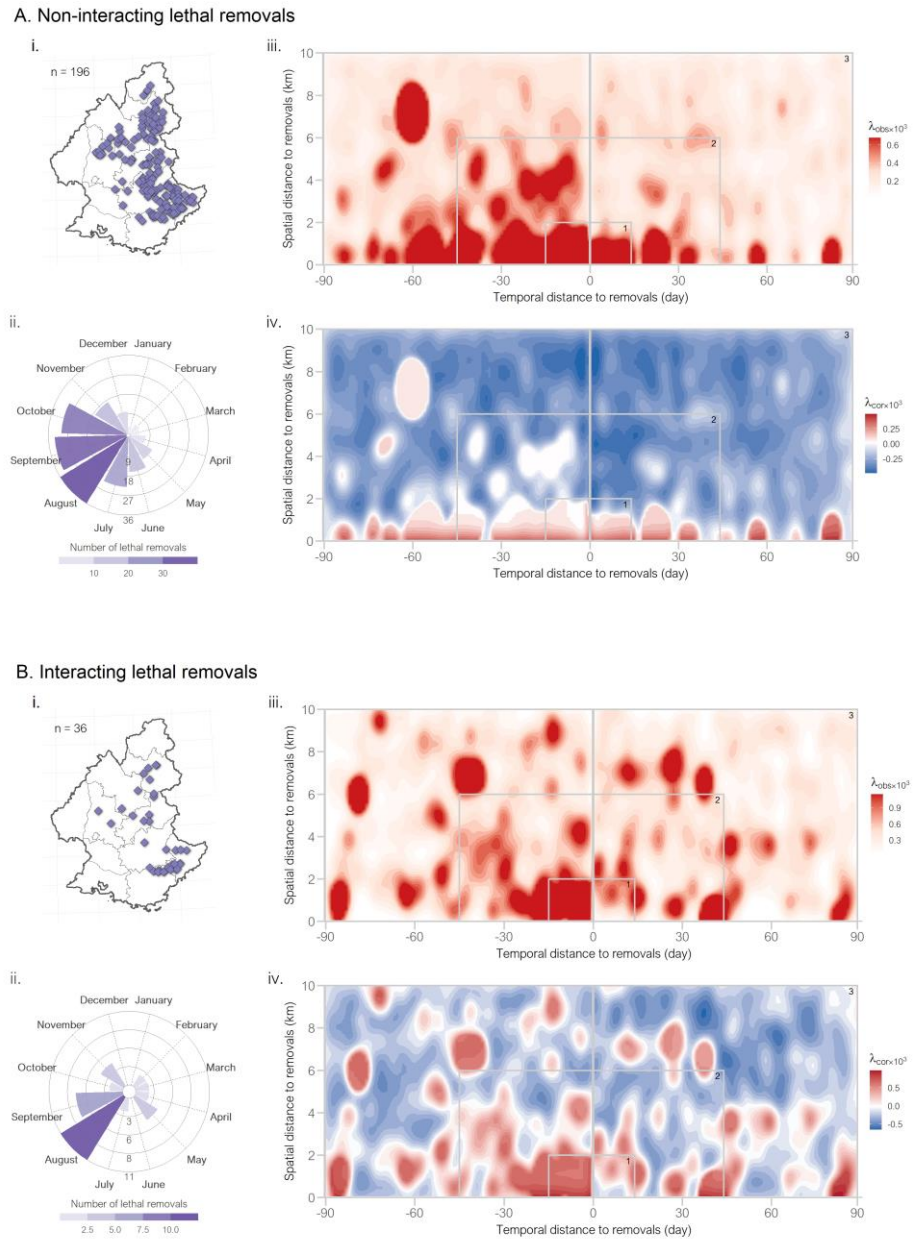

Figure 10. Kernel estimation of attack intensities surrounding lethal removals, detailed for each analyzed subset of removals (all panels except B.) or of groups of removals for the subset of interacting removals (B.). Each panel includes (i) the map of the removal locations or of the centroids of the groups, with the annotated number of involved removals or groups, (ii) the monthly distribution of the removal dates or of the middle dates of the groups, (iii) the observed attack intensities λ_{obs} and (iv) the corrected attack intensities λ_{corr}. The coordinate (0,0) indicates the day before removals and the location of removals. Grey rectangles of subpanels iii and iv delimit the three analysis scales 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days). A value of λ_{corr} lower, equal or higher than zero indicated that the observed attack intensity was lower, equal or higher, respectively, than the attack intensity expected according pastoral use. (Part 1/4)

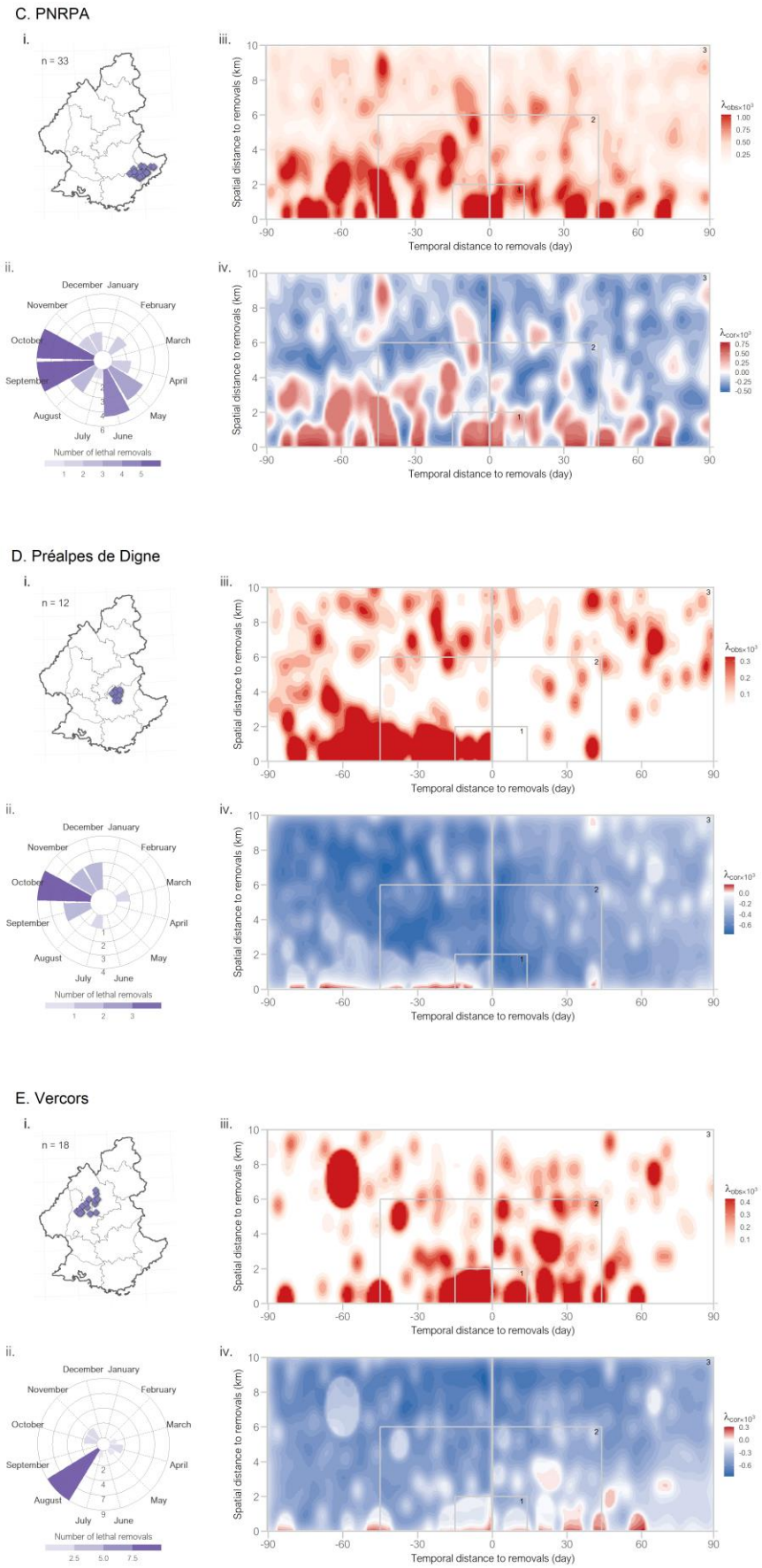

Figure 10. (Part 2/4)

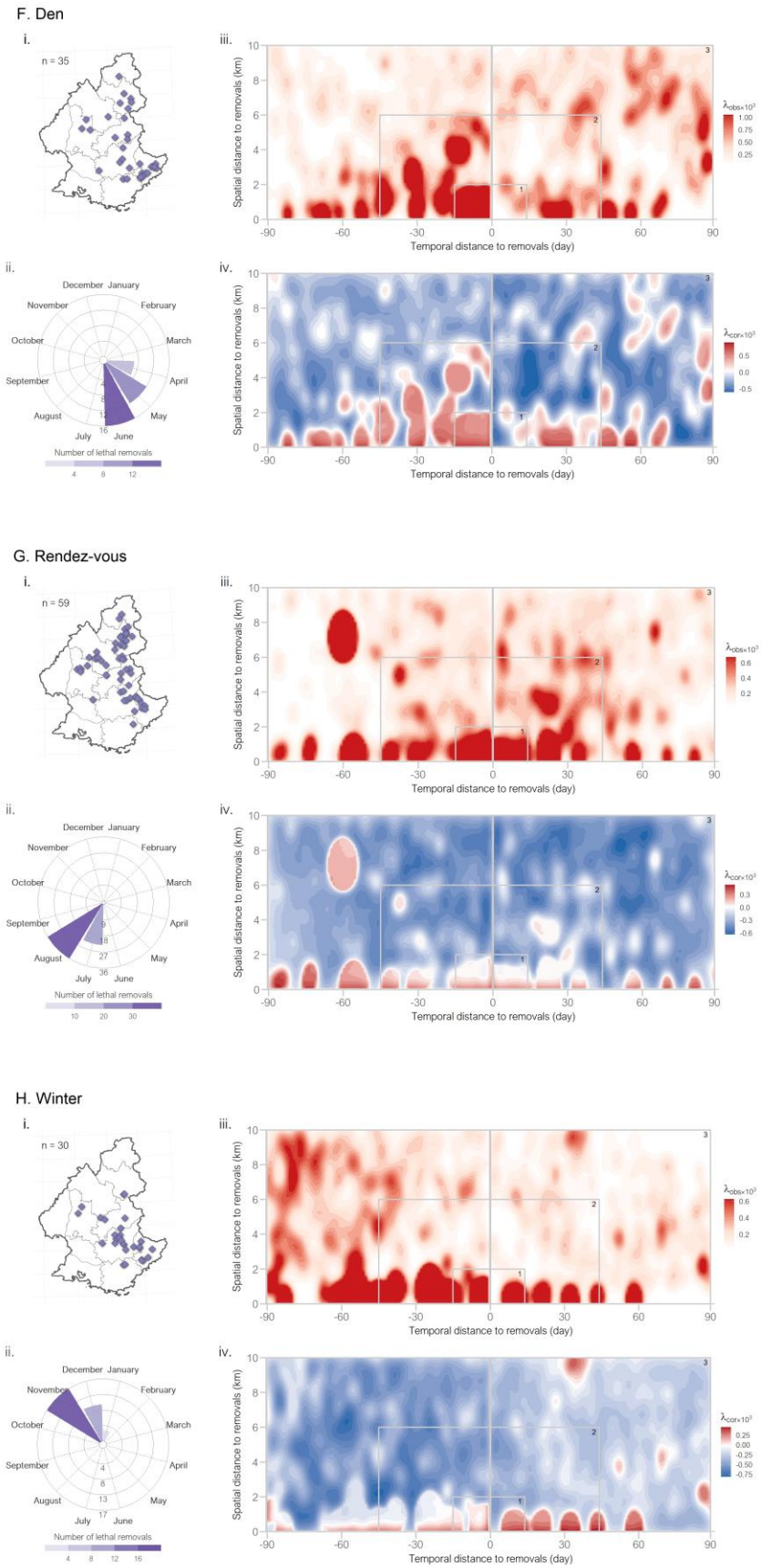

Figure 10. (Part 3/4)

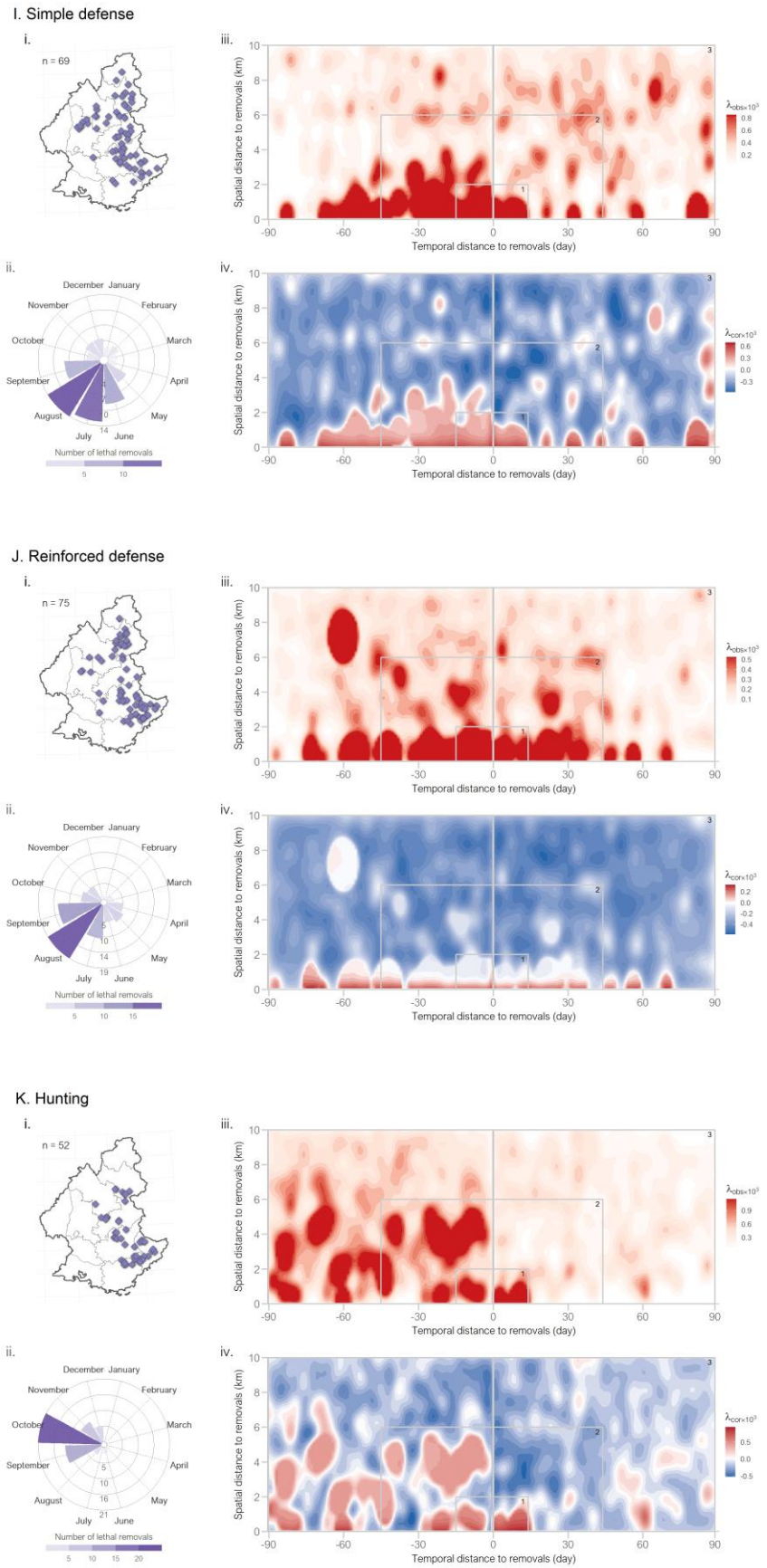

Figure 10. (Part 4/4)

4. Discussion

We evaluated the effects of lethal control of wolves on attack intensity distribution through a kernel density estimation that had never been used before for this topic, through the large number of attack claims surrounding the events of lethal removal of wolves in France. Our method contrasted with the Cox proportional hazard models commonly used by previous studies to estimate the risk of recurrence of a single attack over a fixed area (Bradley et al., 2015; Harper et al., 2008; Santiago-Avila et al., 2018).

Our method provided an efficient visualization of attack intensity distributions in the form of heatmaps over continuous spatial and temporal scales, corrected for sheep presence. The resulting attack intensity trends showed the differences in the attack intensities before and after lethal removals (intra-site comparison) and with comparable areas without removals (BACI design).

The aim of our study was to generalize the spatio-temporal patterns of attack intensity surrounding lethal removal applications, without concealing the potential diversity of these patterns across the French Alps that could result from different situations. This is why we grouped lethal removals into 20 subsets according to their application conditions (geographical, seasonal, administrative) or to the removal results (one or several killed wolves, sex). Our confidence in the representativeness of a pattern however depended on the size of the subset, and we removed too small subsets from the geographical category. In addition, some categories had too unbalanced subset sizes to be explored (*e.g.* age class of killed wolf).

The distribution of the attacks was usually structured by space, with strong spatial aggregations of attacks, especially close to the locations of the lethal removals, and was only subsequently modulated by time. This suggested that some locations may have been more subject to attacks than others.

The trends of attack distributions after lethal removals showed a gradient ranging from important decreases to moderate increases, by way of no changes. Within this gradient, the moderate decrease (between -21% and -8%) was the prevalent effect for the three analyzed spatio-temporal scales. Generally, the smaller the area and the time period surrounding the lethal removals, the more important the decrease of attacks after removals.

We expect these results to reasonably reflect the effects of lethal removals on wolves. Thus, the lethal removals should have generally decreased attack intensities by temporarily decreasing local wolf density or by altering the distribution or the predation behavior of the remaining wolves. However, as in every study, confounding factors may interfere. For this topic, the main risk was to confound the effects of lethal removals on wolves with the effects of livestock distribution dynamics in space and time. We corrected our analysis for livestock distribution based on a pastoral census in the Alps that gave the precise limits of pastures and their months or seasons in use (Dobremez et al., 2016). This type of regional census requires a substantial amount of work. Fine-scale livestock data as provided by this census is therefore generally missing from analyses on predation, including for other parts of France (*e.g.* Gastineau et al., 2019). When integrated, livestock data is generally at large, administrative scales (*e.g.* DeCesare et al., 2018; Šuba et al., 2023). Thus, only two comparative studies (Allen, 2015; Conner et al., 1998) and two correlative studies (Blejwas et al., 2002; Wagner and Conover, 1999) that evaluated lethal control effects on canids corrected their analysis for livestock presence at the pasture level.

However, despite the quality of the livestock census we used, this may not have been enough to prevent the main confounding risk for our study. Annual changes in the use of pastures since the

census may have occurred. In addition, temporary changes in livestock presence are common during a grazing season, as livestock owners and shepherds modulate the use of pastures by their flocks to optimize grazing according to environmental conditions. Among these conditions, pressure due to wolf predation or attempts of predation may encourage livestock owners to remove flocks from some pastures or to reinforce preventive measures. Data on precise husbandry practices, such as preventive measures, were out of the scope of this census. Hence, resulting potential variations in livestock distribution and protection, even small and temporary, may drive changes in attack distribution that would not have been considered in the census and therefore in the livestock correction of our analysis. To a lesser extent, variations in the spatio-temporal distributions of wild ungulates may also impact the distribution of attacks on livestock.

In spite of the limits of the livestock dataset, the intra-site comparison design should have helped to reduce the confounding risks, especially at the smallest scale. Because wolves move over large territories, we acknowledge that focusing on changes happening only in very close proximity to removals could not be enough to evaluate removal effects (Treves et al., 2016). To improve the statistical power of our analysis, especially at the two larger analysis scales, we doubled the intra-site comparison with an inter-site comparison, therefore applying a BACI design, evaluated as robust by Christie et al. (2019). The main limit of this study design is to use appropriate control sites. In our case, this was a challenging task because lethal removals in France were generally authorized and applied in attack hotspots, creating unbalanced initial attack intensities between sites with and without removals. Nevertheless, the buffers of control events had on average 16.7 attacks (± 0.9) against 26.3 (± 20.7) for the removal buffers, suggesting that control sites were also subject to attacks.

If the confounding risks were as low as possible, the gradient in the trends of attack intensities should mainly correspond to different reactions from wolves after the lethal removals according to the situations. The disappearance of attacks immediately after removals like in *Préalpes de Digne* is in favor of the removal of problem individuals (Linnell et al., 1999) or of the drastic reduction in the localized wolf density (Bjorge and Gunson, 1985; Bradley et al., 2015). This density reduction would not result from the removal intensity (only one killed wolf per removal event in this subset) but from an initial low wolf density. However, for most analyzed subsets, attacks persisted after removals at the location of the removals, including at high intensity, even though most removals targeted wolves approaching livestock or attempting attacks. This result suggested that attacks on livestock were more a structural phenomenon than the outcome of some problem individuals. Local wolf density is mainly driven by the abundance and vulnerability of their prey (Mech, 2024). Therefore, we hypothesize that the efficiency of lethal removals is increased in situations with low localized wolf density, resulting from low vulnerable prey biomass (*e.g.* area with a generalization of livestock protection or local conditions that facilitate protection, or denser in wild boar than in roe deer) or resulting from the progressive process of recolonization by wolves in the Alps.

Persistence of attacks in most situations also challenges the hypothesis of pack dissolution (Elbroch and Treves, 2023), as settlement of new wolves at the same location was unlikely to be as fast, even in the dense population of the Western Alps (Marucco et al., 2023). In addition, pack dissolution risks are higher when one or two breeders are killed, and decrease with pack size (Brainerd et al., 2008; Cassidy et al., 2023). In our dataset, only a low number of breeding females were removed (7/105), although the reproduction status was unknown for males. Moreover, one wolf was killed per lethal control on average, mostly in areas with long-term packs. This suggested that pack sizes and the local wolf density could have been only moderately affected by most removals, reducing pack dissolution risks. This would be consistent with the most encountered result of moderate

decrease of attack intensities after removals, and with results from the northern Rocky mountains in the USA, where the probability of recurrence of attacks increased with pack size (Bradley et al., 2015). Nevertheless, low risks of pack dissolution do not disprove possible changes in pack composition further to the removals, that may alter wolf space use, causing remaining or new wolves to move away or closer to the flocks protected by removals or to the neighboring flocks.

Confirming or rejecting these hypotheses about the effects of lethal removals on wolves and therefore on their attacks would have required to have access to pack compositions and space use by wolves at fine spatio-temporal scale, which were unavailable. Collection of these datasets on wolves are particularly difficult on large study area, considering the secrecy of wolves. A trade-off would be to deploy the substantial means required to collect such datasets in a small study area (*e.g.* one wolf territory and its neighboring packs) for a few years, ideally replicated at different locations in the Alps. Effects of lethal control on wolves and their attacks may then be evaluated through promising methods such as animal social network analysis, which was applied to study the reaction of other social animals to human-induced removals (*e.g.* Downing et al., 2023; Goldenberg et al., 2016). Working at small scale would also facilitate a more precise collection of livestock presence and husbandry practices, in order to correct the analyses for the primary risk of confounding factor.

However, variability is inherent to any ecological process, and predation behavior is no exception. A few fine-scale datasets on wolves and livestock would not necessarily explain all the observed responses of wolves to lethal removals and therefore the effects on attacks. Indeed, predation partly relies on random encounters of wolves with their prey, natural (Huggard, 1993) or domestic (Landry et al., 2020). The gradient of effects of lethal removals on attacks we obtained is indicative of this variability. A small number of study sites would increase the risks to miss out this uncertainty surrounding predation behavior and could compromise our abilities to interpret the effects of lethal removals on attacks through their effects on wolves.

A solution would be to upgrade the analysis of observed data by simulations. For example, Wiśniewska et al. (2022) used individual-based modelling to simulate poaching effects on elephant social structures. We also used individual-based modelling to simulate removal effects on wolf population dynamics and on attacks at the scale of a mountain range in the Alps (Grente et al., 2024). This modelling exercise showed that lethal control reduced the risks of predation by maintaining a low wolf density. However, the model strongly depended on assumptions about predation behavior and would greatly benefit from a combination with social network analysis based on observed data at small scale.

5. Conclusion

The lethal management strategy implemented in France from 2011 to 2020—primarily involving the removal of individual wolves in defense situations with protected livestock—can be expected to have produced a moderate reduction in attack intensity following removals. This reduction was generally more pronounced when considering small spatial and temporal scales. However, contextual factors (e.g., geographical or seasonal variations) could lead to deviations from this general pattern, with outcomes ranging from important decreases to moderate increases in attacks. Given that our study design —including livestock correction, small-scale analyses, and a BACI framework— mitigated the main confounding risks related to livestock, we hypothesize that localized wolf density could have explained the variability in lethal removal effectiveness. Our findings support a context-dependent approach to damage management, in line with insights from social sciences (Creti et al., 2022). Future research should focus on understanding wolves' responses

to removals—such as changes in pack composition, space use, and predation behavior—to better interpret the observed variability in attack trends post-removal.

Supplementary information

Two supplementary materials are available online, on Zenodo (https://doi.org/10.5281/zenodo.14893823).

File 1. Supplementary table (Table S1)

File 2. Supplementary figures (Figure S1, Figure S2)

Acknowledgements

We are indebted to the governmental agents in charge of recording attack claims and lethal removals. We are grateful to the regional administration of Auvergne-Rhône-Alpes for the access to the databases of claims and of wolf lethal removals. We are also grateful to INRAE (previously IRSTEA) for the access to the pastoral census. We greatly thank Marion Valeix, John Linnell and Michel Meuret for their valuable comments regarding the first draft of this study as part of the PhD dissertation of Oksana Grente. We also thank members of the scientific council of the National Plan of Action for wolves and livestock breeding activities for their feedback and advices.

Data, scripts and code

Data, scripts and code are available online, on Zenodo (https://doi.org/10.5281/zenodo.14893823) and on gitlab (https://gitlab.com/oksanagrente/Kernel_wolf_culling_attacks_p).

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

Olivier Gimenez and Simon Chamaillé-Jammes are recommenders of the managing board of PCI Ecology.

Funding

This study was funded by a grant from the French Ministry of Ecological and Solidary Transition and the French Ministry of Agriculture and Food as part of the National Plan of Action for wolves and livestock breeding activities.

References

Agreste, 2021. La transhumance collective. Données issues du recensement agricole 2020. [WWW Document]. VizAgreste. URL https://vizagreste.agriculture.gouv.fr/la-transhumance-collective.html (accessed 11.24.23).

Allen, B.L., 2015. More buck for less bang: Reconciling competing wildlife management interests in agricultural food webs. Food Webs 2, 1–9. https://doi.org/10.1016/j.fooweb.2014.12.001

Allen, L.R., 2014. Wild dog control impacts on calf wastage in extensive beef cattle enterprises. Anim. Prod. Sci. 54, 214. https://doi.org/10.1071/AN12356

Arif, S., MacNeil, M.A., 2022. Predictive models aren't for causal inference. Ecology Letters 25, 1741–1745. https://doi.org/10.1111/ele.14033

Ausband, D.E., Mitchell, M.S., Waits, L.P., 2017. Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore. Journal of Animal Ecology 86, 1094–1101. https://doi.org/10.1111/1365-2656.12707

Baddeley, A., Rubak, E., Turner, R., 2015. Spatial Point Patterns: Methodology and Applications with R, CRC Press. ed.

Bjorge, R.R., Gunson, J.R., 1985. Evaluation of Wolf Control to Reduce Cattle Predation in Alberta. Journal of Range Management 38, 483. https://doi.org/10.2307/3899736

Blejwas, K.M., Sacks, B.N., Jaeger, Michael M., McCullough, D.R., 2002. The Effectiveness of Selective Removal of Breeding Coyotes in Reducing Sheep Predation. The Journal of Wildlife Management 66, 451–462. https://doi.org/10.2307/3803178

Bradley, E.H., Robinson, H.S., Bangs, E.E., Kunkel, K., Jimenez, M.D., Gude, J.A., Grimm, T., 2015. Effects of wolf removal on livestock depredation recurrence and wolf recovery in Montana, Idaho, and Wyoming: Effects of Wolf Removal. Jour. Wild. Mgmt. 79, 1337–1346. https://doi.org/10.1002/jwmg.948

Brainerd, S.M., Andrén, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W., Iliopoulos, Y., Jimenez, M.D., Jozwiak, E.A., Liberg, O., Mack, C.M., Meier, T.J., Niemeyer, C.C., Pedersen, H.C., Sand, H., Schultz, R.N., Smith, D.W., Wabakken, P., Wydeven, A.P., 2008. The Effects of Breeder Loss on Wolves. Journal of Wildlife Management 72, 89–98. https://doi.org/10.2193/2006-305

Campitelli, E., 2023. ggnewscale: Multiple fill and colour scales in “ggplot2” (manual).

Campitelli, E., 2021. metR: Tools for easier analysis of meteorological fields (manual). https://doi.org/10.5281/zenodo.2593516

Cassidy, K.A., Borg, B.L., Klauder, K.J., Sorum, M.S., Thomas-Kuzilik, R., Dewey, S.R., Stephenson, J.A., Stahler, D.R., Gable, T.D., Bump, J.K., Homkes, A.T., Windels, S.K., Smith, D.W., 2023. Human-caused mortality triggers pack instability in gray wolves. Frontiers in Ecology and the Environment n/a. https://doi.org/10.1002/fee.2597

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe’s modern human-dominated landscapes. Science 346, 1517–1519. https://doi.org/10.1126/science.1257553

Christie, A.P., Amano, T., Martin, P.A., Shackelford, G.E., Simmons, B.I., Sutherland, W.J., 2019. Simple study designs in ecology produce inaccurate estimates of biodiversity responses. Journal of Applied Ecology 56, 2742–2754. https://doi.org/10.1111/1365-2664.13499

Conner, M.M., Jaeger, Michael M., Weller, T.J., McCullough, D.R., 1998. Effect of Coyote Removal on Sheep Depredation in Northern California. The Journal of Wildlife Management 62, 690–699. https://doi.org/10.2307/3802345

Creti, I., Chezel, E., Mounet, C., Baud, D., Dusseux, P., 2022. Territorialiser la question des loups par les pratiques agri-alimentaires. Une enquête sur les relations biodiversité et alimentation en Belledonne. Journal of Alpine Research | Revue de géographie alpine 110. https://doi.org/10.4000/rga.10634

de Beaufort, F., 1987. Le loup en France: éléments d'écologie historique. Encyclopédie des carnivores de France.

DeCesare, Nicholas.J., Wilson, S.M., Bradley, E.H., Gude, J.A., Inman, R.M., Lance, N.J., Laudon, K., Nelson, A.A., Ross, M.S., Smucker, T.D., 2018. Wolf-livestock conflict and the effects of wolf management: Wolf-Livestock Conflict. Jour. Wild. Mgmt. 82, 711–722. https://doi.org/10.1002/jwmg.21419

Dobremez, L., Bray, F., Borg, D., 2016. Enquête pastorale 2012-2014. IRSTEA.

Downing, B.C., Silk, M.J., Delahay, R.J., Bearhop, S., Royle, N.J., 2023. Culling-induced perturbation of social networks of wild geese reinforces rather than disrupts associations among survivors. Journal of Applied Ecology n/a. https://doi.org/10.1111/1365-2664.14522

Duchamp, C., Boyer, J., Briaudet, P.-E., Léonard, Y., Moris, P., Bataille, A., Dahier, T., Delacour, G., Millisher, G., Miquel, C., Poillot, C., Marboutin, E., 2012. A dual frame survey to assess time– and space–related changes of the colonizing wolf population in France. Hystrix, the Italian Journal of Mammalogy 23, 12. https://doi.org/10.4404/hystrix-23.1-4559

Elbroch, L.M., Treves, A., 2023. Perspective: Why might removing carnivores maintain or increase risks for domestic animals? Biological Conservation 283, 110106. https://doi.org/10.1016/j.biocon.2023.110106

Fabbri, E., Miquel, C., Lucchini, V., Santini, A., Caniglia, R., Duchamp, C., Weber, J.-M., Lequette, B., Marucco, F., Boitani, L., Fumagalli, L., Taberlet, P., Randi, E., 2007. From the Apennines to the Alps: colonization genetics of the naturally expanding Italian wolf (Canis lupus) population. Molecular Ecology 16, 1661–1671. https://doi.org/10.1111/j.1365-294X.2007.03262.x

Fernández-Gil, A., Naves, J., Ordiz, A., Quevedo, M., Revilla, E., Delibes, M., 2016. Conflict Misleads Large Carnivore Management and Conservation: Brown Bears and Wolves in Spain. PLoS ONE 11, e0151541. https://doi.org/10.1371/journal.pone.0151541

Gastineau, A., Robert, A., Sarrazin, F., Mihoub, J.-B., Quenette, P.-Y., 2019. Spatiotemporal depredation hotspots of brown bears, Ursus arctos, on livestock in the Pyrenees, France. Biological Conservation 238, 108210. https://doi.org/10.1016/j.biocon.2019.108210

Goldenberg, S.Z., Douglas-Hamilton, I., Wittemyer, G., 2016. Vertical Transmission of Social Roles Drives Resilience to Poaching in Elephant Networks. Current Biology 26, 75–79. https://doi.org/10.1016/j.cub.2015.11.005

Grente, O., 2021. Understanding the depredation process in grey wolf (Canis lupus) and its interactions with lethal measures: focus on the French Alpine Arc (Biologie des populations et Écologie). Thèse, Université de Montpellier, Montpellier, France.

Grente, O., Bauduin, S., Santostasi, N.L., Chamaillé-Jammes, S., Duchamp, C., Drouet-Hoguet, N., Gimenez, O., 2024. Evaluating the effects of wolf culling on livestock predation when considering wolf population dynamics in an individual-based model. Wildlife Biology e01227. https://doi.org/10.1002/wlb3.01227

Grente, O., Opitz, T., Duchamp, C., Drouet-Hoguet, N., Chamaillé-Jammes, S., Gimenez, O., 2025. Spatio-temporal dynamics of attacks around deaths of wolves: A statistical assessment of lethal control efficiency in France. https://doi.org/10.5281/zenodo.14893823

Grente, O., Saubusse, T., Gimenez, O., Marboutin, E., Duchamp, C., 2022. Wolf depredation hotspots in France: Clustering analyses adjusting for livestock availability. Biological Conservation 267, 109495. https://doi.org/10.1016/j.biocon.2022.109495

Hamilton, N.E., Ferry, M., 2018. ggtern: Ternary Diagrams Using ggplot2. Journal of Statistical Software, Code Snippets 87, 1–17. https://doi.org/10.18637/jss.v087.c03

Harper, E.K., Paul, W.J., Mech, L.D., Weisberg, S., 2008. Effectiveness of Lethal, Directed Wolf-Depredation Control in Minnesota. Journal of Wildlife Management 72, 778–784. https://doi.org/10.2193/2007-273

Hernangómez, D., 2023. tidyterra: tidyverse Methods and ggplot2 Helpers for terra Objects (manual). https://doi.org/10.5281/zenodo.6572471

Hijmans, R.J., Barbosa, M., Ghosh, A., Mandel, A., 2023. geodata: Download geographic data (manual).

Huggard, D.J., 1993. Prey selectivity of wolves in Banff National Park. I. Prey species. Can. J. Zool. 71, 130–139. https://doi.org/10.1139/z93-019

Jęodrzejewska, B., Jęodrzejewski, W., Bunevich, A.N., Minkowski, L., Okarma, H., 1996. Population dynamics of Wolves Canis lupus in Bialowieża Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. Mammal Review 26, 103–126. https://doi.org/10.1111/j.1365-2907.1996.tb00149.x

Knopf, G., 2019. Délimitation des massifs alpins. Nivologie des Alpes du Sud. URL https://nivo06.knobuntu.fr/index.php?option=com_content&view=article&id=400:delimitation-des-massifs-alpins&catid=63&Itemid=408 (accessed 11.27.23).

Kompaniyets, L., Evans, M.A., 2017. Modeling the relationship between wolf control and cattle depredation. PLoS ONE 12, e0187264. https://doi.org/10.1371/journal.pone.0187264

Kutal, M., Duľa, M., Selivanova, A.R., López-Bao, J.V., 2023. Testing a conservation compromise: No evidence that public wolf hunting in Slovakia reduced livestock losses. Conservation Letters n/a, e12994. https://doi.org/10.1111/conl.12994

Landry, J.-M., Borelli, J.-L., Drouilly, M., 2020. Interactions between livestock guarding dogs and wolves in the southern French Alps. Journal of Vertebrate Biology 69. https://doi.org/10.25225/jvb.20078

Lennox, R.J., Gallagher, A.J., Ritchie, E.G., Cooke, S.J., 2018. Evaluating the efficacy of predator removal in a conflict-prone world. Biological Conservation 224, 277–289. https://doi.org/10.1016/j.biocon.2018.05.003

Linnell, J.D.C., Cretois, B., 2018. Research for AGRI Committee – The revival of wolves and other large predators and its impact on farmers and their livelihood in rural regions of Europe. European Parliament, Policy Department for Structural and Cohesion Policies, Brussels.

Linnell, J.D.C., Odden, J., Smith, M., E., Aanes, R., Swenson, J.E., 1999. Large carnivores that kill livestock: do “problem individuals” really exist? Wildlife Society Bulletin 27, 698–705.

Louvrier, J., Duchamp, C., Lauret, V., Marboutin, E., Cubaynes, S., Choquet, R., Miquel, C., Gimenez, O., 2018. Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data. Ecography 41, 647–660. https://doi.org/10.1111/ecog.02874

Marucco, F., Reinhardt, I., Avanzinelli, E., Zimmermann, F., Manz, R., Potočnik, H., Černe, R., Rauer, G., Walter, T., Knauer, F., Chapron, G., Duchamp, C., 2023. Transboundary Monitoring of the Wolf Alpine Population over 21 Years and Seven Countries. Animals (Basel) 13. https://doi.org/10.3390/ani13223551

Mech, L.D., 2024. Wolf population density: prey biomass limits via intrinsic factors. Wildlife Biology 2024, e01358. https://doi.org/10.1002/wlb3.01358

Meuret, M., Moulin, C.-H., Bonnet, O., Garde, L., Nozières-Petit, M.-O., Lescureux, N., 2020. Missing shots: has the possibility of shooting wolves been lacking for 20 years in France’s livestock protection measures? Rangel. J. 42, 401–413.

Ministère de la Transition Ecologique et Solidaire, 2020. Arrêté du 30 décembre 2019 portant expérimentation de diverses dispositions en matière de dérogations aux interdictions de destruction pouvant être accordées par les préfets concernant le loup (Canis lupus), TREL1936320A.

Ministère de la Transition Ecologique et Solidaire, 2018. Arrêté du 19 février 2018 fixant les conditions et limites dans lesquelles des dérogations aux interdictions de destruction peuvent être accordées par les préfets concernant le loup (Canis lupus).

Neuwirth, E., 2022. RColorBrewer: ColorBrewer palettes (manual).

Nichols, J.D., Cooch, E.G., 2025. Predictive models are indeed useful for causal inference. Ecology 106, e4517. https://doi.org/10.1002/ecy.4517

Office National de la Chasse et de la Faune Sauvage, 2019. Bilan hivernal de la population de loup : le seuil des 500 loups est atteint. Office National de la Chasse et de la Faune Sauvage.

Padgham, M., Rudis, B., Lovelace, R., Salmon, M., 2017. osmdata. Journal of Open Source Software 2, 305. https://doi.org/10.21105/joss.00305

Pebesma, E., Bivand, R., 2023. Spatial data science: With applications in R. Chapman and Hall/CRC.

Pedersen, T.L., 2022a. ggfx: Pixel Filters for “ggplot2” and “grid” (manual).

Pedersen, T.L., 2022b. patchwork: The composer of plots (manual).

Poudyal, N., Baral, N., Asah, S.T., 2016. Wolf Lethal Control and Livestock Depredations: Counter-Evidence from Respecified Models. PLoS ONE 11, e0148743. https://doi.org/10.1371/journal.pone.0148743

Poulle, M.-L., Carles, L., Lequette, B., 1997. Significance of ungulates in the diet of recently settled wolves in the Mercantour mountains (southeastern France). Revue d’Ecologie, Terre et Vie 52, 657–368.

R Core Team, 2023. R: A language and environment for statistical computing (manual). R Foundation for Statistical Computing, Vienna, Austria.

Réseau Loup-Lynx, 2024. Bilan annuel du suivi de la population de loups 2022 (No. 17), Lettre d'information du réseau Loup-lynx. Office Français de la Biodiversité.

Santiago-Avila, F.J., Cornman, A.M., Treves, A., 2018. Killing wolves to prevent predation on livestock may protect one farm but harm neighbors. PLoS ONE 13, e0189729. https://doi.org/10.1371/journal.pone.0189729

Šuba, J., Žunna, A., Bagrade, G., Done, G., Ornicāns, A., Pilāte, D., Stepanova, A., Ozoliņš, J., 2023. Does Wolf Management in Latvia Decrease Livestock Depredation? An Analysis of Available Data. Sustainability 15. https://doi.org/10.3390/su15118509

Treves, A., Krofel, M., McManus, J., 2016. Predator control should not be a shot in the dark. Front Ecol Environ 14, 380–388. https://doi.org/10.1002/fee.1312

Treves, A., Krofel, M., Ohrens, O., van Eeden, L.M., 2019. Predator Control Needs a Standard of Unbiased Randomized Experiments With Cross-Over Design. Front. Ecol. Evol. 7, 462. https://doi.org/10.3389/fevo.2019.00462

Wagner, K., K., Conover, M., R., 1999. Effect of Preventive Coyote Hunting on Sheep Losses to Coyote Predation. The Journal of Wildlife Management 63, 606–612. https://doi.org/10.2307/3802649

Walfish, S., 2006. A review of statistical outlier methods. Pharm. technol. 30, 82–88.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. Journal of Open Source Software 4, 1686. https://doi.org/10.21105/joss.01686

Wickham, H., Bryan, J., 2023. readxl: Read excel files (manual).

Wickham, H., Seidel, D., 2022. scales: Scale functions for visualization (manual).

Wielgus, R.B., Peebles, K.A., 2014. Effects of Wolf Mortality on Livestock Depredations. PLoS ONE 9, e113505. https://doi.org/10.1371/journal.pone.0113505

Wikle, C., K., Zammit-Mangion, A., Cressie, N., 2019. Spatio-Temporal Statistics with R. Chapman and Hall/CRC.

Wilke, C.O., Wiernik, B.M., 2022. ggtext: Improved text rendering support for "ggplot2" (manual).

Wiśniewska, M., Puga-Gonzalez, I., Lee, P., Moss, C., Russell, G., Garnier, S., Sueur, C., 2022. Simulated poaching affects global connectivity and efficiency in social networks of African savanna elephants—An exemplar of how human disturbance impacts group-living species. PLoS Comput Biol 18, e1009792. https://doi.org/10.1371/journal.pcbi.1009792

Žunna, A., Ruņģis, D.E., Ozoliņš, J., Stepanova, A., Done, G., 2023. Genetic Monitoring of Grey Wolves in Latvia Shows Adverse Reproductive and Social Consequences of Hunting. Biology 12, 1255. https://doi.org/10.3390/biology12091255